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Under " Classification by Area and Ecological Association "

In " Group A. Species which do not occupy an area of more than 100 sq. miles " for " *Bradypterus grandis* " substitute " *Bradypterus graueri* ".

In " Area occupied 100-500 sq. miles " after " *Tauraco bannermani* MF ", insert " *Bubo vosseleri MF or F*, *Campethera tullbergi* MF,".

After paragraph " Area occupied 100-500 sq. miles " *insert fresh paragraph:—*

" Area occupied 500-2,500 sq. miles : *Francolinus harwoodi*, *F. jacksoni* MF, *Pseudocalyptomena graueri* MF, *Anthus sokokensis* F, *Macronyx sharpei* M, *Melaenornis ardesiaca* MF, *Turdus ludoviciae* MF, *Alethe lowei* MF, *Prinia leontica* M, *Cryptospiza shelleyi* MF, *Estrilda nigriloris*, *Carduelis johannis* M.".

MITES ASSOCIATED WITH RODENTS IN ISRAEL

MICHAEL COSTA

BULLETIN OF
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BY

MICHAEL COSTA

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MITES ASSOCIATED WITH RODENTS IN ISRAEL

By MICHAEL COSTA[1, 2]

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[2] The present address of the writer is : Kibbutz Mishmar Ha'emeq, Israel.

INTRODUCTION

THE material forming the basis of this work was collected by the author during a survey of the parasites of wild mammals and birds in Israel. The survey was made possible by a grant from the National Institute of Health (U.S.A. Public Health Department) and was carried out under the direction of Prof. O. Theodor in the Dept. of Parasitology, the Hebrew University, Jerusalem.

Two papers have been published which deal partly with the acarine fauna of the area covered by the present study. Keegan (1956) in the " Laelaptid and Dermanyssid mites of Egypt, Kenya and the Sudan " deals with eleven of the twenty-four Israel species and subspecies, and Bregetova (1956), working in Russia, includes thirteen species of which six were also listed by Keegan. These numbers demonstrate the somewhat exceptional zoogeographical position of Israel on the limits of both the Ethiopian and the Palaearctic regions (Costa, 1958). A detailed discussion on zoogeography and host-specificity will be given elsewhere.

The classification follows closely Strandtmann & Wharton (1958) and therefore only the most important synonyms have been cited. Morphological terminology follows Evans (1957).

Types of the new species have been deposited at the British Museum (Natural History), paratypes have been deposited at the Hebrew University, Jerusalem (Dept. of Parasitology), and in the collections of the U.S. National Museum.

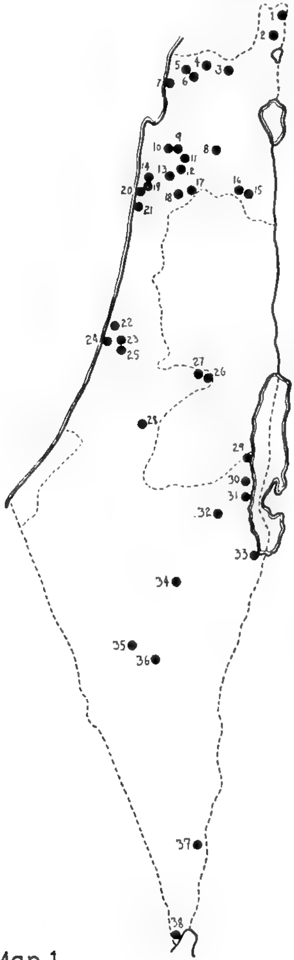
The localities in which the material has been collected are indicated in map 1.

MATERIALS AND METHODS

All the mites dealt with in this paper have been collected from trapped rodents in Israel. The living rodent was placed on a sheet of filter paper in a small transparent jar. It was anaesthetized with sulphuric ether. Most of the mites left the host immediately after the introduction of the ether and crawled on to the filter paper, the remainder were hand-collected from the fur. The rodents were kept alive for haematological and helminthological studies.

The mites were stored in small vials in 70% ethyl alcohol. The descriptions and the camera-lucida drawings were made from temporary mounts of lactic acid (Evans, 1957).

Measurements have been restricted to sclerotized structures which, with the possible exception of the length of the anal shield, are not affected by the degree of compression of the specimen.



Map 1

Map showing the localities in which collections of the material were made.

The spelling adopted here is as far as possible after *The Times Atlas of the World*, Mid-Century Edition, Vol. 11, Map 35. Edited by J. Bartholomew. London, 1959.

Aqua bella (27)
Akko Junction (10)
Beit Alfa (15)
Beit Guvrin (28)
Beit Hakerem (26)
Caesarea (21)
Dalia (13)
Dan (1)
Eyn Gedi (29)
Ha-Makhtesh Hagadol (34)
Holon (22)
Kabri (5)
Me'arat Karmel (19)
Mezada (31)
Mishmar Ha'emeq (12)
Nazareth (8)
Neoth Mordekhai (2)
Nes Ziona (25)
Nir David (16)
Palmahin (24)
Qishon (11)
Raman (36)
Rishon le Zion (23)
Rosh Zohar (32)
Sasa (3)
Sedom (33)
Shavey Zion (7)
Tivon (9)
Umm el Fahm (17)
Wadi Ara (18)
Wadi Masri (38)
Wadi Nafkh (35)
Wadi Seyal (30)
Yekhiam (6)
Yotvata (37)
Zikhron Ya'aocv (14)

HAEMOLAELAPS Berlese, 1910

Type : *Haemolaelaps marsupialis* Berlese, 1910.

A detailed examination of the chaetotaxy of the dorsum of the immature and adult stages of the Israel species of *Haemolaelaps* and *Laelaps* has shown that there is an overall chaetotactic pattern which is relatively constant and easily definable. The basic complement of setae in the adults appears to be 39 pairs, comprising 22 pairs on the " anterior dorsal shield " and 17 pairs on the "posterior dorsal shield ". The position of the setae is indicated by black dots in Text-fig. 1. The basic number may vary by the addition of one or two paired setae (*ax* and *px*1) or by the loss of one or two pairs (e.g. *s*3 or *px*3). The primary chaetotaxy is often supplemented by unpaired accessory setae added at the deutonymphal stage (indicated by white circles in the diagram). These are usually restricted to the region between the J series, but they may extend over the greater part of the " posterior dorsal shield " and even over the " anterior dorsal shield ".

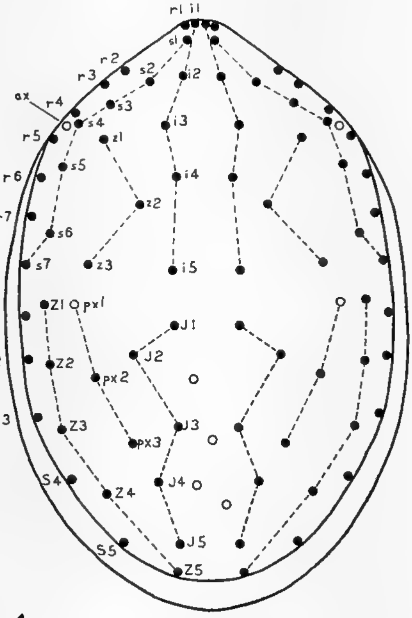


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FIG. 1. Diagrammatic representation of the chaetotaxy of the dorsal shield in the genera *Haemolaelaps* and *Laelaps*.

Although Bregetova (1956) has referred to " the strictly determined number of setae " on the dorsal shield, and has used a system of nomenclature designed to name all the setae, Hirschmann (1957) has been followed here in order to differentiate into the setae of the " anterior dorsal shield " and the " posterior dorsal shield ".

On the basis of the dorsal chaetotaxy the Israel material of *Haemolaelaps* may be divided into the following three groups :

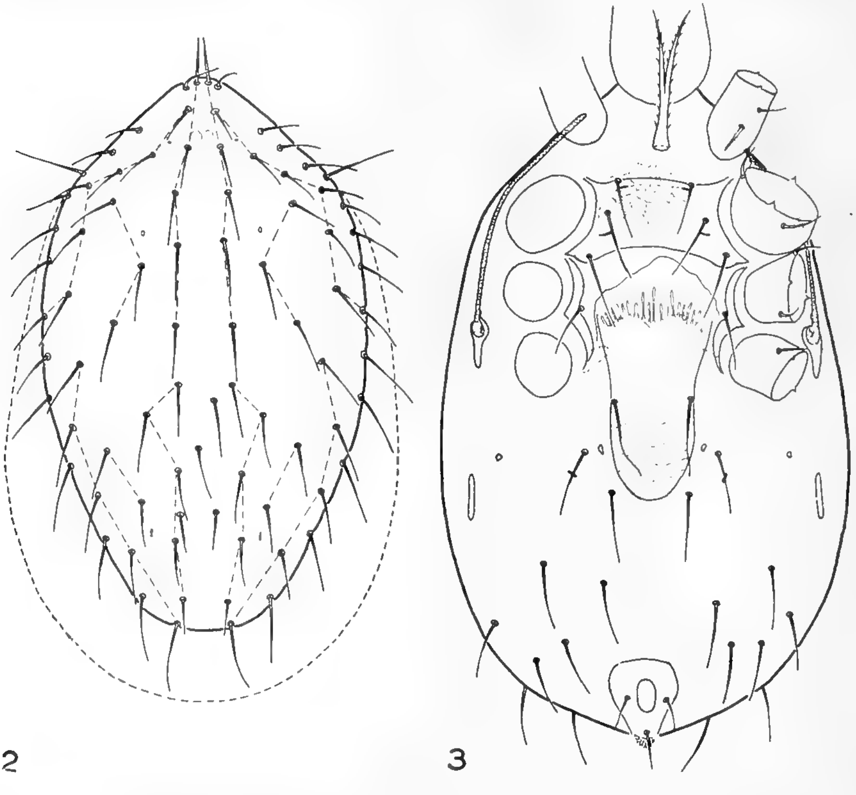
1. Species with 39 paired dorsal setae: *H. glasgowi* (Ewing), *H. androgynus* Bregetova, *H. insculptus* Keegan, *H. ovalis* sp. nov. and *H. hirstionyssoides* sp. nov.
2. Species with 40 paired dorsal setae: *H. longipes* Breg.
3. Species with 41 paired dorsal setae: *H. hirsti* Keegan and *H. centrocarpus* Berlese.

The males of the above-mentioned species may be also grouped according to the sclerotization of the venter; species from gerbillids having the anal shield free while those from other hosts having the anal shield fused with the sternito-ventral shield This confirms the observations of Keegan (1956). *Haemolaelaps insculptus* Keegan is somewhat intermediate in character in having a large sternito-ventral shield abutting the anal shield.

Haemolaelaps androgynus **Bregetova**

Haemolaelaps androgynus Bregetova, 1952.

Female (Text-figs. 2, 3). Dorsal shield 780–810 μ long and 465–495 μ wide. The



Figs. 2–3 *Haemolaelaps androgynus* Breg., female. Fig. 2, dorsal shield. Fig. 3, venter.

mites are rather weakly sclerotized, with the dorsal shield only faintly ornamented. The shield bears 39 pairs of symmetrical setae and a varying number of asymmetrical setae. The J5 setae are half the length or slightly shorter than the Z5 setae. The dorsal setae are distinctly shorter than the ventral setae. Distribution of setae and relative lengths of setae as in Text-fig. 2.

Tritosternum with long undivided base and feathered laciniae. The presternal area is sculptured but the anterior margin of the sternal shield is distinct. The anterior margin of the sternal shield is almost straight, its posterior margin is concave. The postero-lateral corners of the shield project distinctly between coxae II and III. The shield is 93–192 μ long (at mid-line) and 160–165 μ wide (at the level of the second setae), it is ornamented in its anterior part. The anterior pores are almost parallel to the anterior margin, the posterior pores have a slight outward slant. The anterior sternal setae are much shorter than the other sternal setae but longer than the metasternal setae. The weakly sclerotized genital shield is tongue-shaped and expands only slightly behind the genital setae, it is faintly marked with striations.

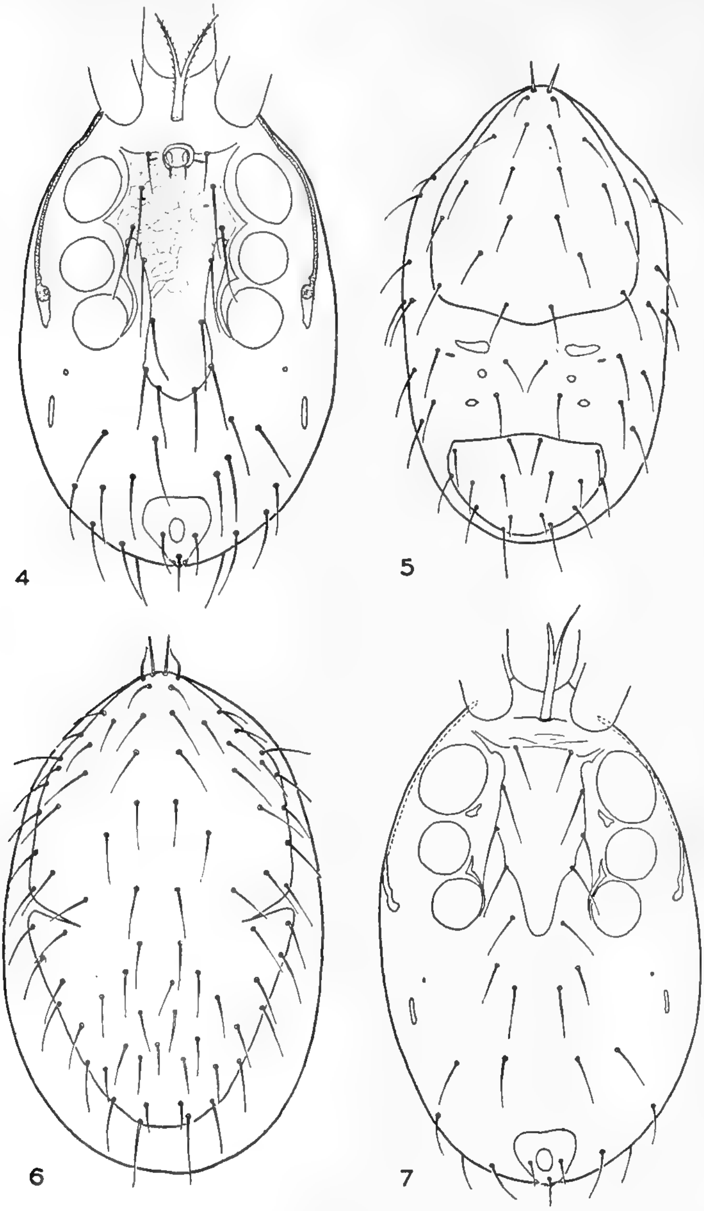
The metapodal shields are narrow and elongated. The anal shield is 145 μ long and 95 μ wide, the paranal setae, inserted near the posterior margin of the anus are slightly longer than the postanal seta. About 7 pairs of setae are inserted on the ventral integument. The peritreme reaches to the middle of coxa I, a peritrematal shield is present. The respective lengths of the legs (excluding pulvilli) are as follows: I—630 μ, II—570 μ, III—675 μ, IV—1, 020 μ.

Chelicerae chelate-dentate, pilus dentilis slightly inflated. The deutosternal teeth are in 6 rows, 3 teeth in each row. The internal posterior rostral setae are longer than the capitular setae and almost three times the length of the external posterior rostral setae. The corniculi are well sclerotized, horn-shaped and pointed.

Male (Text-fig. 4). Dorsal shield 615–630 μ long and 375–390 μ wide (in one male it is 550 μ long and 285 μ wide). The chaetotaxy of the dorsal shield is essentially the same as in the female, the setae are slightly longer. The anal shield is separate from the sternito-ventral shield. The sternito-ventral shield is tongue-shaped and behind the third pair of setae it is separated from the endopodal shields by membraneous integument. The shield bears 7 pairs of setae. The first pair of setae is rather short, only slightly longer than half the length of the third pair. The anal shield is approximately 95 μ long and 90 μ wide, the anus is nearer to the postanal seta than to the anterior margin of the shield. The paranal setae are inserted in line with the middle of the anus or slightly posterior to it, they are longer than the postanal seta.

Deutonymph (Text-figs. 6, 7). Dorsal shield 555–615 μ long and 315–375 μ wide. The sternal shield bears 4 pairs of setae and it is widest at the level of the third setae. The narrow part of the shield does not project behind coxa IV. The peritreme reaches beyond the posterior margin of coxa I.

Protonymph (Text-fig. 5). The anterior dorsal shield is 270–300 μ long and 225–240 μ wide. The sternal shield bears 3 pairs of setae, the third pair being the longest. The posterior margin of the shield forms an obtuse angle. There are 3 pairs of normal ventral setae and one pair of minute setae between coxae IV. The peritreme reaches almost to the anterior margin of coxa III.



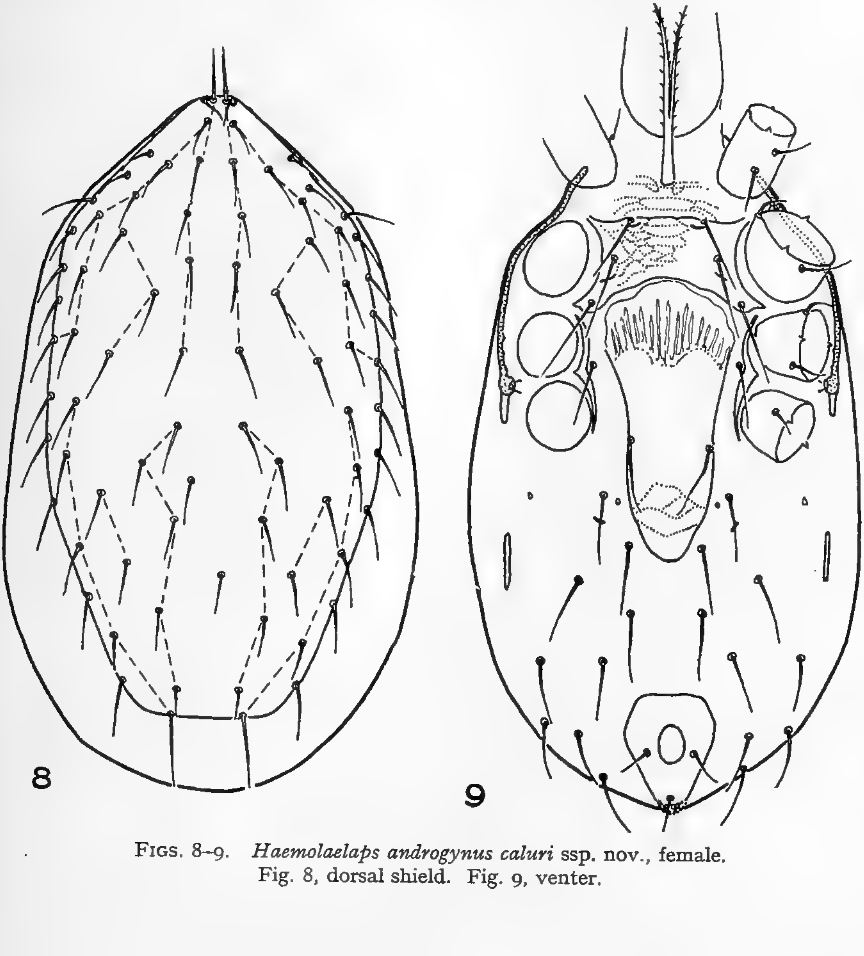
FIGS. 4–7. *Haemolaelaps androgynus* Breg. Fig. 4, venter of male. Fig. 5, dorsum of protonymph. Fig. 6, dorsal shield of deutonymph. Fig. 7, venter of deutonymph.

HOSTS AND LOCALITIES. All the specimens were taken off *Gerbillus* (*Dipodillus*) *dasyurus* at the following dates and localities : 4 pn, 1 dn—Ha-Makhtesh Hagadol, 26–xii.1954 ; 1 dn—ditto ; 1 pn, 2 dn, 4 ♀—Raman, 12.iv.1955 ; 2 pn, 22 dn, 11 ♂, 7 ♀—Wadi Masri, 16.iv.1955 ; 2 pn, 6 dn, 2 ♂—ditto ; 1 ♀, Umm el Fahm, 18.viii.1955.

NOTES. The Israel material differs slightly in the measurements from those given by Bregetova (1956) and in the form of the dorsal shield which is less ovoid in shape. Only one female (the specimen from Umm el Fahn) has comparable dimensions, the dorsal shield measuring 690 μ long and 450 μ wide. Its sternal shield is only 80 μ long. The dorsal shield in this specimen is rounder than in the other specimens and it bears no asymmetrical setae.

Haemolaelaps androgynus caluri ssp. nov.

FEMALE (Text-figs. 8, 9). Dorsal shield 645–735 μ long and 330–420 μ wide. The



FIGS. 8–9. *Haemolaelaps androgynus caluri* ssp. nov., female. Fig. 8, dorsal shield. Fig. 9, venter.

lateral margins of the posterior part of the shield are convergent. The posterior end of the shield is markedly truncated. The dorsal setae are shorter than the ventral setae. The shield bears 39 pairs of symmetrical setae, many specimens (about 50%) have in addition one or more asymmetrical setae. The mites are only weakly sclerotized.

Tritosternum with long shaft and feathered laciniae. The presternal area is faintly ornamented. The sternal shield is 54–64 μ long (at mid-line) and 134–147 μ wide (at level of second setae), the shorter shields being the widest. The anterior margin of the shield is practically straight, the posterior margin is rather deeply concave. The postero-lateral corners of the shield project between coxae II and III. The pores are very distinct, slightly crescent-shaped and almost parallel to the anterior and the posterior margins of the shield respectively. The shield is ornamented with fine striations. The sternal setae are simple and elongated, the first setae are longer than the sternal shield. The metasternal setae are only slightly shorter than the first sternal setae, about two-thirds of the third sternal setae.

The genital shield is tongue-shaped and narrow, it is ornamented with faint striations. The metapodal shields are very narrow and elongated. Approximately 8–9 pairs of long setae are inserted on the ventral integument. The anal shield is 102–118 μ long and 80–96 μ wide. The paranal setae are slightly longer than the postanal seta, they are inserted near the posterior margin of the anus. The peritreme reaches slightly beyond the middle of coxa I. A small peritrematal shield is present.

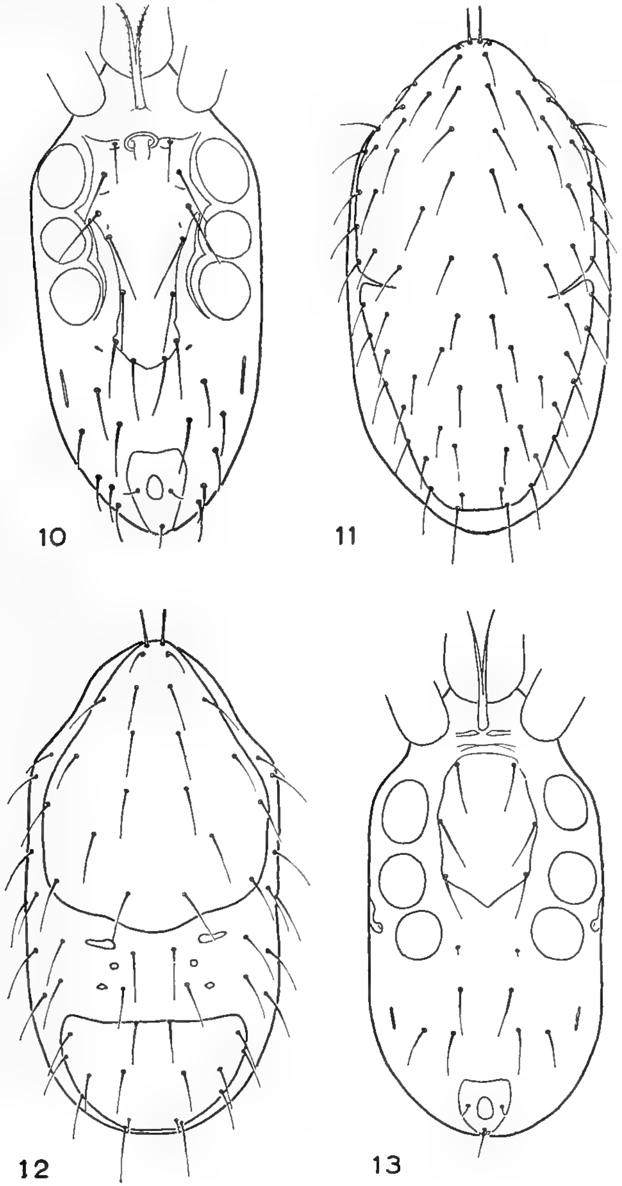
The respective lengths of legs (excluding pulvilli) are as follows: I—480 μ; II—420 μ; III—465 μ; IV—675 μ. Chelicerae chelate-dentate, pilus dentilis slightly inflated. The deutosternal teeth are arranged in 6 rows, mainly 4 teeth in each row. The internal posterior rostral setae are long, longer than the capitular setae.

Male (Text-fig. 10). Dorsal shield 480–540 μ long and 255–300 μ wide. Chaetotaxy essentially the same as in the female. The anal shield is separate from the sternito-ventral shield which bears 7 pairs of setae. The sternito-ventral shield is tongue-shaped, behind the third pair of setae it is separated from the endopodal shields by a strip of membraneous integument as in *H. androgynus*. The anal shield is 90–97 μ long and 67 μ wide. The peritreme reaches beyond the posterior margin of coxa I.

Deutonymph (Text-fig. 11). Dorsal shield 480–540 μ long and 225–300 μ wide. Chaetotaxy as in female. The sternal shield bears 4 pairs of setae and it projects slightly beyond coxae IV. The peritreme reaches to the middle of coxa I. Approximately 11 pairs of ventral setae are inserted on the ventral integument.

Protonymph (Text-figs. 12, 13). Anterior dorsal shield 230 μ long and 190 μ wide. The sternal shield is widest at the second pair of setae, the posterior margin of the shield forms an obtuse angle. Three pairs of normal ventral setae and one pair of minute setae between coxae IV are inserted on the ventral integument. The peritreme reaches to the middle of coxa III.

Hosts and localities. All specimens were recovered from *Sekeetamys calurus* at the following localities and dates: 3 dn, 7 ♀—Raman, 25.x.1954; 6 pn, 4 dn, 1 ♂, 4 ♀—Wadi Masri, 16.iv.1955; 2 pn, 2 dn, 1 ♂, 2 ♀—ditto; 2 ♂—ditto; 3 pn, 6 dn,



FIGS. 10–13. *Haemolaelaps androgynus caluri* ssp. Fig. 10, venter of male. Fig. 11, dorsal shield of deutonymph. Fig. 12, dorsum of protonymph. Fig. 13, venter of protonymph.

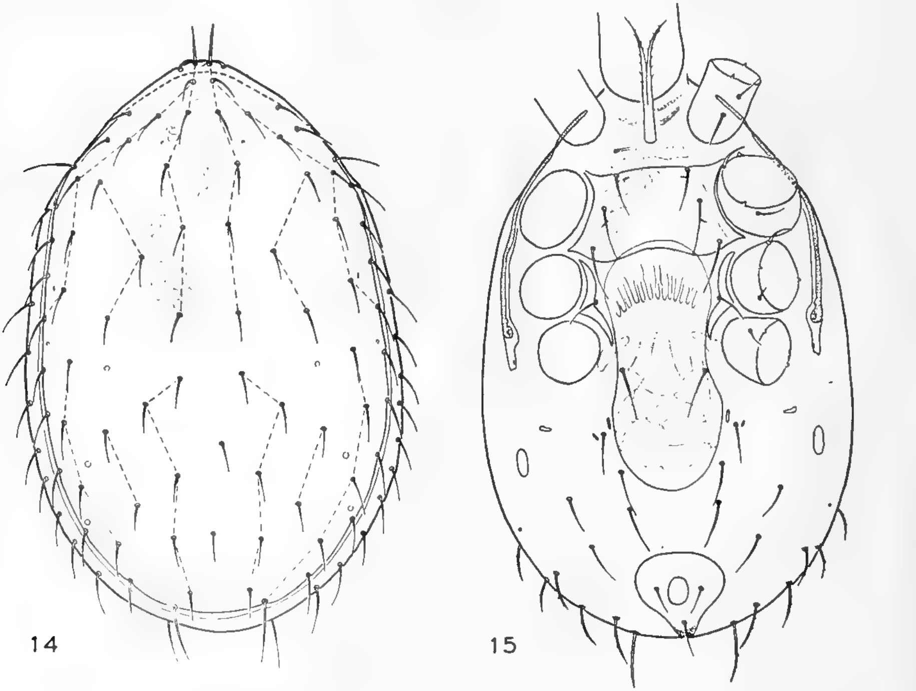
6 ♂—ditto ; 2 pn, 5 dn, 6 ♂, 4 ♀—ditto, 1.xi.1955 ; 1 pn, 8 dn, 11 ♂, 10 ♀—ditto, 5.xii.1955 ; 6 pn, 9 dn, 11 ♀—ditto ; 3 ♂, 8 ♀— Mezada, 29.ii.1956 ; 9 pn, 10 dn, 5 ♂, 9 ♀—ditto.

NOTES. The form found on *Sekeetamys calurus* differs from *Haemolaelaps androgynus* in the following constant features : it is much smaller without any overlapping of size, its dorsal shield is more truncated, its sternal shield is much shorter (relatively to its width as well as absolutely) and the first sternal setae are longer. As these features are mainly ones of degree, the forms occurring on *Sekeetamys calurus* are considered as a new subspecies.

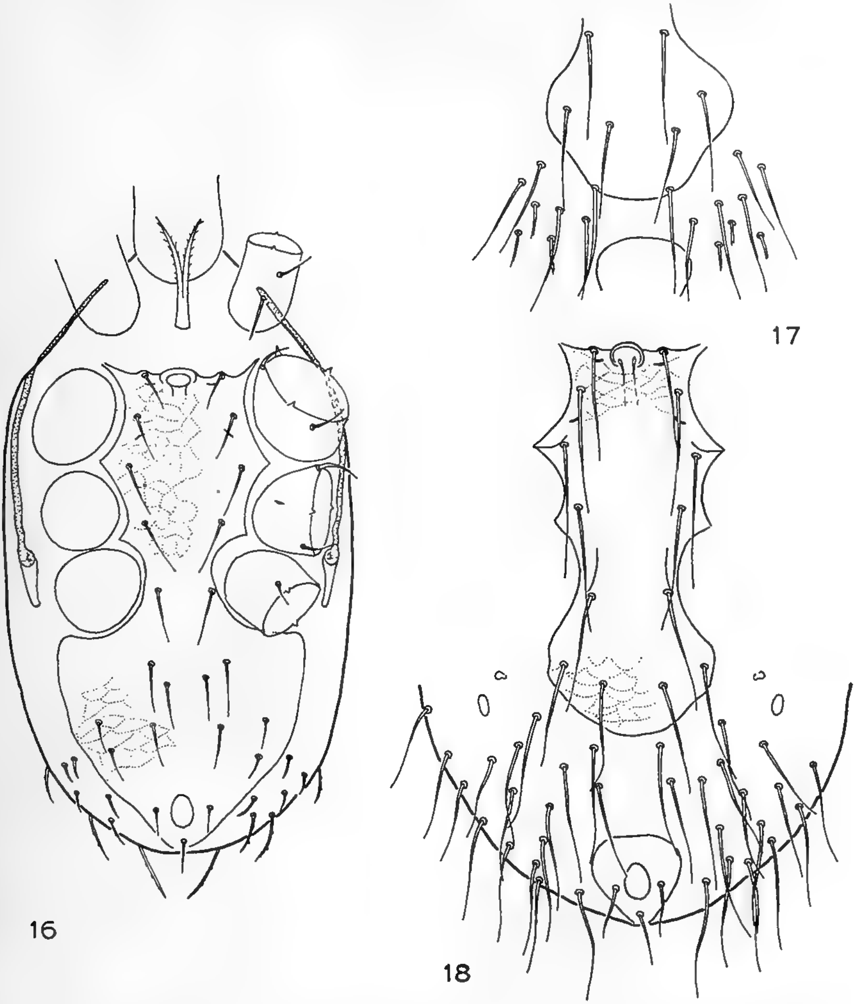
Haemolaelaps glasgowi (Ewing)

Laelaps glasgowi Ewing, 1925.
Atricholaelaps glasgowi, Wharton, 1938.
Haemolaelaps glasgowi, Strandtmann, 1949.

FEMALE (Text-figs. 14, 15). The dorsal shield is oval, it is 675–720 μ long and 435–480 μ wide. The shield is sculptured on its anterior part and is ornamented with striations throughout. On the shield are a number of pores, 2 pairs of pores near the postero-lateral margin of the dorsal shield are especially prominent. The shield



FIGS. 14–15. *Haemolaelaps glasgowi* (Ewing,) female. Fig. 14, dorsum. Fig. 15, venter.



FIGS. 16–18. Fig. 16, *Haemolaelaps glasgowi* (Ewing), venter of male. Figs. 17–18, *Haemolaelaps hirsti* Keegan, venter of the male, showing variation in the outline of the sternitiventral shield.

bears 39 pairs of simple setae which are shorter than the smooth ventral setae, a varying number of asymmetrical setae may also be present. The shield has a distinct double border, the marginal setae are inserted on the inner margin.

The tritosternum is distinct and its laciniae are well feathered. The presternal area is faintly ornamented and the anterior margin of the sternal shield is well defined. The sternal shield is 93–109 μ long (at mid-line) and 144–157 μ wide (at the level of the second sternal setae). The anterior margin is only slightly convex, the posterior margin is concave and weakly emarginate. The shield is ornamented throughout with striations. The anterior pores are parallel to the anterior margin, the posterior pores have an outward slant. The sternal setae are short, even the second setae barely project beyond the posterior margin of the sternal shield. The metasternal setae are only slightly shorter than the first sternal setae.

The genital shield is tongue-shaped, it is expanded behind the genital setae. The shield bears one pair of simple setae and it is ornamented with striations. The anal shield is pear-shaped, it is 96–100 μ long and 105–118 μ wide. The paranal setae are inserted in line with the middle of the anus. The metapodal shields are elongate-oval. Five pairs of simple setae are inserted on the ventral integument, as well as a number of latero-ventral setae which are barbed, mainly on their outer curvature. The peritreme reaches slightly beyond the middle of coxa I.

The coxae are rather short and stumpy, the respective lengths of the legs (excluding pulvilli) are as follows: I—570 μ; II—480 μ; III—495 μ; IV—675 μ. The chelicerae are chelate-dentate, the pilus dentilis on the fixed finger is highly inflated in its proximal part, its terminal portion is slender and recurved.

MALE (Text-fig. 16). The dorsal shield is 540–585 μ long and 300–315 μ wide. The shape and the chaetotaxy of the dorsal shield are essentially the same as in the female. The holoventral shield bears 23 setae (including the anal setae); it is ornamented with striations throughout. The shield expands behind coxae IV, it includes the metapodal shields. Many of the setae that are inserted on the postero-lateral integument are barbed on their outer curvature. The spermatophoral process of the movable finger is extremely long and its distal portion is recurved.

HOSTS AND LOCALITIES. All specimens were recovered from *Microtus guentheri* at the following dates and localities: 1 ♀—Mishmar Ha'emeq, 10.i.1953; 12 ♀—ditto, 14.v.1955; 1 ♀—Neoth Mordekhai, 20.v.1955; 3 ♂—Mishmar Ha'emeq, 23.xii.1955 (out of nest material).

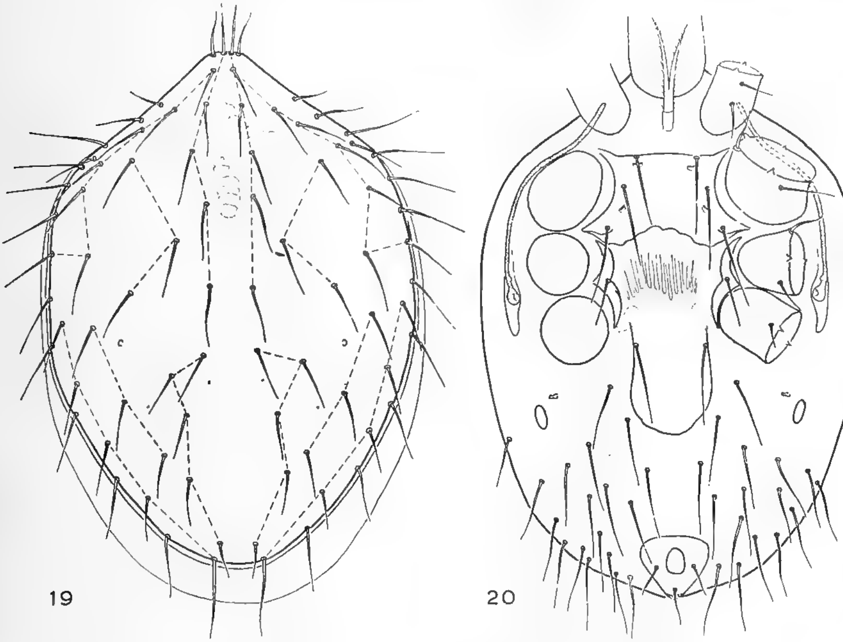
NOTES. Strandtmann & Wharton (1958) have already pointed out that this widespread mite represents a species complex. No attempt will be made here to deal with the complex as a whole, although the following points should be mentioned: Bregetova (1956) states that *Haemolaelaps glasgowi* has only 38 pairs of dorsal setae (setae *s3* are missing). Females from Japan (*ex Rattus norvegicus*) in the collection of the British Museum are identical with the females from Astrakhan. In the Israel material, the females have 39 pairs of dorsal setae as well as a number of asymmetrical setae on the posterior dorsal shield. Specimens from South Africa (examined by the courtesy of Dr. W. Till) have the same chaetotaxy as the material from Israel although in most specimens the dorsal setae are more elongated.

Haemolaelaps hirsti Keegan

Haemolaelaps hirsti Keegan, 1956.

FEMALE (Text-figs. 19, 20). Dorsal shield oval, it is 1,125–1,215 μ long and 810–855 μ wide. The shield bears 41 pairs of setae (*ax* and *px1* in addition to the normal 39 pairs). The setae on the posterior half of the shield are distinctly shorter than the ventral setae. Some of the setae, mainly the postero-marginal ones, may be slightly barbed. Setae J5 are less than half the length of setae Z5. The shield has a distinct double margin and it is well sculptured, mainly on its anterior part.

The tritosternum is very distinct and its laciniae are feathered. The presternal area is ornamented and the anterior margin of the sternal shield may be indistinct. The sternal shield is 150–180 μ long (at mid-line) and 225–250 μ wide (at the level of the second setae). The anterior margin is practically straight, the posterior margin is markedly concave and emarginate in various degrees. The anterior pores are parallel to the anterior margin of the shield, the posterior pores have a distinct outward slant. The shield is only very faintly ornamented and its surface seems to be granulated. The sternal setae are very long, the first setae are only slightly shorter than the second and third setae which are of equal length. The metasternal setae are slightly less than half the length of the third sternal setae.



FIGS. 19–20. *Haemolaelaps hirsti* Keegan, female. Fig. 19, dorsum. Fig. 20, venter.

The genital shield is only weakly sclerotized, it does not expand posteriorly to the genital setae. The genital setae are elongated and may almost reach the posterior margin of the shield. The metapodal shields are elongate-oval. The anal shield is fairly triangular, it is 173–183 μ long and 160–173 μ wide. The paranal setae are usually of the same length as the postanal seta, in some specimens they appear to be longer. The number of setae inserted on the ventral membrane is 17–20 pairs (it may be higher in more compressed specimens), some of the setae, mainly the postero-lateral ones, are slightly barbed. The peritrene reaches to the middle of coxa I, a peritrematal shield is present.

Of the two ventral setae on coxa I, the proximal seta is distinctly longer and stouter than the distal seta. On femur I are 2 well-developed dorsal, spur-like setae and a smaller dorsal, spur-like seta on trochanter I. The respective lengths of the legs (excluding pulvilli) are as follows: I—990 μ; II—900 μ; III—1,005 μ; IV—1,200 μ. Chelicerae chelate-dentate, pilus dentilis not inflated, with a curved tip. The deutosternal teeth are arranged in 6 rows, 4–6 teeth in each row.

MALE (Text-figs. 17, 18). Dorsal shield 990–1,020 μ long and 675–705 μ wide. The chaetotaxy is essentially the same as in the female. The anal shield is separate from the sternito-ventral shield which bears 7–8 pairs of long (160–205 μ) setae. The shape of the posterior margin of the shield is variable (Text-figs. 17, 18) and therefore a certain variation can be found in the number of setae it bears and in its distance from the anal shield. The shield may be faintly ornamented, mainly in its anterior and posterior portions. The chelicerae bear elongated spermatophoral processes.

DEUTONYMPH. The dorsal shield has distinct lateral incisions, it is 900 μ long and 630 μ wide. The chaetotaxy is as in the female. The sternal shield is broadest mid-way between the second and the third sternal setae, its hind end does not reach as far as the posterior margin of coxae IV. Four pairs of simple setae are inserted on the shield. Approximately 15 pairs of setae are inserted on the ventral integument, the posterior ones are slightly barbed.

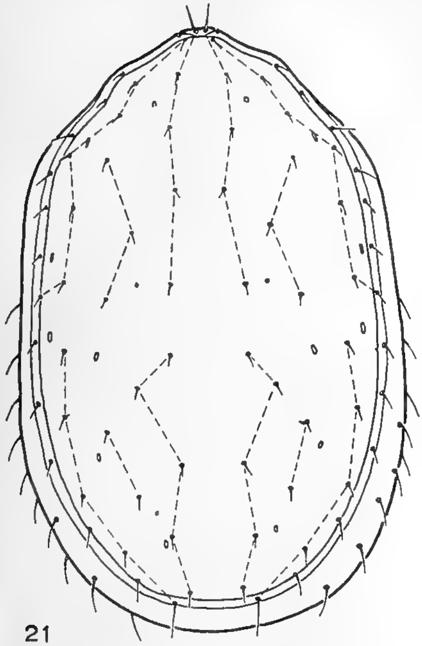
PROTONYMPH. The anterior dorsal shield is 420 μ long and 400 μ wide, it bears 11 pairs of fairly long setae. The setae of the posterior row on the pygidial shield are longer than the other setae on the shield, they are slightly barbed. The sternal shield is broadest at the level of the second setae and it is ornamented throughout. Four to five pairs of real ventral setae and a pair of minute setae between coxae IV are inserted on the ventral integument. Three to four pairs of postero-lateral setae may be slightly barbed.

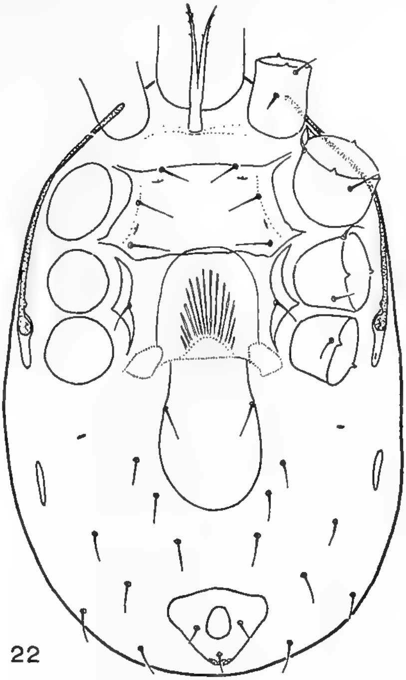
HOSTS AND LOCALITIES. 7 ♂, 10 ♀—*Gerbillus allenbyi*, Caesarea, 23.vii.1954; 1 ♂, 10 ♀—ditto; 5 ♂, 8 ♀—ditto; 3 ♂, 2 ♀—ditto; 2 ♂, 3 ♀—Ma'agan Mikhael, 26.ix.1955; 1 ♀—ditto; 5 pn, 5 dn, 8 ♂, 16 ♀—Rishon le Zion (Dunes).

NOTES. This species has been determined by comparison with a paratype female in the collection of the British Museum (N.H.). Keegan (1956) described a similar species, *Haemolaelaps ewingi* from *Gerbillus gerbillus* basing the differences mainly on the relative length of the sternal shield and on the length of the genital setae. As these differences are in rather variable characters, it may be possible that these two species are in fact synonymous. This conclusion has been reached on purely zoogeographical speculations, unfortunately no specimens of *H. ewingi* were available at the time of the study.

Haemolaelaps hirstionyssoides sp. nov.

FEMALE (Text-figs. 21, 22). The dorsal shield is ovoid with well-developed shoulders it is broadest posterior to coxae IV. The shield is 555–585 μ long and 330–375 μ wide. The shield bears 39 pairs of very minute setae (some of them can be seen clearly only with high magnification). The shield may be faintly ornamented on its anterior





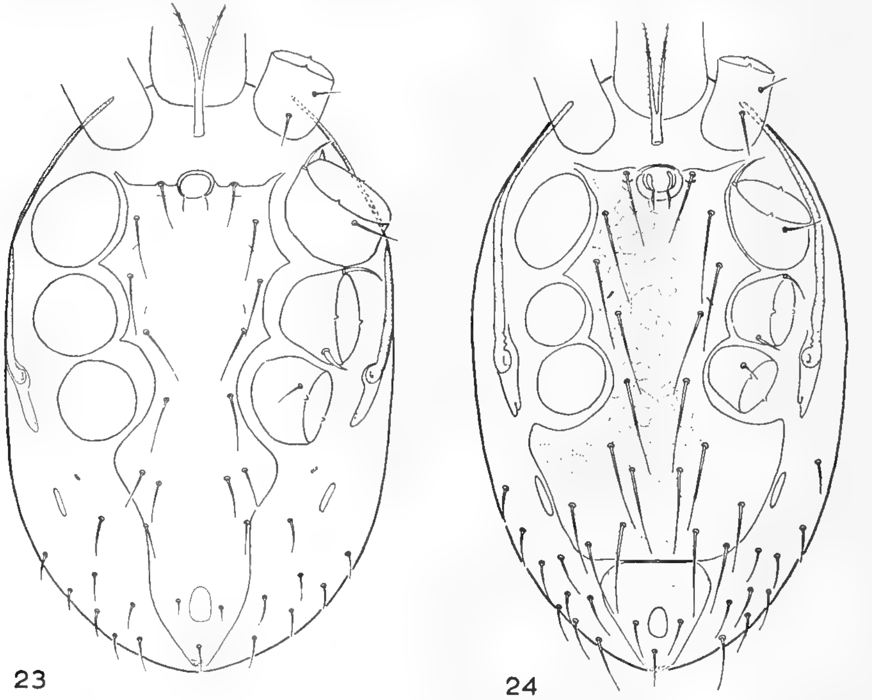
FIGS. 21–22. *Haemolaelaps hirstionyssoides* sp. nov., female. Fig. 21, dorsum. Fig. 22, venter.

part and it has many distinct pores. The dorsal shield has a double border, consisting of a thinner marginal stripe on which most of the marginal setae are inserted.

The tritosternum is rather translucent, the laciniae are only sparsely feathered. The sternal shield is 86–93 μ long (at mid-line) and 130–140 μ wide (at the level of the second setae), its anterior margin is rather indistinct and slightly convex, its posterior margin is almost straight, weakly emarginate and irregular. The shield is granulated throughout, without any other ornamentation. The sternal setae are extremely short, even the second sternal setae do not reach the posterior margin of the shield. The metasternal setae are of the same length as the sternal setae. The anterior pores are parallel to the anterior margin, the posterior pores are almost parallel to the lateral borders of the shield.

The genital shield is tongue-shaped and rather rounded, it surface is granulated throughout. The shield bears one pair of short genital setae. The anal shield is 80–85 μ long and 90–93 μ wide. The anus is nearer to the postanal seta than to the anterior margin of the shield. The paranal setae are inserted in line with the middle of the anus. The anal setae are very short. The metapodal shields are narrow and elongated. Five pairs of smooth setae are inserted on the ventral integument. The setae of the postero-lateral integument are weakly barbed on their outer curvature.

The proximal seta on coxa I is stouter and shorter than the distal seta. Coxa II has a distinct sharp spine on its antero-dorsal rim. The legs are rather stumpy and short, their respective lengths (excluding pulvilli) are as follows: I—495 μ; II—360 μ; III—360 μ; IV—435 μ. Leg II is much stouter than the other legs. Chelicerae chelate-dentate, the movable finger is rather curved, the pilus dentilis is hair-like. The deutosternal teeth are in 6 rows, 2–4 teeth in each row. The gnathosomal setae are short, the internal posterior rostral setae being the longest.



FIGS. 23–24. Fig. 23, venter of male of *Haemolaelaps hirstionyssoides* sp. nov. Fig. 24, venter of male of *Haemolaelaps insculptus* Keegan.

MALE (Text-fig. 23). The dorsal shield is 450–465 μ long and 300–315 μ wide. The chaetotaxy of the dorsal shield is essentially as in the female. The rather narrow holoventral shield bears 19 setae, including the anal setae. The first 5 pairs of setae are distinctly longer and stouter than the other setae on the shield. The holoventral shield is granulated almost throughout, the area occupied by the anal shield is faintly ornamented with striations. The peritreme reaches slightly beyond the middle of coxa I. The postero-ventral seta on coxa III is very stout. The legs are rather short and stumpy.

HOSTS AND LOCALITIES. 1 ♂, 44 ♀—*Spalax ehrenbergi*, Zikhron Ya'aqov, 8.iv.1954; 1 ♂, 1 ♀ ditto, Beit Hakerem, 21.xii.1952; 1 ♀—*Mus musculus*, Akko. Junction, 22.ii.1956.

NOTES. This species is rather interesting in having the habitus of a *Hirstionyssus*. Superficially one is inclined to consider this to be a *Hirstionyssus* without coxal spurs, for the following reasons : granulated surface of the ventral shields, narrow holoventral shield of male, short and stumpy legs. However, the character of the deutosternal teeth as well as the chelate-dentate chelicerae indicate clearly the position of this species. *Haemolaelaps hirstionyssoides* seems to be most closely related to *Haemolaelaps glasgowi*.

Haemolaelaps insculptus Keegan

Haemolaelaps insculptus Keegan, 1956.

FEMALE (Text-figs. 25, 26). The dorsal shield is oval, it is 600–690 μ long and 420–465 μ wide. The shield is heavily sclerotized and sculptured. Thirty-nine pairs of setae are inserted on the dorsal shield. The dorsal setae are markedly shorter than the ventral setae. Some of the setae, mainly the marginal ones, are slightly barbed. Setae J5 are approximately half the length of setae Z5.

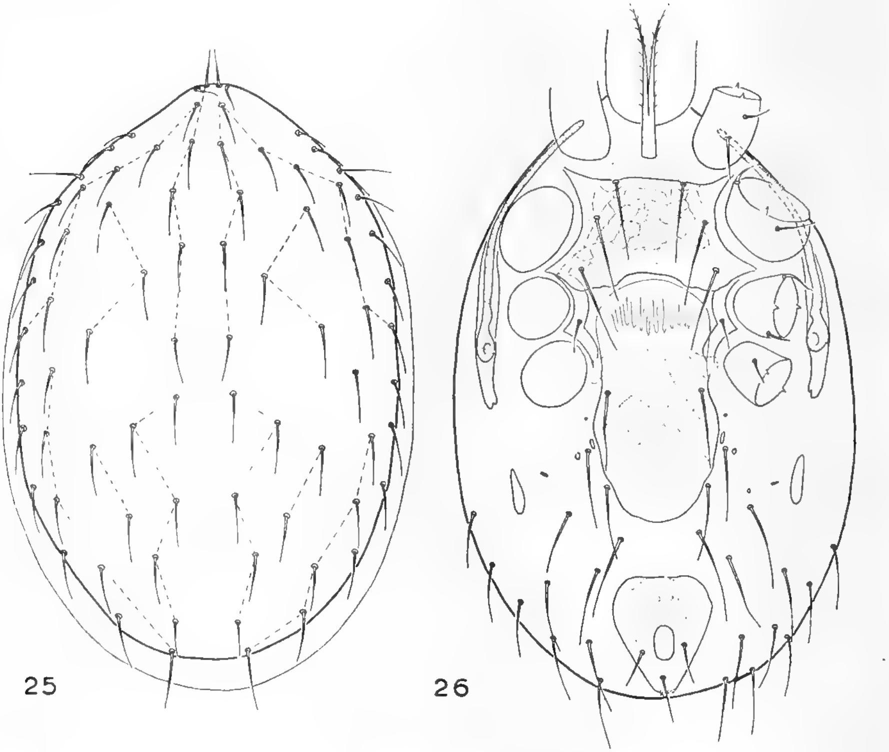
Tritosternum with long shaft and feathered laciniae. The distance between the base of the tritosternum and the anterior margin of the sternal shield is very narrow. The sternal shield is 110 μ long (at mid-line) and 145–150 μ wide (at the level of the second setae). The shield is heavily sclerotized and markedly sculptured on its anterior part. The anterior margin is straight between the bases of the first pair of setae, the posterior margin is concave. The sternal setae are long, but the setae of the first pair do not reach the posterior margin of the shield. The short metasternal setae are inserted on well-sclerotized endopodal shields which are attached to the sternal shield. The length of the metasternal setae is approximately one-third of the length of the third sternal setae.

The genital shield is broadest immediately behind the genital setae, it is well marked with striations. Only one pair of setae is inserted between the genital and the anal shields. The length of the long ventral setae is approximately 85–90 μ, the posterior setae may be slightly barbed. The metapodal shields are elongated and narrow. The anal shield is 112 μ long and 112 μ wide, its anterior margin is almost straight, with rounded corners. The distance of the anus from the anterior margin of the anal shield is much greater than the length of the anus. The paranal setae are usually inserted on a line slightly anterior to the middle of the anus, their length roughly equals the length of the postanal seta. The anal shield is ornamented. The peritreme reaches slightly beyond the posterior margin of coxa I, a peritrematal shield is present.

The coxae are ornamented. Of the two ventral setae on coxa I, the proximal seta is markedly larger and stouter than the distal seta. The respective lengths of the legs (excluding pulvilli) are as follows : I—445 μ ; II—435 μ ; III—435 μ ; IV—630 μ. Most of the setae on tarsus and tibia II are thick and spine-like.

Chelicerae chelate-dentate, the pilus dentilis is only slightly inflated. The deutosternal teeth are arranged in 6 rows of 3 (rarely 4) teeth.

MALE (Text-fig. 24). The males are markedly smaller than the females. The dorsal shield is 450–480 μ long and 255–270 μ wide. The chaetotaxy of the dorsal shield is essentially the same as in the female. The anal shield is separated from the sternito-ventral shield. The sternito-ventral shield is markedly sculptured throughout and it bears 10 pairs of long setae. It is broadest immediately behind coxa IV and reaches to the anterior margin of the anal shield. The metapodal shields and the anal shield are as in the female. Setae on tarsus II thick and spine-like as in the female.



Figs. 25–26. *Haemolaelaps insculptus* Keegan, female. Fig. 25, dorsal shield. Fig. 26, venter

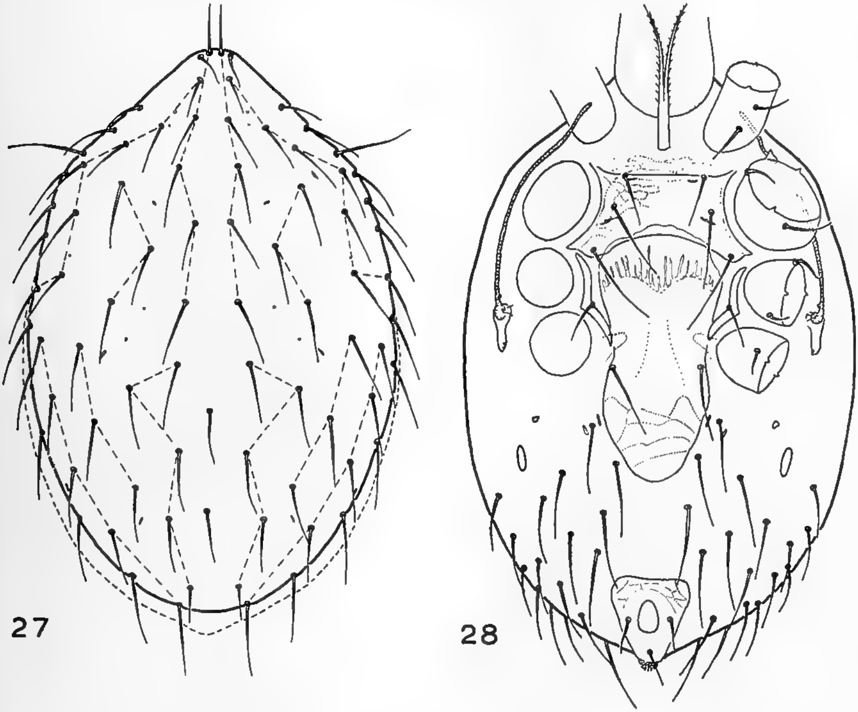
Hosts and localities. 6 ♂, 3 ♀—*Gerbillus pyramidum*, Holon, 12.vii.1954; 1 ♀—*Gerbillus allenbyi*, Holon, 12.vii.1954; 1 ♂, 2 ♀—*G. pyramidum*, Holon, 2.ix.1954; 3 ♀—ditto; 1 ♂, 1 ♀—*G. allenbyi*, Ma'agan Mikhael, 26.ix.1955; 2 ♀—ditto; 4 ♂, 16 ♀—*G. pyramidum*, Rishon le Zion (Dunes); 4 ♂, 12 ♀—*Meriones sacramenti*, Rishon le Zion (dunes); 3 ♂, 11 ♀—ditto.

Notes. This species was previously known only from Egypt. According to the distribution of its hosts, our area might well be on the northern limit of the distribution of the species. The material from Israel differs somewhat from the typical material, mainly in being larger, but the mites are undoubtedly conspecific.

Haemolaelaps longipes Bregetova

Haemolaelaps longipes Bregetova, 1952.
Haemolaelaps aegyptius Keegan, 1956 *syn. nov.*

FEMALE (Text-figs. 27, 28). The dorsal shield is ovoid, it is 855–900 μ long and 570–600 μ wide. The shield bears 40 pairs of setae (the additional pair is *px*1) as well as some asymmetrical setae. The dorsal setae are only slightly shorter than the ventral setae. Setae J5 slightly over half the length of setae Z5.



FIGS. 27–28. *Haemolaelaps longipes* Breg., female. Fig. 27, dorsal shield. Fig. 28, venter.

Tritosternum with long shaft and feathered laciniae, relatively weakly sclerotized. The presternal area is ornamented but the anterior margin of the sternal shield is usually well defined. The sternal shield is 85–110 μ long (at mid-line) and 192–202 μ wide (at the level of the second setae). The anterior margin between the first sternal setae is straight, the posterior margin is concave. The sternal setae are very long, the metasternal setae are slightly longer than half thelength of the third sternal setae. The sternal shield, although only weakly sclerotized, is sculptured on its anterior two-thirds. The pores are slightly crescent-shaped, the anterior pores are parallel to the anterior margin, the posterior pores have a slight outward slant.

The genital shield is weakly sclerotized but ornamented with striations ; it is widest behind the genital setae. The shield is flanked by two pairs of setae, it is constricted and narrowing just opposite the posterior flanking setae. The anal shield is 145 μ long and 122–128 μ wide. The paranal setae are inserted slightly posterior to the middle of the anus, they are slightly longer than the postanal seta. The metapodal shields are very narrow and elongated. Fifteen to sixteen pairs of setae are inserted on the ventral integument. The tubular part of the peritreme reaches slightly beyond the middle of coxa I ; a peritrematal shield is present.

The two ventral setae on coxa I are of subequal length, the proximal seta is much stouter than the distal seta. All coxae are slightly sculptured. The respective lengths of the legs (excluding pulvilli) are as follows : I—795 μ ; II—705 μ ; III—780 μ ; IV—1,065 μ.

Chelicerae chelate-dentate. The pilus dentilis on the fixed finger is only slightly inflated. The internal posterior rostral setae are very long (approximately 95 μ), longer than the capitular setae, almost three times the length of the outer posteror rostral setae. The deutosternal teeth are arranged in 6 rows, 4–5 teeth in each row.

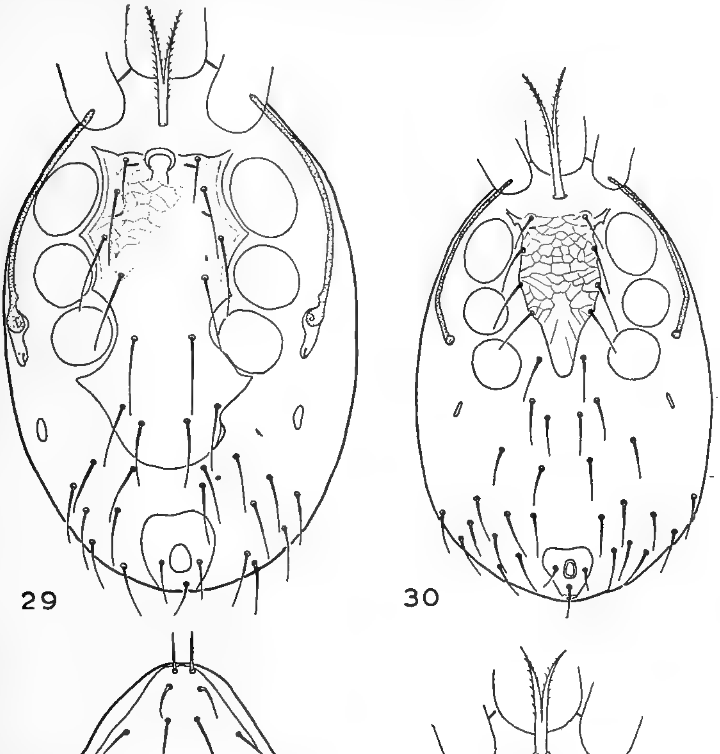
MALE (Text-fig. 29). The dorsal shield is 570 μ long and 390 μ wide. The chaetotaxy of the dorsal shield is essentially the same as in the female. The anal shield is separate from the sternito-ventral shield. The sternito-ventral shield bears 7 pairs of long setae of which the first pair is the shortest. The shield although only weakly sclerotized, is ornamented throughout with striations. The paranal setae are slightly longer than the postanal seta. The peritreme reaches to the middle of coxa I.

DEUTONYMPH (Text-fig. 30,). The dorsal shield has distinct lateral incisions ; it is 600–690 μ long and 345–430 μ wide. The chaetotaxy is the same as in the female. The sternal shield is ornamented, it bears 4 pairs of long setae, which are longer than the ventral setae. The shield is broadest at the level of the third setae and tapers off behind the fourth pair. It does not project behind coxae IV. The peritreme reaches to the middle of coxa I. Other characters as in the female.

PROTONYMPH (Text-figs. 31, 32). The anterior dorsal shield is 345 μ long and 300 μ wide, it bears 11 pairs of long setae. The setae on the pygidial shield are fairly long, except J5 which are only slightly over half the length of setae Z5. The sternal shield is ornamented on its anterior part, its anterior margin is hardly distinguishable from the ornamented presternal area. Three pairs of normal ventral setae and one pair of minute setae between coxae IV are inserted on the ventral membrane. The peritreme reaches to the middle of coxa III.

HOSTS AND LOCALITIES. 14 pn, 3 dn, 11 ♀—*Meriones crassus*, Raman, 12.iv.1955 ; 2 pn, 2 dn, 1 ♂, 2 ♀—*Gerbillus dasyurus*, Rosh Zohar, 21.viii.1955 ; 1 pn, 2 dn, 4 ♂—*Nesokia indica*, Sedom.

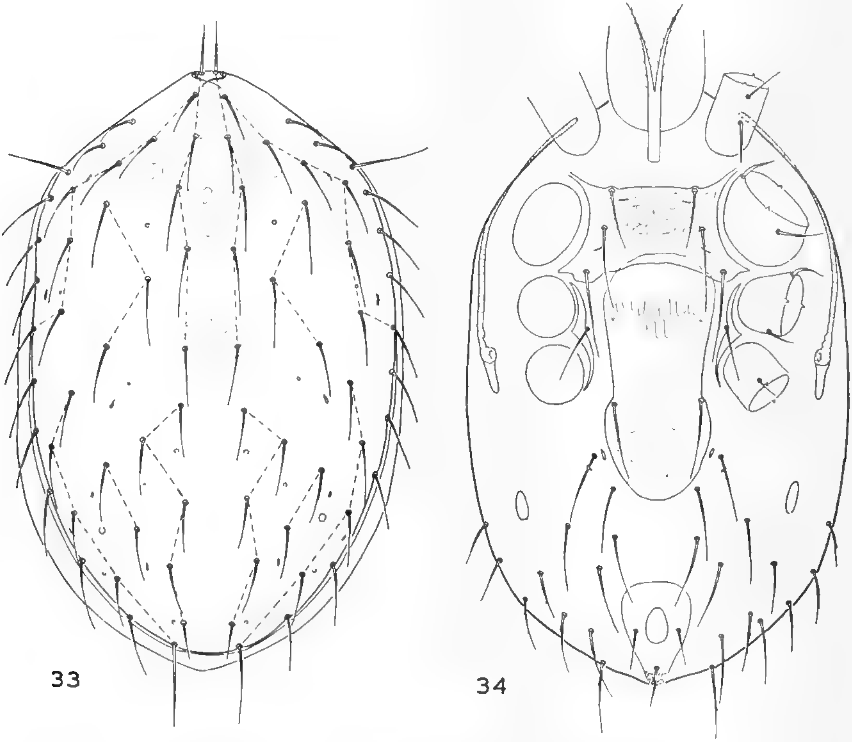
NOTES. *Haemolaelaps aegyptius* Keegan, 1956, is considered to be a synonym of *Haemolaelaps longipes* Bregetova, 1952. The paratype female of *H. aegyptius* in the collection of the British Museum (N.H.) having been compared with material of *H. longipes*, also in the collection. The most important diagnostic feature is the additional pair of setae in the *px* series (*px*1). Keegan (1956) lists this species from a wide range of gerbillids as well as from *Jaculus jaculus* and from *Rattus rattus*.



FIGS. 29–32. *Haemolaelaps longipes* Breg. Fig. 29, venter of male. Fig. 30, venter of deutonymph. Fig. 31, dorsum of protonymph. Fig. 32, venter of protonymph.

Haemolaelaps ovalis sp. nov.

FEMALE (Text-figs. 33, 34). The dorsal shield is ovoid and covers most of the dorsal surface. It is 735–795 μ long and 450–495 μ wide. The mites are well sclerotized. The dorsal shield is ornamented on its anterior part, bears 39 pairs of setae and in some of the specimens (roughly 25%), one or two additional asymmetrical setae. Setae J5 are slightly less than half the length of setae Z5.



FIGS. 33–34. *Haemolaelaps ovalis* sp. nov., female. Fig. 33, dorsal shield. Fig. 34, venter.

The strongly sclerotized tritosternum has a long shaft and feathered laciniae. The presternal area is faintly striated but the anterior margin of the sternal shield is well defined. The sternal shield is 90–102 μ long (at mid-line) and 160–172 μ wide (at the level of the second setae). The anterior margin of the sternal shield is fairly straight between the first pair of setae, the posterior margin is concave and slightly irregular. The pores are parallel to the anterior and to the posterior margin respectively. The shield is ornamented mainly on its anterior half. The well-sclerotized postero-lateral corners of the shield project between coxae II and III. The bases of the first pair of setae are situated on the anterior margin of the shield and the setae do not reach the posterior margin of the shield. Their length is approximately two-thirds of the length of the second setae. The metasternal setae are about half the length of the third setae.

The genital shield is tongue-shaped, it expands posteriorly to the genital setae and it is faintly ornamented with striations. The anal shield is 118–128 μ long and 96–109 μ wide. The paranal setae are inserted at the level of the middle of the anus, they appear to be slightly longer than the postanal seta. The metapodal shields are narrow and elongated. The peritreme reaches to the middle of coxa I. Five pairs of smooth setae are inserted on the ventral integument, and 6–7 latero-ventral pairs are slightly barbed.

The legs are relatively short, their respective lengths (excluding pulvilli) are as follows: I—630 μ; II—600 μ; III—616 μ; IV—870 μ.

Chelicerae chelate-dentate. The pilus dentilis on the fixed finger is only slightly inflated. There are 6 rows of deutosternal teeth, 3–4 teeth in each row.

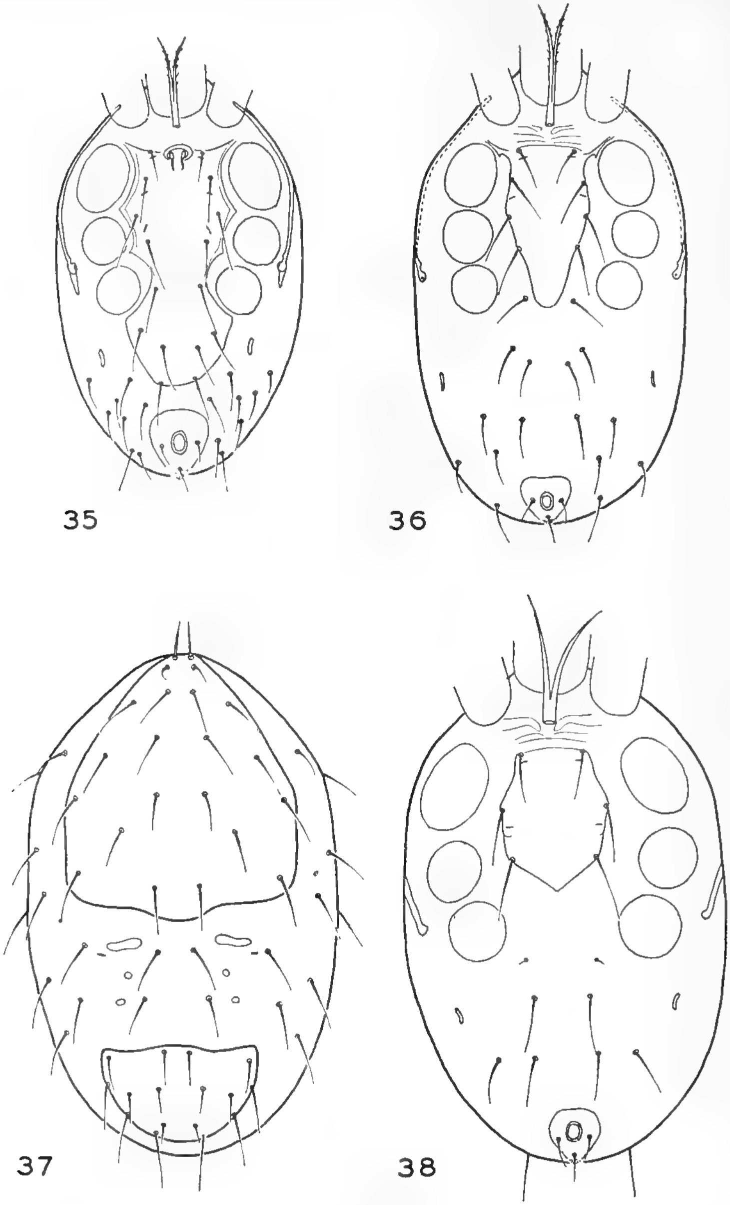
MALE (Text-fig. 35). The dorsal shield is 585–615 μ long and 360–405 μ wide. The chaetotaxy is essentially the same as in the female. Only one out of ten specimens examined had additional asymmetrical setae. The anal shield is separate from the sternito-ventral shield. The sternito-ventral shield bears 8 pairs of setae and is throughout ornamented with striations. Chelicerae with long, slightly curved, spermatophoral process.

DEUTONYMPH (Text-fig. 36). The dorsal shield is 480–570 μ long and 270–345 μ wide. The chaetotaxy of the dorsal shield is as in the female. The sternal shield bears four pairs of simple setae, it does not project behind coxae IV. The peritreme extends to the middle of coxa I. Eight to ten pairs of setae are inserted on the ventral membrane.

PROTONYMPH (Text-figs. 37, 38). The anterior dorsal shield is 255–270 μ long and 225–240 μ wide. The median setae on the pygidial shield are markedly shorter than the marginal setae. The sternal shield is very pointed at its posterior margin. The distance between the setae of the second pair of the sternal setae is markedly greater than the distance between the setae of the first pair. Three pairs of ventral setae of normal length and one pair of minute setae between coxae IV are inserted on the ventral membrane. The peritreme is short and does not reach to the level of the hind margin of coxa III.

HOSTS AND LOCALITIES. All specimens were recovered from *Meriones tristrami* at the following localities and dates: 18 pn, 13 dn, 3 ♂, 2 ♀—Mishmar Ha'emeq, 21.i.1952; 1 pn, 5 ♂, 12 ♀ (and numerous specimens in alcohol)—Nir David, 15.ii.1953; 7 pn, 2 dn, 2 ♂, 1 ♀—Shavei Zion, 22.viii.1955.

NOTES. The new species which is similar to *Haemolaelaps longipes* Breg. differs from it in the following features: it has no additional pair of setae in the *px* series; it is markedly smaller; its first sternal setae are distinctly shorter than the sternal shield; setae J5 are shorter.

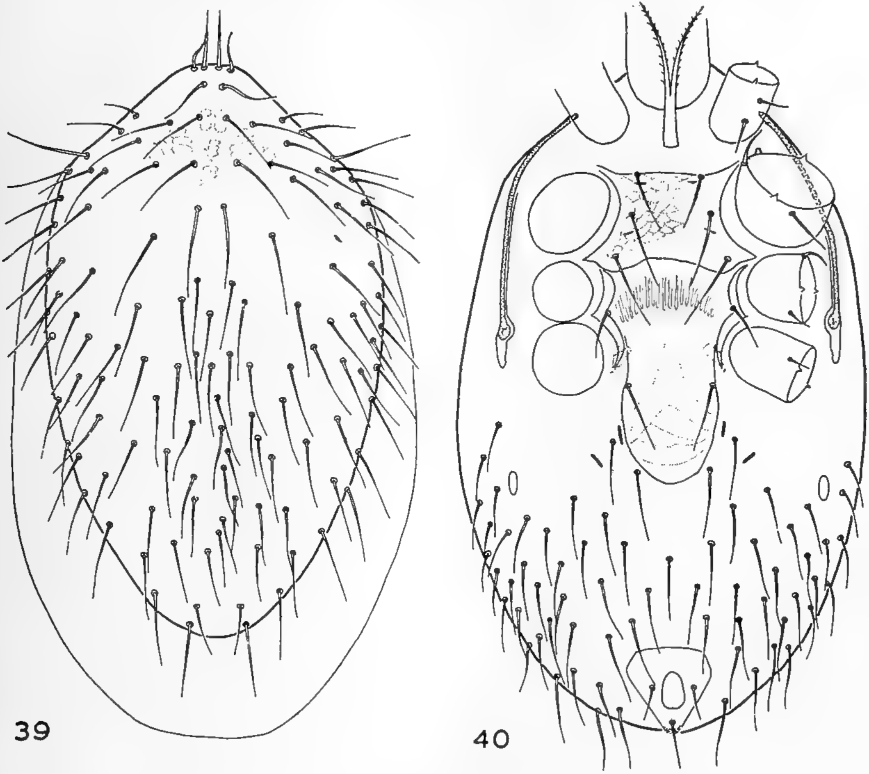


FIGS. 35–38. *Haemolaelaps ovalis* sp. nov. Fig. 35, venter of male. Fig. 36, venter of deutonymph. Fig. 37, dorsum of protonymph. Fig. 38, venter of protonymph.

Haemolaelaps centrocarpus Berlese, 1811

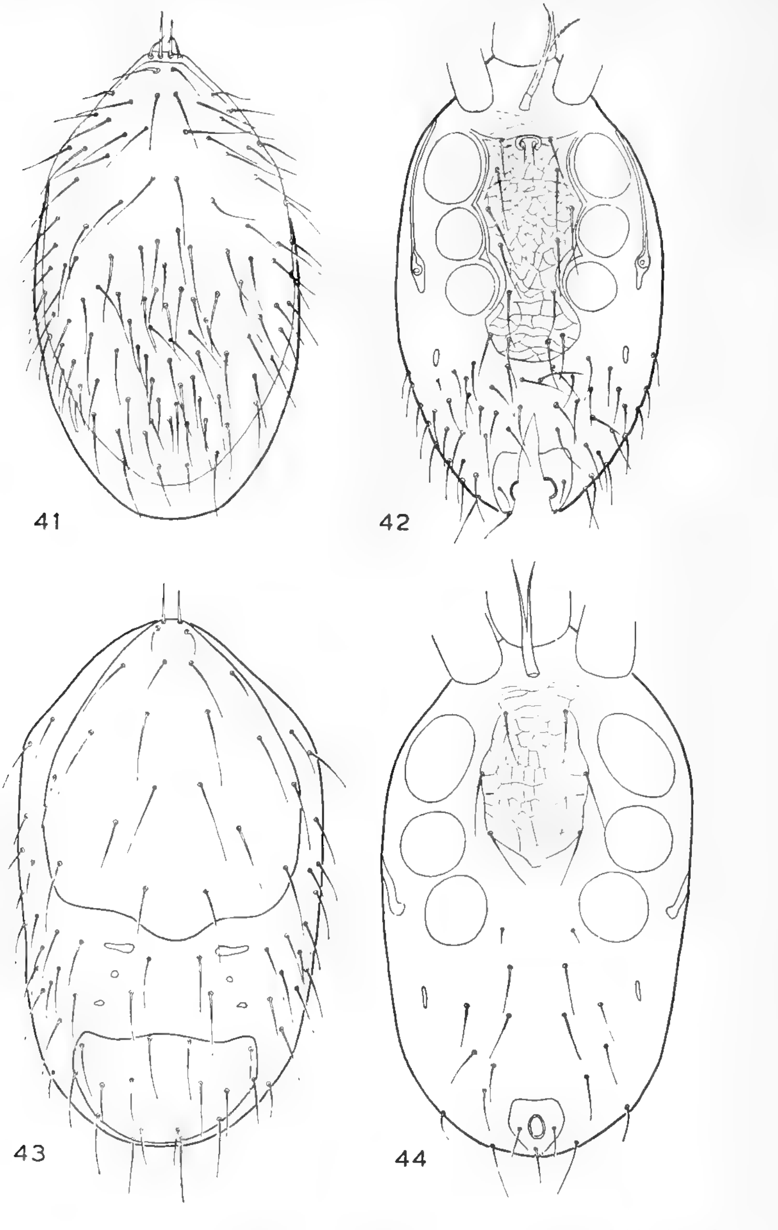
Haemolaelaps centrocarpus Berlese, 1911

FEMALE (Text-figs. 39, 40). The dorsal shield is 1,020–1,080 μ long and 615–690 μ wide. In addition to the regular paired setae (including apparently setae *ax* and *px*1) the shield has 25–30 asymmetrical neosetae, mainly on its posterior part. The number of setae on the dorsal shield is therefore approxinately 110. All the setae are of normal length. Setae J5 are about three-quarters of the length of setae Z5.



FIGS. 39–40. *Haemolaelaps centrocarpus* Berlese female. Fig. 39, dorsal shield. Fig. 40, venter.

The tritosternum is well defined and has feathered laciniae. The presternal area is ornamented, but the anterior margin of the sternal shield is distinct. The sternal shield is 150–170 μ long (at mid-line) and 192–198 μ wide (at the level of the second sternal setae). The anterior margin of the shield is fairly straight, the posterior margin is concave. The anterior pores are parallel to the anterior margin of the shield, the posterior pores have a very slight outward slant. The shield is well ornamented throughout. The first sternal setae are markedly shorter than the second and third setae which are approximately of equal length. The metasternal setae are slightly over half the length of the third sternal setae.



FIGS. 41–44. *Haemolaelaps centrocarpus* Berlese. Fig. 41, dorsal shield of male. Fig. 42, venter of male. Fig. 43, dorsum of protonymph. Fig. 44, venter of protonymph.

The genital shield is only weakly sclerotized, it bears one pair of long genital setae which are slightly longer than the adjacent setae. The anal shield is triangular with a fairly straight anterior margin. It is approximately 160 μ long and 135 μ wide. The paranal setae are inserted in line with the middle of the anus and seem to be of equal length to the postanal seta. Approximately 35 pairs of setae are inserted on the ventral integument, most of the postero-lateral setae are slightly barbed. The peritreme reaches slightly beyond the posterior margin of coxa I. A peritrematal shield is present.

The two ventral setae of coxa I are of about the same length, the proximal seta is much stouter than the distal seta. On the proximal dorsal surface of femur I are two spur-like setae, a similar, somewhat smaller seta, is inserted on the trochanter. The respective lengths of the legs (excluding pulvilli) are as follows: I—975 μ; II—855 μ; III—990 μ; IV—1,290 μ.

The chelicerae are chelate-dentate, the pilus dentilis is only very slightly inflated and has a curved tip. The deutosternal teeth are arranged in 6 rows, 3–5 teeth in each row.

MALE (Text-figs. 41, 42). The dorsal shield is 705–735 μ long and 405–480 μ wide, its chaetotaxy is essentially the same as in the female. The anal shield is separate from the sternito-ventral shield which bears 7–8 pairs of setae. The shape and the extent of the posterior margin of the shield are variable (as in *H. hirsti*, see Text-figs. 17, 18) and there is therefore a certain variation in the number of setae it bears and in its distance from the anal shield. The shield is distinctly ornamented throughout. The chelicerae bear elongated spermatophoral processes.

DEUTONYMPH. The dorsal shield is 630–660 μ long and 390–410 μ wide. Its chaetotaxy is as in the female. The sternal shield is widest between the second and the third setae; it is ornamented throughout and its posterior margin does not project beyond the hind margins of coxae IV.

PROTONYMPH (Text-figs. 43, 44). The anterior dorsal shield is 315 μ long and 270 μ wide. The number of setae on the dorso-lateral integument is higher than usual. Five to six pairs of setae are inserted on the ventral integument, a pair of minute setae is inserted between coxae IV. The sternal shield is faintly ornamented.

HOSTS AND LOCALITIES. 1 ♀—*Gerbillus allenbyi*, Holon, 12.vii.1955; 2 ♀—*Gerbillus pyramidum*, ditto; 1 ♂, 1 ♀—*G. allenbyi*, Caesarea, 23.vii.1954; 7 ♀—ditto; 2 ♂, 15 ♀—ditto; 2 ♀—*G. pyramidum*, Palmahim, 2.ix.1954; 1 pn, 2 dn, 1 ♀—*Meriones sacramenti*, Holon, 9.xi.1954; 3 pn, 1 dn, 10 ♀—*Gerbillus gerbillus*, Yotvata, 14.iv.1955; 1 dn, 3 ♂, 3 ♀—*G. allenbyi*, Ma'agan Mikhael, 26.ix.1955; 1 ♂—ditto; 2 ♀—*M. sacramenti*, Nes Ziona, 22.v.1957; 2 dn, 10 ♀—*M. sacramenti*, Rishon le Zion (Dunes); 1 ♂, 46 ♀—*G. pyramidum*, ditto.

NOTES. This species, although obviously related to *Haemolaelaps hirsti*, is most easily separated from the other species of *Haemolaelaps* by its large size and by its numerous long accessory setae.

LAELAPS C. L. Koch, 1839

Lange (1955) in his review on the genus *Laelaps* in the U.S.S.R. proposed a number of subgenera but Strandtmann & Wharton (1958) and Tipton (1960) did not adopt

Lange's subgeneric concepts. Tipton recognized four or five more or less distinct species groups separable on the basis of the distance between the epigynal setae.

Although the present study deals only with five species, it seems worth while to point out that they fall into three, clearly defined groups :

1. Species with 38 pairs of dorsal setae (only setae *px2* are inserted between the J and Z series), the male having a separate anal shield. This group includes only *Laelaps pachypus* C. L. Koch.

2. Species with 39 pairs of dorsal setae, femur I with very elongate and wavy dorsal setae ; the internal posterior rostral setae being rather short. This group includes *Laelaps ekstremi* Zachvatkin and *Laelaps agilis longispinosus* ssp. nov.

3. Species with 39 pairs of dorsal setae, femur I with only slightly elongated, straight and stout dorsal setae, the internal posterior rostral setae being very elongated. This group includes *Laelaps algericus* Hirst and *Laelaps acomydis* sp. nov.

In the present study the old nomenclature will be followed.

Although *Echinolaelaps echidninus* (Berlese) occurs in Israel (Gratz, 1957), it is not included in the present study as it has been recovered only from *Rattus norvegicus* in the Haifa port area.

Laelaps acomydis sp. nov.

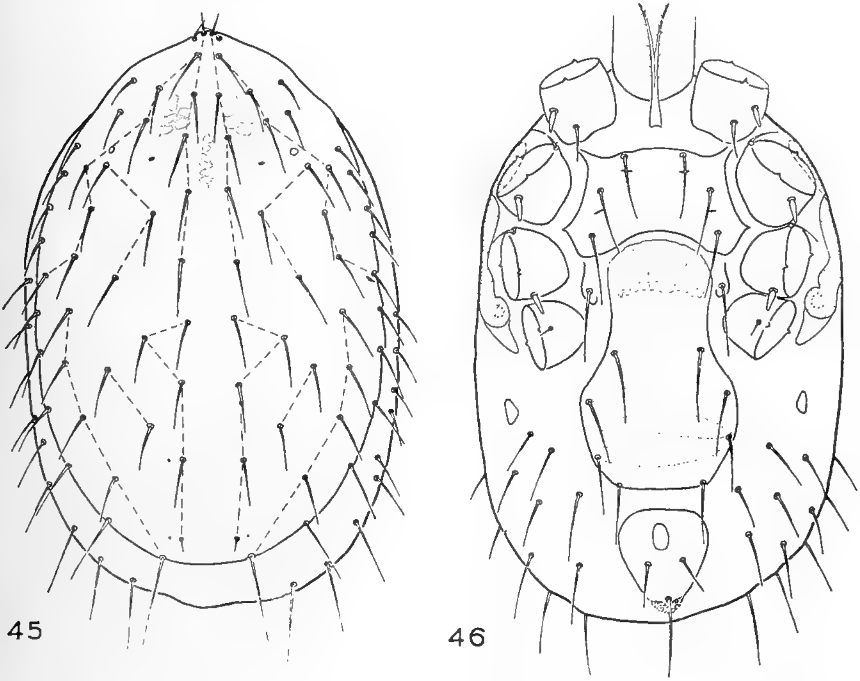
FEMALE (Text-figs. 45, 46). The dorsal shield is ovoid and rather narrow, 525–540 μ long and 345–360 μ wide, it bears 39 pairs of setae. All the setae are simple and slender Setae J5 short (approximately 24 μ), setae Z5 long (approximately 86 μ). The anterior part of the shield is sculptured and has two pairs of distinct pores. Two setae, *px2* and *px3* are inserted between the J and Z series.

The tritosternum is well developed and has clearly defined, sparsely feathered laciniae. The presternal area is weakly ornamented, the anterior margin of the sternal shield is distinct. The sternal shield is 80 μ long (at mid-line) and 140 μ wide (at the level of the second setae). The anterior margin is only slightly convex, the posterior margin is markedly concave. The sternal shield has prominent posterolateral corners which project at the level of the third sternal setae. The shield is ornamented with transverse striations. The anterior and the posterior pores are nearly horizontal. The first sternal setae do not reach the hind margin of the sternal shield. The metasternal setae are of the same length as the third sternal setae, they are inserted on small indistinct shields.

The genito-ventral shield is flask-shaped, broadest at the level of the second pair of setae. The distance between the setae of the first pair is approximately equal to the distance between the setae of the fourth pair. The shield is weakly ornamented with transverse striations.

The anal shield is roughly triangular, 108 μ long and 100 μ wide. The paranal setae are inserted usually at a point beyond the hind margin of the anus, their length is approximately 45 μ. The postanal seta is about 80 μ in length. The peritreme is very broad and conspicuous and extends anteriorly to the anterior margin of coxa II. A small peritrematal shield is present. The metapodal shields are in the form of elongated triangles with their bases directed externally. Eight to nine pairs of setae are located on the ventral membrane.

Legs I and II are stumpy while legs III and IV are more slender, their respective lengths (excluding pulvilli) being as follows: I—300 μ; II—300 μ; III—330 μ; IV—360 μ. Femur I bears dorsally straight, stout and not very elongated setae. Coxa I with a proximal seta and a distal spur, coxae II and III with spurs, coxa IV with a small, hair-like, seta.



FIGS. 45–46. *Laelaps acomydis* sp. nov., female. Fig. 45, dorsum. Fig. 46, venter.

There are 6 rows if deutosternal teeth, 2–3 denticles in each row. The corniculi are horn-shaped, their proximal portions are broad and their distal parts are attenuated. The internal posterior rostral setae are longer than the corniculi (approximately 32 μ long), similar to the corresponding setae in *Laelaps algericus* (Text-fig. 65).

MALE (Text-fig. 71). Markedly smaller than the female and much narrower. The dorsal shield is 420–460 μ long and 240–255 μ wide. The dorsal shield bears more ornamentation than that of the female. The chaetotaxy of the dorsal shield is essentially the same as in the female. The holoventral shield bears 23 setae (anal setae included), and is ornamented with fine striations. Tarsus IV (118 μ in length) with simple setae only.)

HOSTS AND LOCALITIES. All the specimens, except 2 , were recovered from *Acomys cahirinus* at the following localities and dates: 2 ♀—Beit Alfa, 15.ii.1953; 6 ♀—

Beit Guvrin, 5.viii.1954; 1 pn, 1 dn, 13 ♀—ditto; 2 ♂, 14 ♀—Nazareth, 17.viii.1955; 5 ♀—Wadi Ara, 18.viii.1955; 5 ♂, 50 ♀—Kabri, 22.viii.1955; 11 ♂, 24 ♀—Mishmar Ha'emeq, 28.x.1955; 2 ♂, 22 ♀—ditto; 2 ♂, 18 ♀—Carmel (Tivon), 22.ix.1956; 3 ♂, 5 ♀—Mishmar Ha'emeq, 26.ix.1956; 1 ♀—*Sekeetamys calurus*, Wadi Masri, 1.xi.1956; 1 ♀—*Meriones tristrami*, Shavei Zion, 22.viii.1955.

NOTES. The new species seems to have a marked preference for *Acomys cahirinus* and it is actually the first *Laelaps* species recorded from the murine genus *Acomys*. In the key provided by Zumpt (1950) for the Ethiopian species of *Laelaps* the new species keys out as *Laelaps nuttalli* Hirst. It is obviously related to this species, but can be separated from it mainly by its broader and shorter peritreme which does not project beyond the anterior margin of coxa II (in *L. nuttalli* the peritreme projects anteriorly up to the middle of coxa I). Minor differences may also be found in the length of setae J5 which are longer in *L. nuttalli*. Moreover the sternal shield of *L. nuttalli* is longer and its hind margin is less concave. The males can be separated by the length of the peritreme and by the length of the setae on tarsus IV, which are approximately 38 μ long in *L. nuttalli* and about 29 μ long in *L. acomydis*.

In the key provided by Tipton (1960) the new species keys out as *L. lamborni* Hirst, however, it differs from the latter in the shape and the length of the sternal shield (approximately 120–130 μ in *L. lamborni*) and in the shape of the metapodal shields which are short and oval in *L. lamborni*. The setae on tarsus IV of the female are shorter in *L. acomydis* (approximately 32 μ) than in *L. lamborni* (approximately 50 μ).

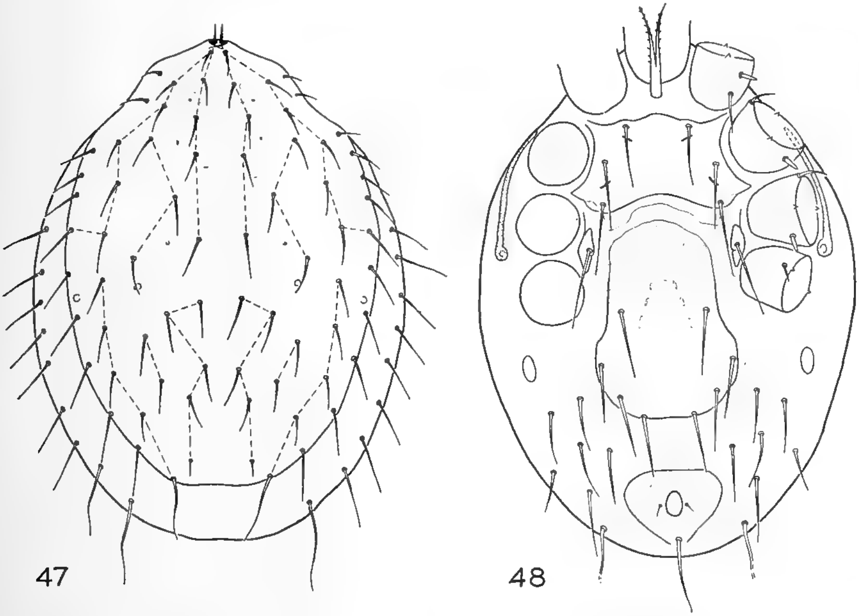
Laelaps agilis longispinosus ssp. nov.

FEMALE (Text-figs. 47, 48). The dorsal shield is ovoid, it is 660–690 μ long and 470–500 μ wide. This mite is rather robust and well sclerotized. Thirty-nine pairs of setae are inserted on the dorsal shield. The posterior setae on the dorsal shield and those on the lateral membrane are rather wavy. Setae J5 are very short and do not reach the posterior margin of the dorsal shield. The anterior part of the shield is ornamented. There are many distinct pores on the shield. Two setae, *px2* and *px3*, are inserted between the J and Z series.

The tritosternum has well-developed but sparsely feathered laciniae. The presternal area is only weakly sculptured. The anterior margin of the sternal shield is very convex, the posterior margin is strongly concave. The shield is 128–140 μ long (at mid-line) and 192–200 μ wide (at the level of the second setae). The anterior pores are slightly crescent-shaped with an inward slant, the posterior pores have an outward slant. First, second, third sternal and metasternal setae are gradually increasing in length in that order. The metasternal shields are well sclerotized, they are spindle-shaped.

The genito-ventral shield is broad, expanding half-way between the first and the second pair of setae and broadest at the level of the second pair. The posterior margin of the shield, between the setae of the fourth pair, is straight. The shield has no transverse striations. The second pair of setae is much nearer to the third pair than to the first pair. The metapodal shields are ovoid. The anal shield is distinctly ornamented around the anus. The shield is 100 μ long and 138 μ wide.

The paranal setae are inserted near the middle of the length of the anus and their length is approximately equal to the width of the anus. The postanal seta is very long, about five times the length of the paranal setae. The peritreme extends beyond the middle of coxa II.

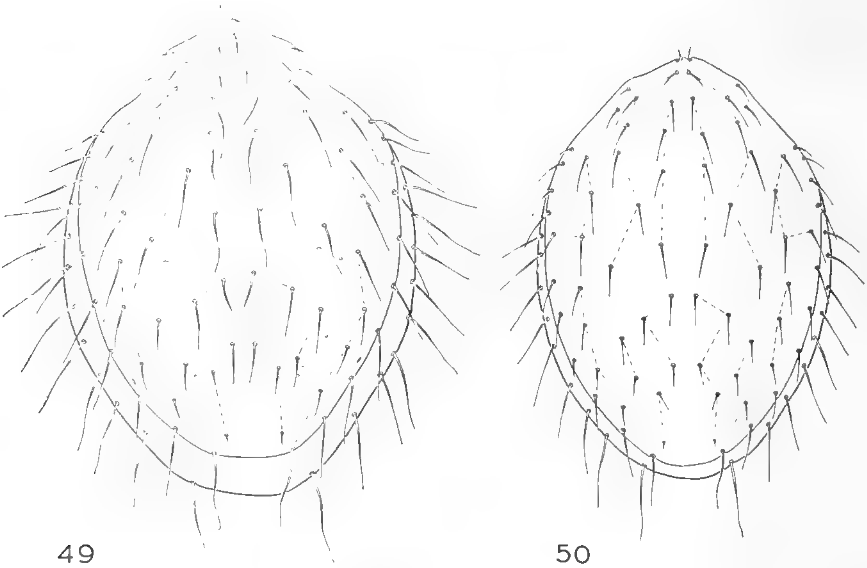


FIGS. 47–48. *Laelaps agilis longispinosus* ssp. nov., female. Fig. 47, dorsum. Fig. 48, venter.

The legs are robust, the fourth pair being the longest, approximately 615 μ (excluding pulvillus). The dorsal setae on femur I are very long and wavy. Coxa I with a piliform proximal seta, the distal seta being a blunt spur, coxae II and III with blunt spurs, coxa IV with a rather sharp spine. There are 6 rows of deutosternal teeth, 2–4 teeth in each row. The corniculi are broad at their bases and rather narrow in their distal halves. The internal posterior rostral setae (approximately 25 μ long) are shorter than the corniculi.

MALE (Text-figs. 49–53). The dorsal shield is 630–690 μ long and 445–490 μ wide. The chaetotaxy is essentially the same as in the female, but with much longer wavy setae on the anterior portion of the shield. The holoventral shield bears 21 setae (including the anal setae). The most distinctive feature of the male is leg IV which bears very long spines on the tarsus, the tibia and the genu.

DEUTONYMPH (Text-figs. 54, 55). The dorsal shield is 585 μ long and 405 μ wide. Setation as in the female. The anterior margin of the sternal shield is indistinct, the presternal area is weakly ornamented. The sternal shield bears 4 pairs of setae of approximately equal length. The posterior part of the shield, behind the fourth pair of setae, is in the shape of a broad tongue, almost touching the pair of setae adjacent to it. The peritreme is short, reaching to the middle of coxa III. The anal shield is 108 μ long and 118 μ wide. Anal setae as in the female. About 10 pairs of ventral setae.

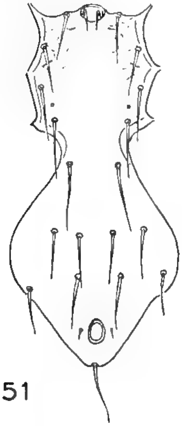


Figs. 49–50. Fig. 49, *Laelaps agilis longispinosus* ssp. nov., dorsum of the male. Fig. 50, *Laelaps agilis* C. L. Koch (from *Apodemus sylvaticus*, Gt. Britain), dorsum of male.

Protonymph (Text-figs. 56, 57). The anterior dorsal shield is 345 μ long and 315 μ wide, it bears 11 pairs of setae. Most of the setae are of equal length, the outer posterior setae being the longest. All the setae on the pygidial shield, except the very short J5 and the very long Z5, are almost of the same length. The shape of the shield is as in Text-fig. 58, rather pointed at its posterior end. Anal shield and setae as in female.

Larva (Text-figs. 58, 59). The body (excluding capitulum) is about 525 μ long and 405 μ wide. The larva, which in the genus *Laelaps* is non-feeding, has a very translucent cuticle through which the nymphal legs may be seen. The finely reticulated dorsum bears 14 pairs of small setae as well as 2 pairs of posterior setae, position and relative lengths of setae as in Text-fig. 59. The tritosternum stands out distinctly and is not feathered. There are 11 ventral setae (including anal setae), and the postanal seta is the longest seta on the ventral surface.

Hosts and localities. All specimens were recovered from *Apodemus sylvaticus* at the following localities and dates: 1 pn, 2 ♂, 15 ♀—Sasa, 4.iv.1954; 1 dn, 3 ♂, 17 ♀—ditto; 22 ♀—ditto; 9 ♀—ditto; 1 larva, 1 pn, 1 dn, 4 ♂, 2 ♀—Yekhiam, 14.ii.1955; 9 ♂, 8 μ—Mishmar Ha'emeq, 28.ix.1956.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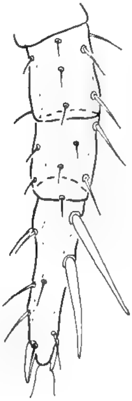
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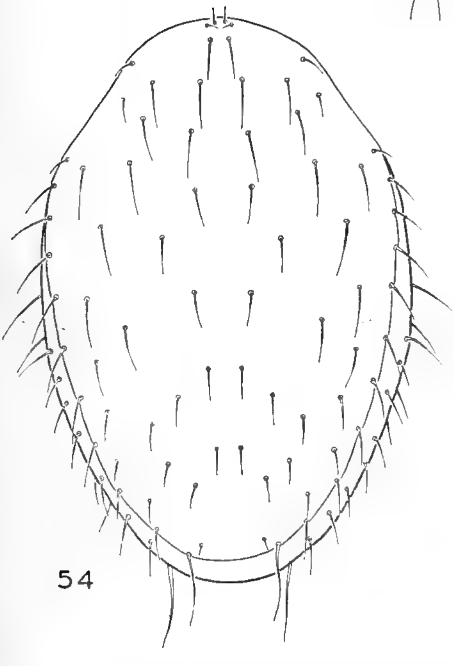
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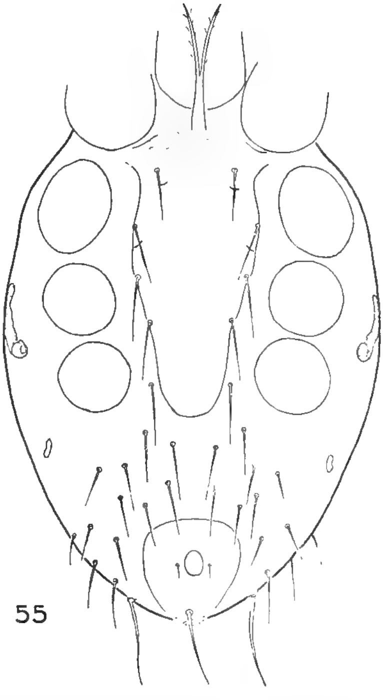
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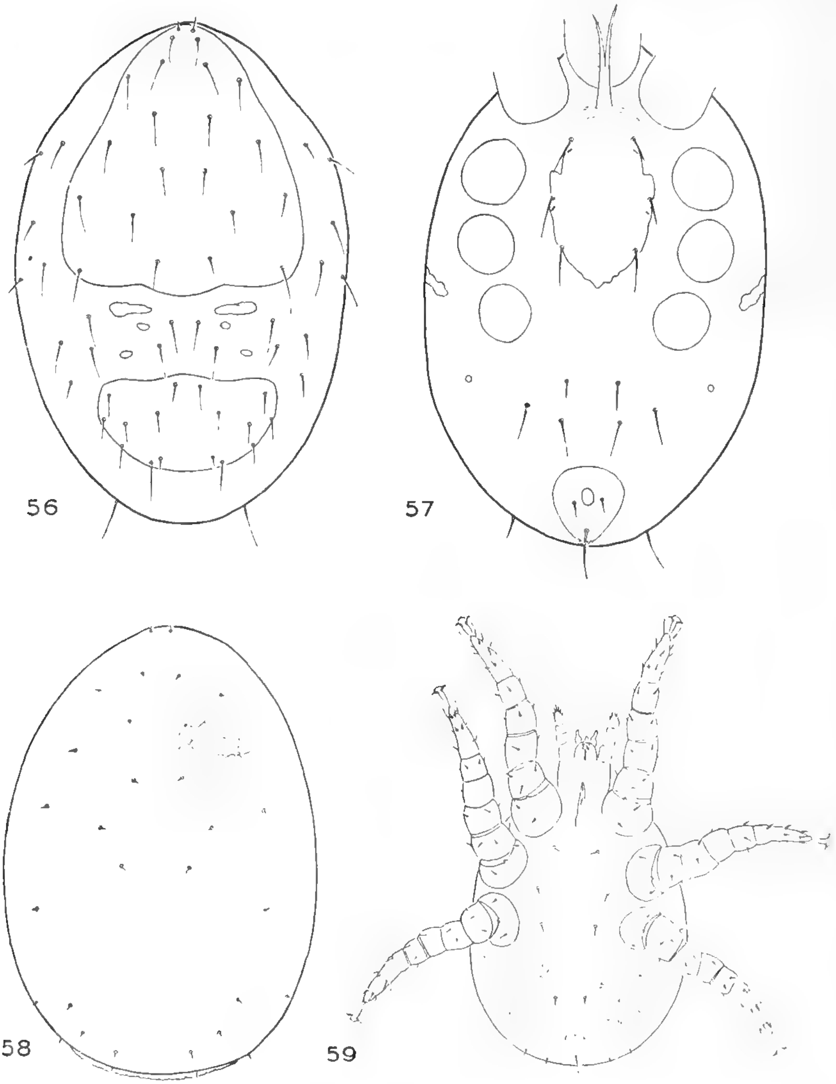
FIGS. 51–55. Fig. 51, *Laelaps agilis longispinosus* ssp. nov., venter of male. Fig. 52, *L. a. longispinosus* ssp. nov., leg IV of the male. Fig. 53, *Laelaps agilis* C. L. Koch, leg IV of the male. Fig. 54, *L. a. longispinus* ssp. nov., dorsum of deutonymph. Fig 55, *L. a. longispinosus* ssp. nov., venter of deutonymph.



FIGS. 56–59. *Laelaps agilis longispinosus* ssp. nov. Fig. 56, dorsum of protonymph. Fig. 57, venter of protonymph. Fig. 58, dorsum of larva. Fig. 59, venter of larva.

NOTES. The material from Israel on which this description is based was compared carefully with material of *Laelaps agilis* C. L. Koch in the collection of the British Museum (N.H.). Although no significant difference could be found between the females of *L. agilis* and the Israel material, the males were seen to be markedly different. The males of the Israel material are more robust, have much longer setae and also differ in the setation of leg IV by having elongated and stout setae on the tibia and on the genu (Text-figs. 50, 51, 53, 54). It is therefore proposed to create the new subspecies *Laelaps agilis longispinosus* for the material from Israel. The host of these specimens *Apodemus sylvaticus* seems also to be the main host of *L. agilis* which has been recorded only from rodents of the genus *Apodemus* (Tipton, 1960).

The female of *Laelaps oraniensis* Hirst (only sex described) is also very closely related to *L. agilis* and could not be separated from the Israel females. The type material of *L. oraniensis* was collected off " field-mice " Mt. Marabut, Oran, which is well within the range of *A. sylvaticus* and it seems probable that this species was the host. Unfortunately the status of *L. oraniensis* cannot be assessed until males from the type locality and the type host are available for examination.

In a recent review of the genus *Laelaps* by Tipton (1960) the name *L. oraniensis* Hirst is assigned to a *Laelaps* species recovered from *Otomys* sp. (Gerbillinae), a rodent not occurring in the type locality. This species differs, according to Tipton's description from both *L. agilis* and the type material of *L. oraniensis* Hirst in the number of dorsal setae (stated to be 31 pairs only), as well as in the pattern of their relative position on the anterior part of the dorsal shield. The males have only short setae on tarsus IV (according to the drawing given by Tipton). It seems therefore that *L. oraniensis* Hirst sensu Tipton is a different species, apparently related to *L. nuttalli* Hirst.

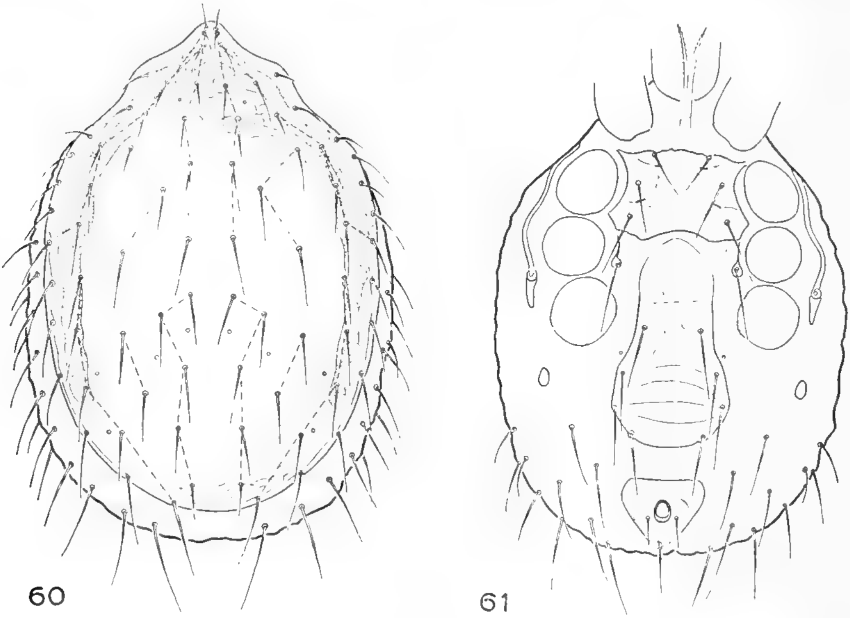
Laelaps algericus **Hirst**

Laelaps algericus Hirst, 1925.

FEMALE (Text-figs. 60, 61). The dorsal shield is 675–705 μ long and 480–510 μ wide (Hirst gives the length of the body without capitulum as 0·70 mm.). The most distinctive feature of this mite is the heavily sclerotized and pigmented band on the anterior and lateral margins of the dorsal shield. There is no sign of this sclerotization in the nymphal stages, the male is unknown. The dorsal shield is slightly ornamented, mainly on its anterior part. The shield bears 39 pairs of setae, all simple. Setae J5 are about half the length of setae Z5. Two setae, *px2* and *px3*, are inserted between the J and the Z series.

Tritosternum apparently with long shaft and with short, sparsely feathered laciniae. The presternal region is sclerotized and sculptured but the anterior margin of the sternal shield is well defined. The sternal shield is heavily sclerotized and slightly ornamented, mainly around the setae. The anterior margin of the shield is irregularly straight, and the central third of the hind margin is concave. The shield is 122–134 μ long (at mid-line) and 160–173 μ wide (at the level of the second setae). The anterior pores are nearly horizontal, the posterior pores are slightly at an angle. First, second, third sternal and metasternal seta gradually increasing in length in that order.

The genito-ventral shield is pear-shaped, broadest at the third pair of setae. The hind margin is almost straight and the shield is ornamented with striations. The faintly sculptured anal shield has a truncate anterior margin, and it is slightly wider than long. The paranal setae are inserted in line with the posterior margin of the anus and their length is about half that of the postanal seta. The metapodal shields are irregularly oval, almost round. Ten pairs of setae are inserted on the ventral membrane. These are slightly longer than the dorsal setae. The peritreme extends anteriorly to the level of the posterior margin of coxa I and a narrow peritrematal shield is present.

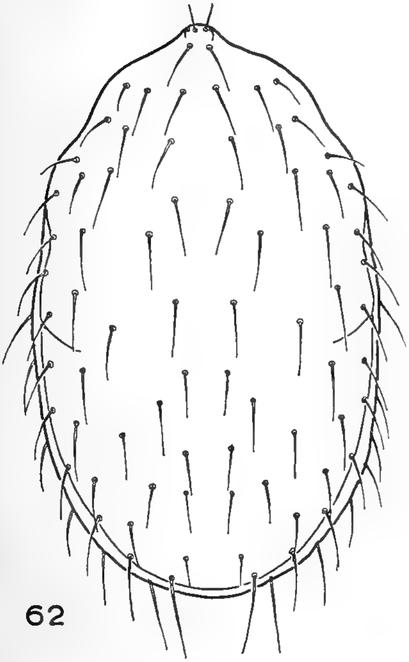


FIGS. 60–61. *Laelaps algericus* Hirst., female. Fig. 60, dorsum, Fig. 61, venter.

The legs are of the usual laelaptid type. The dorsal setae of femur I are much shorter than the setae on the dorsal shield. Coxae I, II and III bear blunt spurs. Tarsus IV with spiniform setae but without spurs. There are 6 rows of deutosternal teeth, 2–4 denticles in each row. The corniculi are distinct and horn-shaped. The chelicerae are chelate-dentate, the pilus dentilis is slightly inflated with a characteristic hook-like shape. The internal posterior rostral setae are very long (approximately 42 μ), much longer than the corniculi.

DEUTONYMPH (Text-figs. 62, 63). The dorsal shield is 570 μ long and 340 μ wide. Chaetotaxy the same as in the female. The sternal shield is elongated, its anterior

FIGS. 62–65. *Laelaps algericus* Hirst. Fig. 62, dorsum of deutonymph. Fig. 63, venter of deutonymph. Fig. 64, dorsum of protonymph. Fig. 65, ventral view of the gnathosoma of the protonymph.



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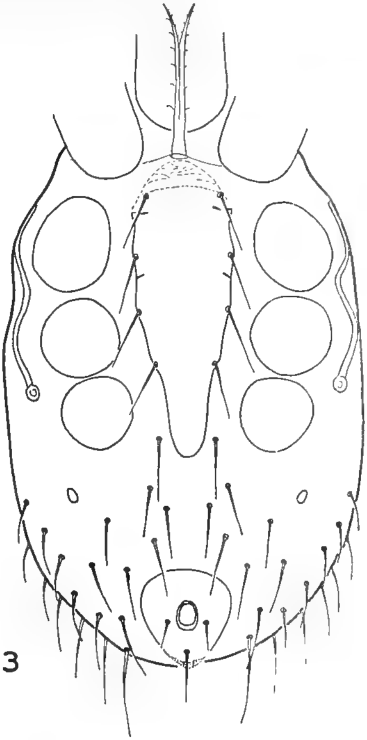

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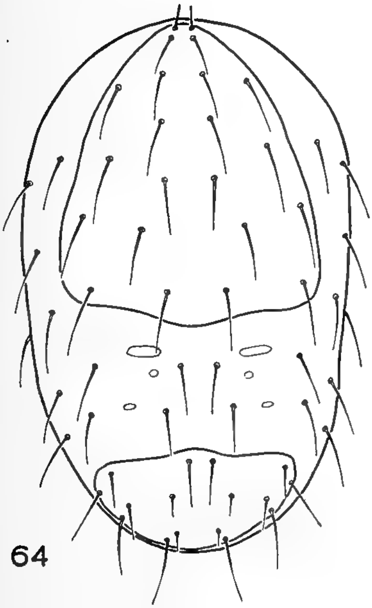

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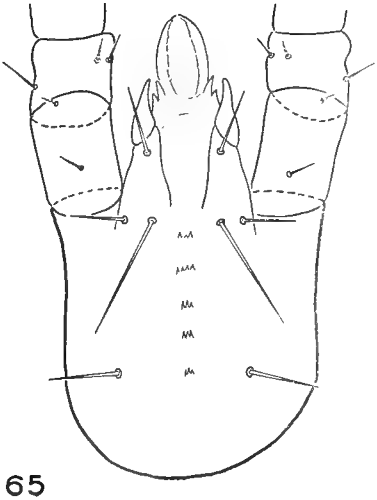

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border is indistinct, the presternal area is faintly ornamented. The sternal shield bears 4 pairs of setae which are of about equal length. Two small oval metapodal shields are present. The anal shield has a rounded anterior margin, anal setae as in the female. The peritreme reaches to the anterior margin of coxa II. The long internal posterior rostral setae are very conspicuous.

PROTONYMPH (Text-figs. 64, 65). The three pairs of platelets between the anterior shield and the pygidial shield are very well defined. Setae J4 and J5 on the pygidial shield are very short. The sternal plate has an indistinct anterior margin and it is broadest at the level of the second pair of setae. Three pairs of normal setae and one pair of minute setae between coxae IV, are inserted ventrally. An additional pair of elongated strong setae is inserted at the posterior end of the body. The long internal posterior rostral setae are conspicuous (Text-fig. 66).

HOSTS AND LOCALITIES. On *Mus musculus*, Mishmar Ha'emeq : 2 ♀ -23.xii.1952 ; 2 ♀—26.xii.1952 ; 1 ♀—13.ii.1953 ; 4 ♀—21.ii.1953 ; 14 ♀—21.ii.1953 ; 3 ♀—22.ii.1953 ; 1 dn—22.ii.1953 ; 12 ♀—13.ii.1954 ; 12 ♀—13.ii.q954 ; 12 ♀—24.i.1955 ; 5 ♀—i.1955 ; 3 ♀.1.ii.1956 ; 8 ♀—13.ii.1958 ; Aqua Bella : 2 ♀—3.ii.1954 ; 5 ♀—16.vii.1957 ; Carmel : 2 pn, 22 ♀—22.ii.1956 ; Kishon : 5 ♀—16.vii.1957. Mishmar Ha'emeq, on *Microtus guentheri*, 1 ♀—21.iii.1953.

NOTES. The type material was taken from " *Mus algericus* " (apparently *Apodemus sylvaticus algirus* Pomel, 1856) and has been recorded from *Mus musculus* and *Crocidura olivieri* (Bregetova, 1956 ; Keegan, 1956). In Israel this species seems to be host-specific on *M. musculus* (the one female from *M. guentheri* may have originated from a *M. musculus* trapped at the same time.

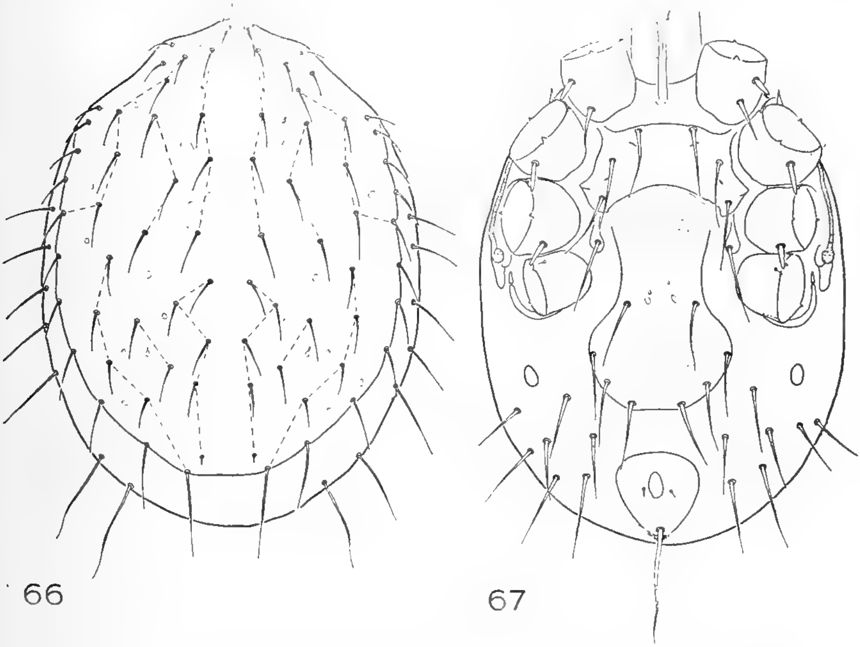
Laelaps ekstremi **Zachvatkin**

Laelaps ekstremi Zachvatkin, 1948.
Laelaps jettmari, Bregetova, 1956.

FEMALE (Text-figs. 66, 67). The dorsal shield is 570 μ long and 435 μ wide, it bears 39 pairs if simple setae. The most diagnostic feature of the dorsal setation is the lateral position of setae *r*1 in relation to setae *i*1 (in most other species of *Laelaps* setae *r*1 lie rather posteriorly to setae *i*1). Setae J5 are very short, approximately 9–10 μ while setae Z5 are very long, approximately 110 μ. The dorsal shield is slightly ornamented on its anterior part and it is provided with many distinct pores. The usual *px*2 and *px*3 setae occur between the J and Z series. All the dorsal setae are simple and their distribution and relative lengths are shown in Text-fig. 66.

The tritosternum has long, very slightly feathered, laciniae. The sternal shield is well sclerotized, it is 77 μ long (at mid line) and 116 μ wide (at the level of the second pair of setae). The anterior margin is very distinct and convex, while the posterior margin is markedly concave. The anterior pores are slightly crescent-shaped with an inward slant, the posterior pores have an outward slant. The first pair of sternal setae is longer than the sternal shield and project beyond the hind margin of the shield. The metasternal setae are not longer than the third pair of sternal setae. The metasternal shields are drop-shaped, almost reaching the posterior margin of the sternal shield.

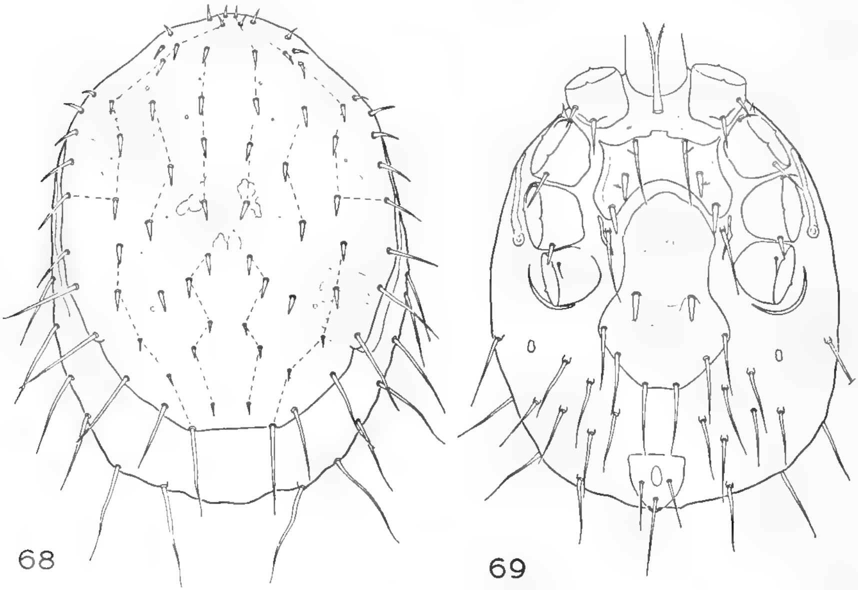
The genito-ventral shield is flask-shaped, very narrow in front of the first pair of setae (approximately 102 μ at this level), broadest at the level of the second pair of setae (approximately 180 μ wide). The shield is ornamented with transverse striations. The posterior margin of the genito-ventral shield is truncated. The anal shield is 105 μ long and 106 μ wide. The paranal setae are very short (19 μ) while the postanal seta is long (128 μ) and wavy. There are about 7 pairs of ventral setae on the membrane. The metapodal shields are oval and well sclerotized. The peritreme reaches to the middle of coxa I, a peritrenatal shield is present, not connected to the very distinct parapodal shield.



FIGS. 66–67. *Laelaps ekstremi* Zachvatkin, female. Fig. 66, dorsum. Fig. 67, venter.

The legs are rather short, the first and second pair more robust, the third and fourth pairs more slender. Leg IV (excluding pulvillus) is 435 μ long. The dorsal setae of femur I are very long and wavy. On coxa I there is a proximal piliform seta and a distal blunt spur ; coxae II and III with blunt spurs (the spur of coxa II being longest) coxa IV bears ventrally only a small, almost hair-like, seta. There are 6 rows of deutosternal teeth, 2–3 denticles in each row. The corniculi are horn-shaped, the internal posterior rostral setae (approximately 16 μ long) are shorter than the corniculi.

MALE (Text-figs. 72, 73). The dorsal shield is 570 μ long and 425 μ wide. The chaetotaxy and the ornamentation of the dorsal shield are essentially the same as in the female. The holoventral shield is well ornamented, especially on its posterior part. The shield, which bears 21 setae (including anal setae), is broadest immediately behind coxae IV and tapers off behind the last row of setae. The setae on the holoventral shield are shorter than the setae on the ventral and the lateral membranes. The metapodal shields are almost circular. The peritreme reaches to the middle of coxa II. A small peritrematal shield is present, it is rather distant from the parapodal shield which is much smaller than in the female. The legs are rather short, coxa III bears a blunt spur, coxae I and II bear sharp spines, coxa IV has a small seta. Tarsus IV (96 μ long, excluding pulvillus) bears 2 blunt short spurs distally and a similar spur on the row preceding them.



Figs. 68–69. *Laelaps pachypus* C. L. Koch, female. Fig. 68, dorsum. Fig. 69, venter.

Hosts and localities. 2 ♂, 7 ♀—*Cricetulus migratorius*, Dalia, 13.v.1955.

Notes. Bregetova (1956) synonymized *L. ekstremi* Zachvatkin with *L. jettmari* Vitzthum. It has been found, however, that the female of *L. jettmari* differs in the following points from *L. ekstremi* :

(*a*) Setae *r*1 are posterior to setae *i*1 ;

(*b*) the sternal shield is much longer, it is 160 μ long ;

(*c*) the first sternal setae are short and do not reach the hind margin of the sternal shield ;

(*d*) the genito-ventral shield is broad and has no narrow neck.

I consider therefore that the validity of *Laelaps ekstremi* Zachvatkin, 1948, should be re-established.

Laelaps pachypus C. L. Koch

Laelaps pachypus C. L. Koch, 1839.
Tetragonyssus microti Ewing, 1933.
Laelaps kochi Oudemans, 1936.
Laelaps (*Hyperlaelaps*) *amphibius* Zachvatkin, 1948.
Laelaps (*Hyperlaelaps*) *arvalis* Zachv., 1948 *syn. nov.*

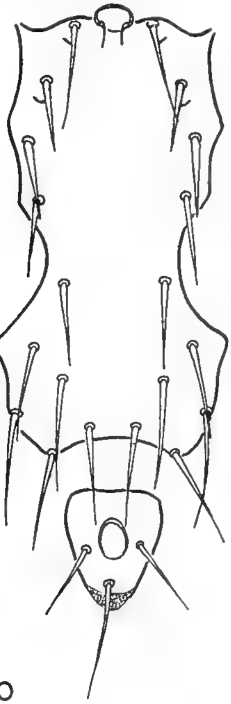
FEMALE (Text-figs. 68, 69). The dorsal shield is 540–570 μ long and 435–450 μ wide, 38 pairs of short, spiniform setae are inserted on it. Five pairs of setae (Z3, Z4 and J3–J5) on the posterior part of the shield are much smaller than the spines on the anterior part of the shield. The marginal setae of the dorsal shield are gradually increasing in size from short spiniform setae on the anterior margin to long and rather wavy setae on the posterior margin of the shield. Setae J5 are short (approximately 19 μ), setae Z5 are long (approximately 118 μ). Only one seta, *px2*, lies between the J and Z series. The dorsal shield is ornamented with scale-like ornamentations on the anterior part of the shield, and with transverse striations on its posterior part. Many punctuations are scattered over the surface of the shield.

The tritosternum has long laciniae which are sparsely feathered with very short hairs. The sternal shield which is heavily sclerotized, is 77 μ long (at mid-line) and 195 μ wide (at the level of the second pair of setae). The anterior pores have a steep inward slant, the posterior pores have a slight inward slant. The anterior margin of the shield is convex, in many specimens with a slight projection in the middle (Text-fig. 69). The hind margin of the shield is deeply concave. The presternal area is only faintly ornamented. The first sternal setae are long and project beyond the hind margin of the sternal shield. The second and third sternal setae are short spurs with jagged tips so as to have the appearance of broken setae. The metasternal setae are apparently not inserted on metasternal shields, their length being approximately the same as that of the first sternal setae.

The genito-ventral shield is flask-shaped, broadest at the second pair of setae. The shield is ornamented with transverse striations. The third pair of setae is nearer to the second pair than to the fourth pair. The setae of the fourth pair are very near to each other. About 10 pairs of ventral setae are inserted on small projections of the integument. The metapodal shields are small, irregularly oval. The anal shield is 80 μ long and 90 μ wide. The paranal setae are long (77 μ), about two-thirds of the length of the postanal seta (118 μ). The peritreme reaches to the middle of coxa II, no peritrematal shield is discernible.

The first three legs are rather stumpy, the fourth pair is more slender and elongated. The respective lengths of the legs (excluding pulvilli) are as follows: I—360 μ; II—360 μ; III—375 μ; IV—555 μ. Coxa I bears two sharp spines, the proximal spine is much longer than the distal spine; coxa II bears a long spine, coxa III a short spine and coxa IV bears a hair-like seta. There are 6 rows of deutosternal teeth, 2 denticles in the first row and one denticle in each of the other rows. All rostral setae are short, the corniculi tapering off rather sharply.

MALE (Text-fig. 70). The dorsal shield is 525 μ long and 390 μ wide. The dorsal shield covers the dorsum more completely than in the female. The anal shield is separate from the sternito-ventral shield which bears 10 pairs of setae. The setae of the second and third pair are stouter than the other setae on the shield. The hind margin of the shield is concave. The anal shield is 83 μ long and 77 μ wide, the anal setae as in the female. Tarsus IV bears simple setae only, it is 122 μ long (excluding pulvillus). Chelicerae with long spermatophoral processes.



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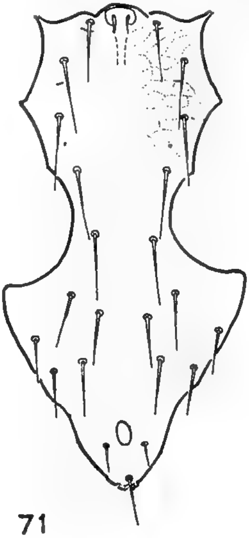

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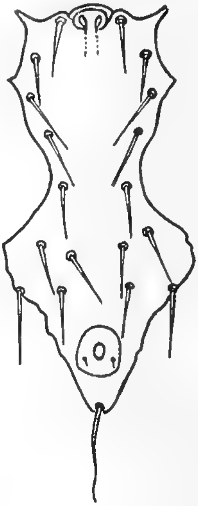

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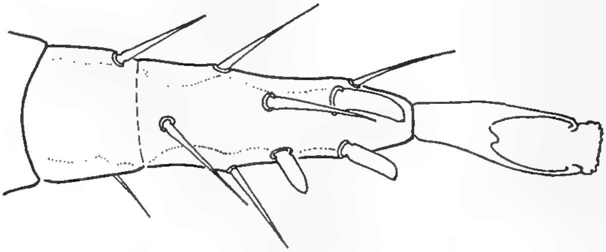

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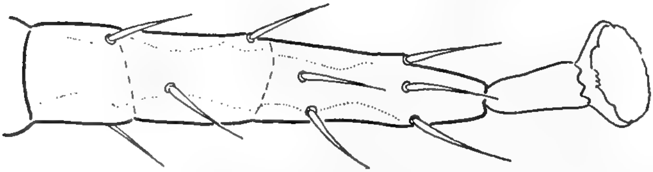

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Figs. 70–74. Fig. 70, *Laelaps pachypus* C. L. Koch, venter of male. Fig. 71, *Laelaps acomysi* sp. nov., venter of male. Fig. 72, *Laelaps ekstremi* Zachv., venter of male. Fig. 73, *Laelaps ekstremi* Zachv., tarsus IV of male. Fig. 74, *Laelaps acomydis* sp. nov., tarsus IV of male.

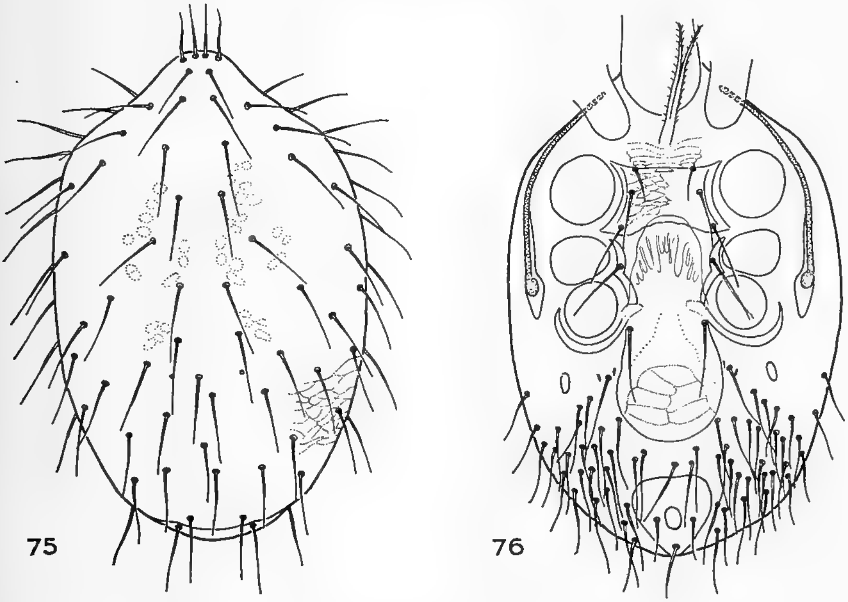
Hosts and localities. This mite has been recovered in Israel only from *Microtus guentheri*, at the following localities and dates : 7 ♀—Mishmar Ha'emeq, 2.i.1953 ; 4 ♀—ditto ; 1 ♂, 1 ♀—ditto, 10.i.1953 ; 1 ♀—Neoth Mordekhai, 20.v.1955.

Notes. The name *Laelaps pachypus* C. L. Koch has been adopted here for reasons summarized by Strandtmann & Wharton (1958). It seems to the writer that *L.* (*H.*) *arvalis* and *L.* (*H.*) *amphibius* are at the opposite ends of a series of intergrading forms of the same species. It may well be probable that the forms occurring on *Arvicola terrestris*, one of the larger microtines, are rather bigger than the forms occurring on the smaller microtines. Even if these differences were constant, both would merely be subspecies of *Laelaps pachypus* C. L. Koch. It is therefore considered that *L.* (*H.*) *arvalis* Zachv., 1948 should be placed in synonymy with *L. pachypus* C. L. Koch, 1839.

Androlaelaps marshalli Berlese

Androlaelaps marshalli Berlese, 1911.
Androlaelaps africanus Zumpt, 1950.
Androlaelaps africanoides Zumpt & Patterson, 1950.

Female (Text-figs. 75, 76). The dorsal shield covers practically the whole of the dorsal surface, it is 1,095–1,155 μ long and 675–735 μ wide. The dorsal setae are very long (e.g. *i*5 is approximately 175 μ long). The arrangement of the posterior dorsal setae is irregular owing to the appearance of neosetae. Setae *r*1 are of about



Figs. 75–76. *Androlaelaps marshalli*, Berlese, female. Fig. 75, dorsum. Fig. 76, venter.

the same length as setae *i*1 (approximately 125 μ), but whereas setae *i*1 are stout and straight, setae *r*1 are wavy. The dorsal shield is ornamented and striated throughout.

The tritosternum is well developed, with long feathered laciniae. The presternal area is ornamented and the anterior margin of the sternal shield is not very well defined. The sternal shield is 130 μ long (at mid-line) and 203–210 μ long (at the level of the second pair of setae), it is heavily ornamented. The anterior margin of the shield is slightly concave, the posterior margin is concave and emarginate. The first pair of sternal setae is considerably shorter than the other sternal setae, they do not reach the posterior margin of the sternal shield. The anterior pores have a slight inward slant, the posterior pores have a slight outward slant. The metasternal setae are inserted on well-developed endopodal shields.

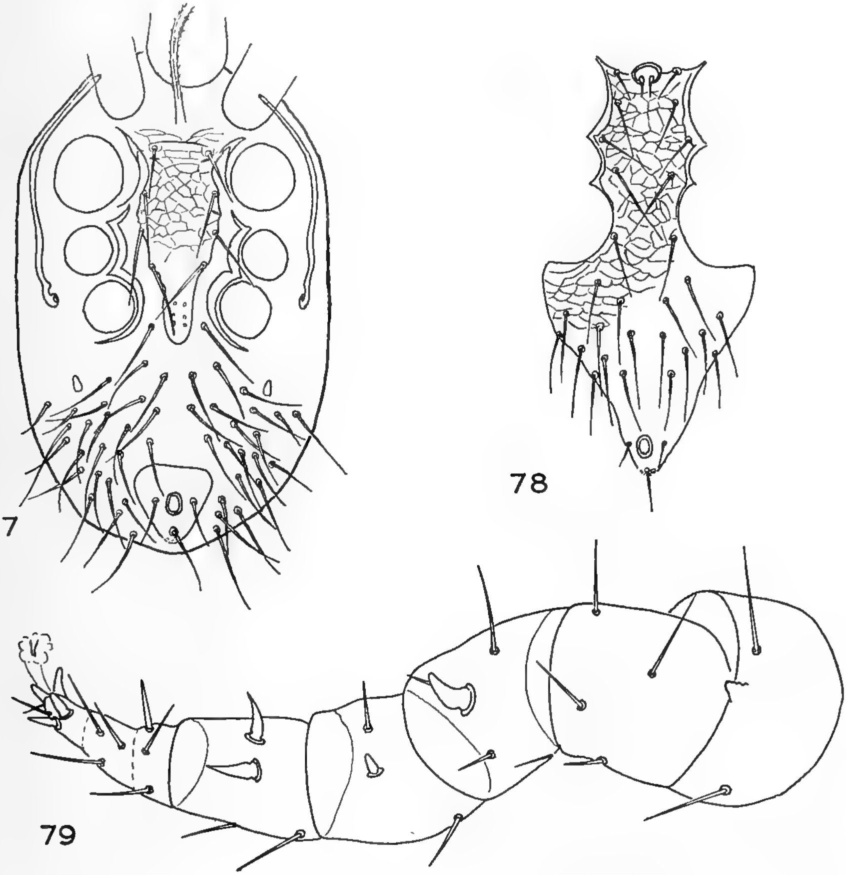
The genital shield bears one pair of setae, it is moderately expanded behind coxa IV with a semicircular convex hind margin. The shield is flanked by a pair of setae, each of which is accompanied by two small elongated platelets. The posterior part of the shield is ornamented with very distinct striations. The metapodal shields are oval and elongated. The anal shield is almost triangular, it is 175–185 μ long and 175–188 μ wide, its anterior margin is slightly concave. The paranal setae are slightly shorter than the postanal seta, they are inserted in a line with the middle of the anus. The anus is more distant from the anterior margin of the anal shield than from the postanal seta. Numerous long and simple setae (approximately 25–28 pairs) are inserted on the ventral membrane. The peritreme reaches beyond the middle of coxa I, a peritrematal shield is present.

The second pair of legs is much stouter than the other pairs. Spurs are present on the ventral side of the femur, genu, tibia and tarsus. Coxa I with its anterior margin serrated. Leg IV is very slender and long, it is approximately 1,275 μ long (excluding pulvillus). The chelicerae are chelate-dentate, with a non-inflated pilus dentilis on the fixed finger. At the base of the movable digit a well-developed brush of many setae is present. The corniculi are well sclerotized, elongated and lanceolate. The internal posterior rostral setae are the longest of the gnathosomal setae (approximately 145 μ long), much longer than the corniculi. There are 6 rows of deutosternal teeth, 5 teeth in each row.

MALE (Text-fig. 78). The dorsal shield is 945–990 μ long and 585–625 μ wide. The chaetotaxy is essentially the same as in the female. The holoventral shield is very expanded immediately behind coxae IV and it is markedly ornamented throughout. The shield bears 31 setae (including anal setae), the setae of the first pair are rather short. The paranal setae are inserted in line with the middle of the anus they are slightly longer than the postanal seta. Legs and spurs on legs essentially as in the female, length of leg IV—1,095 μ. The chelicerae have well-developed spermatophoral processes. There are 6 rows of deutosternal teeth, 2–5 teeth in each row.

DEUTONYMPH (Text-figs. 77, 79). The dorsal shield is 840–945 μ long and 570–615 μ wide. The lateral incisions of the dorsal shield are very prominent. The dorsal chaetotaxy is the same as in the female. The sternal shield bears 4 pairs of setae, the first pair is markedly shorter than the other pairs. The shield is heavily ornamented, it is broadest at the level of the second setae and narrows after the fourth pair. The narrow part of the shield is without ornamented striations but it is marked by 3 pairs of distinctly lighter spots. The shield does not project beyond coxa IV. The anal shield and leg II are similar to those of the female.

HOSTS AND LOCALITIES. 3 dn, 2 ♂, 11 ♀—*Gerbillus allenbyi*, Caesarea, 23.vii.1954; 1 dn, 6 ♀—ditto; 1 ♂, 5 ♀—ditto; 8 ♀—ditto; 1 ♀—*Jaculus jaculus*, Palmahim, 2.ix.1954; 1 dn, 1 ♀—*Gerbillus pyramidum*, Palmahim, 4.ii.1955; 14 ♀—ditto; 3 ♂, 1 ♀—*G. allenbyi*, Ma'agan Mikhael, 26.ix.1955; 1 dn, 9 ♀—*Meriones sacramenti*, Rishon le Zion (Dunes).

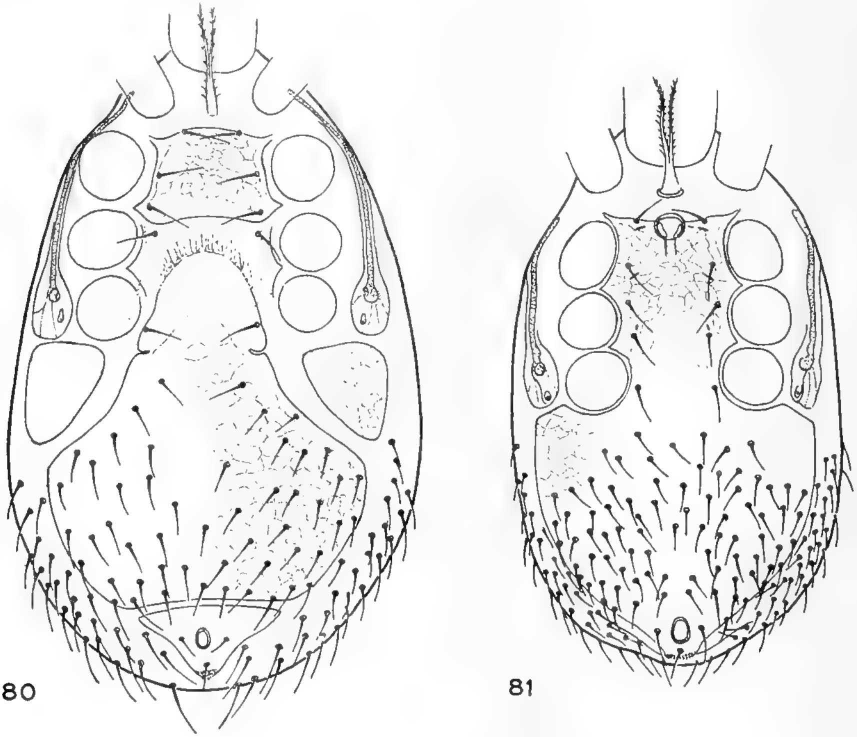


FIGS. 77–79. *Androlaelaps marshalli* Berlese. Fig. 77, venter of deutonymph. Fig. 78, venter of male. Fig. 79, ventral view of leg II of the deutonymph.

NOTES. This species was determined after comparing it with camera lucida drawings of the type specimen, kindly provided by Dr. G. O. Evans. Regarding the synonymy of this species I have arrived at the same conclusions as Keegan (1956).

Eulaelaps stabularis (Koch)

Gamasus stabularis C. L. Koch, 1836.
Hypoaspis stabularis, G. &. R. Canestrini, 1882.
Laelaps oribatoides Michael, 1892.
Laelaps stabularis Berlese, 1903.
Eulaelaps stabularis, Hirst, 1914.
Eulaelaps arcualis Trägårdh, 1912.
Eulaelaps oudemansi Turk, 1944.



FIGS. 80–81. *Eulaelaps stabularis* (Koch). Fig. 80, venter of female. Fig. 81, venter of male.

FEMALE (Text-fig. 80). Robust, heavily sclerotized and very setous mites. The dorsal shield is oval, broadest posterior to coxa IV. The shield is 1,005–1,050 μ long and 660–690 μ wide, it is covered with numerous setae, most densely on its lateral and posterior parts.

The tritosternum is well discernible and has pilose laciniae. The sternal shield is 145 μ long (at mid-line) and 175–185 μ wide (at the level of the second setae), it is well sclerotized and ornamented. The sternal setae are short, the first pair barely reaching beyond the middle of the sternal shield.

The genito-ventral shield is very expanded, sclerotized and ornamented, it bears 50–60 setae. The metapodal shields are very large, triangular in shape, well sclerotized and ornamented. The anal shield is much wider than long, approximately 110 μ long and 230 μ wide. The peritreme reaches slightly beyond the posterior margin of coxa I, a well-developed peritrematal shield is present.

The chelicerae are chelate-dentate, a small non-inflated pilus is present on the fixed finger. A row of very small setae is present on the base of the movable finger. The corniculi are horn-shaped. There are 10 rows of deutosternal teeth, 6–8 teeth in each row.

The legs are relatively short, legs of pair II being stouter than the others.

MALE (Text-fig. 81). The dorsal shield is 750 μ long and 450 μ wide. The chaetotaxy of the dorsal shield is essentially the same as in the female. The holoventral shield covers practically the whole venter, it is well sclerotized and ornamented. The shield bears approximately 90–100 setae. The peritreme reaches only to the level of the anterior margin of coxa II.

HOSTS AND LOCALITIES. 2 ♀—*Meriones tristrami*, Beit Hakerem, 30.xii.1952; 1 ♀—*M. tristrami*, Mishmar Ha'emeq, 13.ii.1953; 8 ♀—*M. tristrami*, Tel Amal, 15.ii.1953; 4 ♀—ditto; 2 ♂, 364 ♀—ditto; 3 ♀—*M. tristrami*, Mishmar Ha'emeq, 22.ii.1953; 1 ♀—*Mus musculus*, ditto; 1 ♀—*Apodemus mystacinus*, Tivon, 9.iii.1953; 1 ♀—*M. musculus*, Aqua Bella, 3.ii.1954; 4 ♀—*Apodemus sylvaticus*, Dan, 1.iv.1954; 1 ♀—*Microtus guentheri*, Neoth Mordekhai, 20.v.1955.

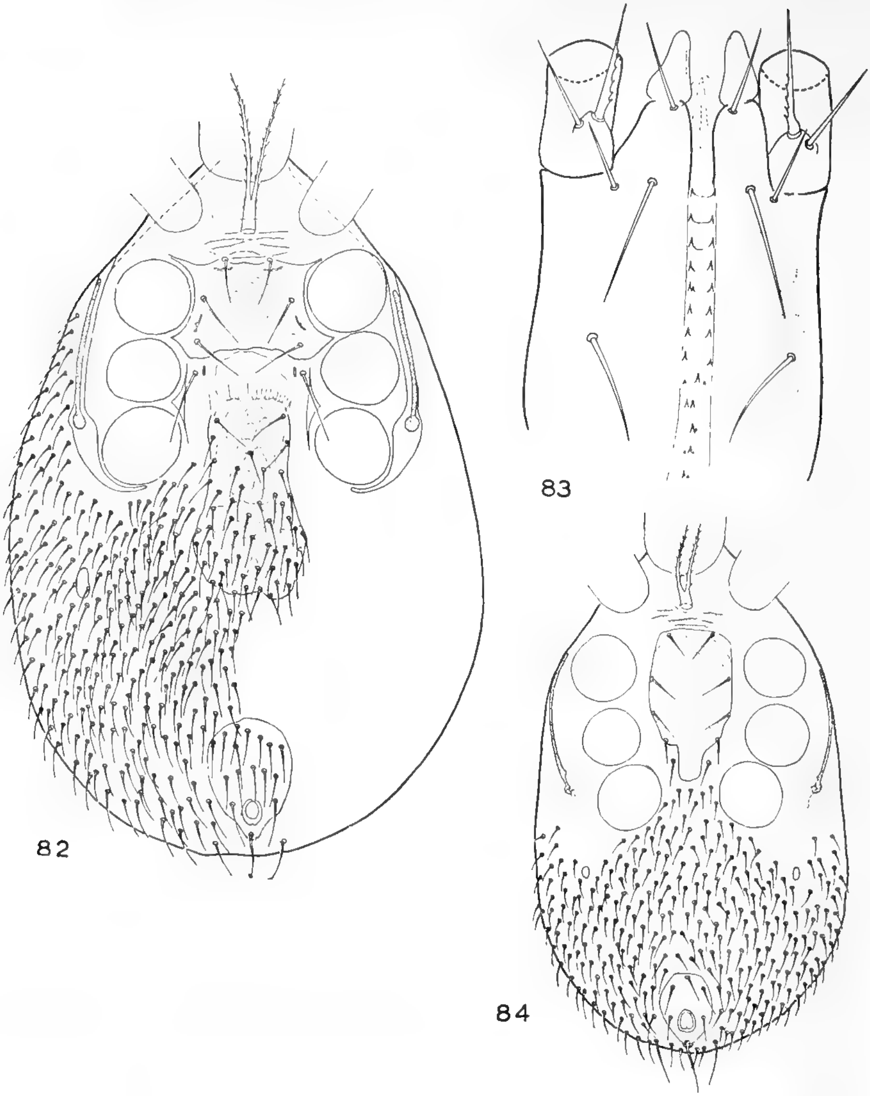
NOTES. This species is a well known and widespread cosmopolitan species with many hosts (Strandtmann & Wharton, 1958). It apparently does not occur in the southern parts of Israel. It is worth while to mention the extremely high infestation of one specimen of *M. tristrami* with 2 ♂ and 364 ♀, which is an unsurpassed record in this collection. The same rodent was also infested with numerous specimens of *Haemolaelaps ovalis* sp. nov.

Haemogamasus horridus Michael

Haemogamasus horridus Michael, 1892.
Euhaemogamasus horridus, Keegan, 1951.
Haemogamasus horridus var. *arvicolarum* Berlese, 1920.
Haemogamsus arvicularum Turk, 1945.

FEMALE (Text-figs. 82, 83). The dorsal shield is 1,260–1,290 μ long and 810–870 μ wide, it is densely covered with setae. Setae *i*1 are stouter than the other setae on the shield, they are approximately 85 μ long. The dorsal setae range from 40–90 μ in length. The shorter setae are inserted on the anterior part of the shield and they lengthen gradually towards the posterior part. There are no distinctly larger pairs of setae on the posterior margin of the shield. The distance between the dorsal setae is 16–40 μ and all the setae on the shield are smooth.

The tritosternum has long feathered laciniae, and on each side of its base a small tooth projects, at a distance of about two-thirds from its proximal end. The presternal area is sculptured, the striations having tiny, posteriorly directed spines. The sternal shield is 163–176 μ long (at mid-line) and 208 μ wide (at the level of the second pair of setae). The anterior margin is nearly straight, while the posterior margin is concave and slightly emarginate. The anterior pores are crescent-shaped, elongated and almost parallel to the anterior margin of the shield. The posterior pores lie



Figs. 82–84. *Haemogamasus horridus* Michael. Fig. 82, venter of female. Fig. 83, ventral view of the gnathosome of the female. Fig. 84, venter of deutonymph.

almost at right angles to the anterior pores, being parallel to the lateral margins of the shield. The shield is ornamented with striations, it bears three pairs of smooth setae. The setae of the first pair are rather short and barely project beyond the middle of the shield. No accessory setae are carried on the sternal shield. The metasternal setae are slightly shorter than the third sternal setae and each metasternal seta is flanked on its medial side by a small carrying a pore. Well developed endopodal shields lie on the uter sides of the metasternal setae.

The flask-shaped genito-ventral shield has an irregular posterior margin, and is ornamented throughout with striations. It bears 52 (in a second ♀, 53) setae. The pair of anterior setae are not longer than the other setae on the shield. The anal shield which bears 16 setae is pear-shaped, it is approximately 225 μ long and 160 μ wide. The anus is located at some distance from the anterior margin of the shield. Numerous setae are inserted on the interscutal membranes. The tubular part of the peritreme reaches to the middle of coxa II, it is surrounded by a peritrematal shield which reaches anteriorly to the gnathosoma, while posteriorly it is attached to the parapodal shields. The distal rims of the leg segments are serrated, the respective lengths of the legs (excluding pulvilli) being as follows: I—1,170 μ; II—900 μ; III—1,020 μ; IV—1,380 μ.

The chelicerae are chelate-dentate. The fixed digit has a hooked tooth on its distal end and slightly posterior to this are two additional, even more projecting teeth. The movable finger, which has a rather broad base, has three teeth at its inner distal end. On the ventral side of the palpal coxa there are two setae, the inner one being barbed on its medial side (Text-fig. 83). These are the only barbed setae on this species The gnathosomal setae are smooth and the corniculi are rounded and membraneous. There are 13 rows of deutosternal teeth, the anterior rows having 2 rather large teeth in each row. The relative lengths and the arrangement of deutosternal teeth is shown in Text-fig. 84. The tectum forms an obtuse angle at its anterior margin and is bordered by membraneous fimbriae.

DEUTONYMPH (Text-fig. 84). The dorsal shield is 795 μ long and 510 μ wide. The chaetotaxy of the dorsal shield, the tritosternum and the presternal area are the same as in the female. The sternal shield bears 4 pairs of setae and narrows abruptly behind the fourth pair of setae into a finger-like projection. The shield is ornamented and terminates anteriorly to the mid-line of coxa IV. The peritreme apparently reaches to the middle of coxa II and is not accompanied by any shield. The anal shield bears 6 setae.

HOSTS AND LOCALITIES. The only material of this species in the collection (4 dn, 2 ♀) was taken off *Apodemus mystacinus* (not from nest), at Tivon, 24.ii.1956.

NOTES. The status of *Haemogamasus arvicularum* Turk is discussed in detail by Keegan (1951), and this author considered that it should be placed in synonymy with *H. horridus* Michael. The Tivon material has been compared with the type specimen of *H. horridus* Michael and was found to differ mainly in relation to the shape of the sternal shield, which in the Tivon material is wider than long. However the specimens from Tivon agree rather closely with Turk's description of *H. arvicularum*. Among the differences between *H. horridus* and *H. arvicularum* is the presence of a larger number of setae on the genito-ventral shield of the latter and it is interesting to note that in the Tivon specimens, which are apparently on the southern limit of the distribution of this species, the number of setae on the genito-ventral shield and on the anal shield is even greater than that noted for *H. arvicularum*. It might be possible in the future to separate *H. horridus* from different areas into subspecies.

For the time being the conclusions reached by Keegan (1951) have been accepted here.

Hirstionyssus arcuatus (C. L. Koch)

Dermanyssus arcuatus C. L. Koch, 1839.
Liponyssus arcuatus, Oudemans, 1913.
Hirstionyssus arcuatus, Fonseca, 1948.
Dermanyssus albatus Koch, 1839.
Hirstionyssus talpae Zemska, 1954.

FEMALE (Text-figs. 85, 86). The dorsal shield is 540–570 μ long and 300–330 μ wide, it is broadest behind the fourth pair of legs. The shield bears 26 pairs of small setae. The marginal setae as well as the setae on the anterior part of the shield, are longer than those on the central part. The shield is faintly ornamented.

The tritosternum is membraneous and translucent and very hard to discern from underlying structures, its base is rather broad and trapezoid in outline. The presternal area is sculptured with transverse lines. The anterior margin of the sternal shield is slightly convex, while the posterior margin is deeply concave, the concavity ascending up to the line of insertion of the second pair of setae. The sternal shield is 29–35 μ long (at mid-line) and 109–135 μ wide (at the level of the second pair of setae). The sternal pores are very small and indistinct. The sternal setae are much longer than the dorsal setae while the metasternal setae are slightly shorter than the sternal setae.

The genital shield is tongue-shaped, it is broadest slightly behind the point of insertion of the genital setae. The anal shield is much longer than wide, it is 115 μ long and 70 μ wide. The paranal setae, which are only slightly shorter than the postanal seta, are inserted slightly anterior to the middle line of the anus. About 12 pairs of setae lie on the ventral membrane. The peritreme extends to the middle of coxa I.

The legs are rather slender, their respective lengths (excluding pulvilli) being: I—375 μ; II—315 μ; III—300 μ; IV—390 μ. Coxa I bears two ventral setae, the proximal seta being longer and stouter; coxa II bears the usual anterior-dorsal spine and one postero-ventral spine; coxa III bears two postero-ventral spines while coxa IV bears a small postero-ventral spine. The chelicerae are narrow and edentate. The deutosternal teeth are arranged in irregular rows of single teeth, alternating on both sides of the median line.

MALE (Text-figs. 87, 88, 89). The dorsal shield is 485 μ long and 300 μ wide, with parallel sides but slightly ovoid in shape. The shield bears 28 pairs of setae. The marginal setae on the posterior part of the shield are inserted at some distance from the edge of the shield. The holoventral shield, which bears 19 setae (anal setae included), is granulated. The 18–20 pairs of setae which lie on the ventral membrane

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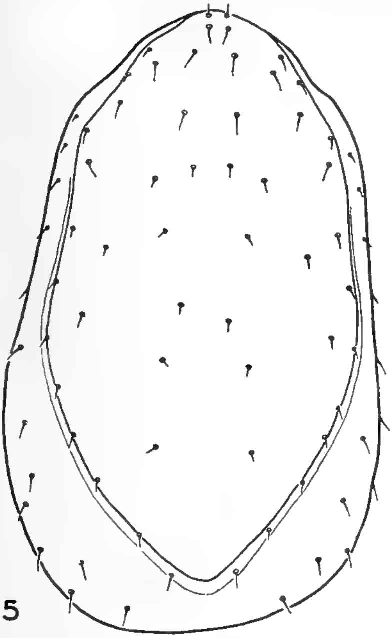
FIGS. 85–89. *Hirstionyssus arcuatus* (C. L. Koch.) Fig. 85, dorsum of female. Fig. 86, venter of female. Fig. 87, dorsum of male. Fig. 88, venter of male. Fig. 89, coxae II–IV of male.



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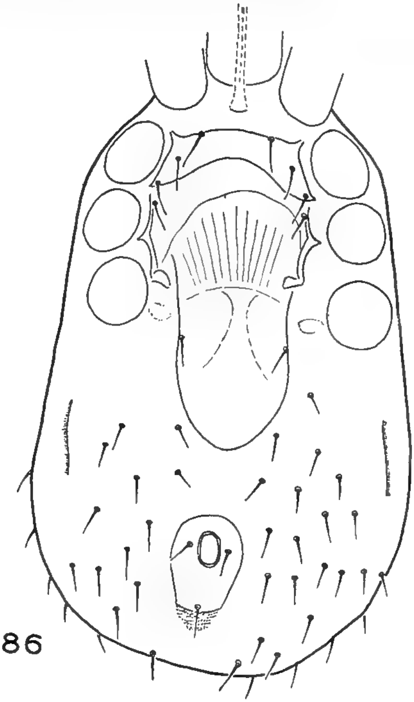

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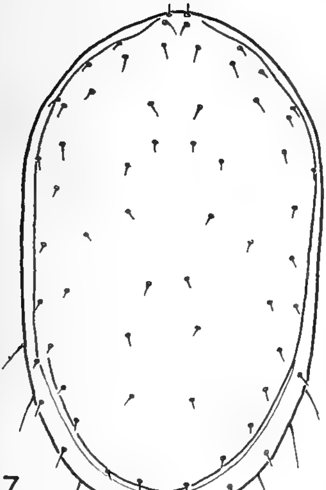

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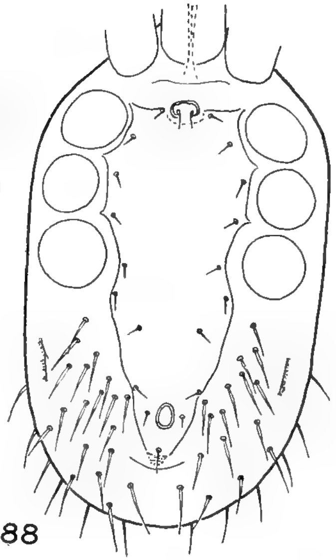

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are distinctly longer than the setae on the holoventral shield. The paranal setae are inserted anterior to the middle line of the anus. The peritreme reaches to the middle of coxa I. The lengths of the legs (excluding pulvilli) are as follows: I—330 μ; II—285 μ; III—300 μ; IV—360 μ. The chelicerae carry spermatophoral processes of medium length. The arrangement of the deutosternal teeth and the coxal spines, as in the female.

HOSTS AND LOCALITIES. Numerous specimens off *Rattus rattus*, Mishmar Ha'emeq, 22.xi.1952; 3 ♀—*Gerbillus* (*Dipodillus*) *dasyurus*, Wadi Nafkh, 11.iv.1955; 1 ♀—ditto; 1 ♂, 8 ♀—*Microtus guentheri*, Mishmar Ha'emeq, 13.v.1955; 1 ♀—*M. guentheri*, Neoth Mordekhai, 20.v.1955.

NOTES. The four females taken off *G. dasyurus* have a much smaller spine on coxa II than the specimens from the other hosts. However, as this was the only difference detected, these are considered to be *arcuatus*.

Hirstionyssus craticulatus Keegan

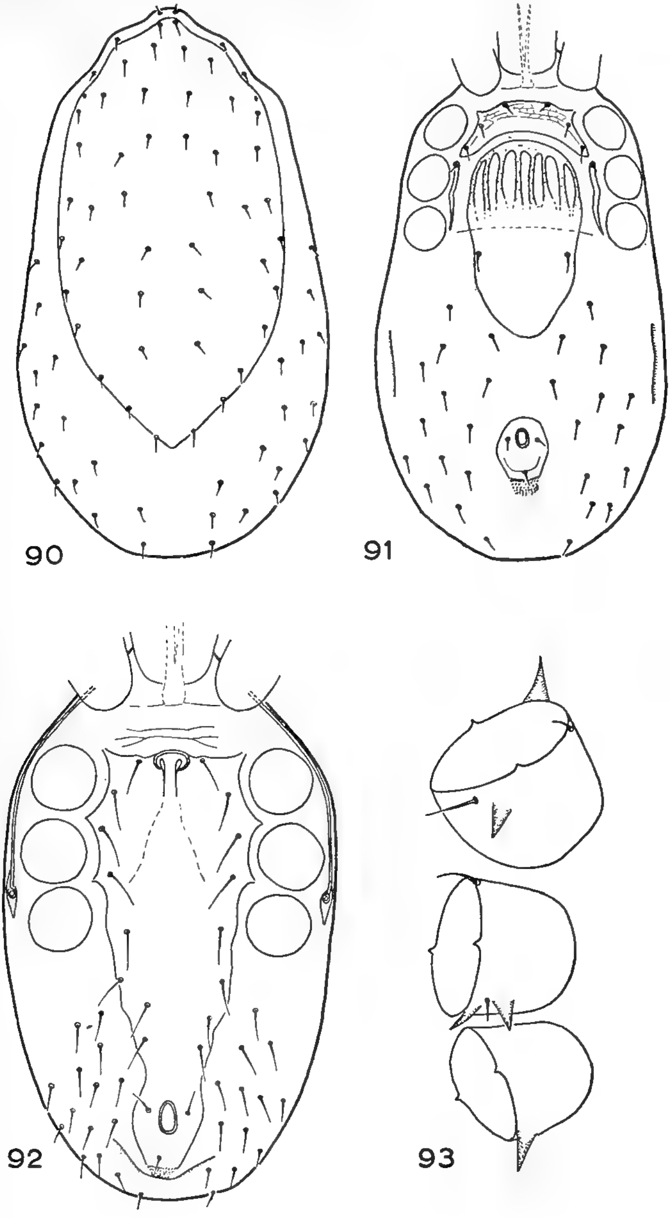
Hirstionyssus craticulatus Keegan, 1956.

FEMALE (Text-figs. 90, 91). The dorsal shield is ovoid, it is 420–465 μ long and 225–240 μ wide. The shoulders are well pronounced and the shield is attenuated posteriorly. The shield bears 25 pairs of setae. The setae which are inserted on the anterior part of the shield are slightly longer and stouter than those inserted on the posterior part. The surface of the shield is ornamented with fine striations which form irregular polygons.

The tritosternum is membraneous and translucent, and difficult to discern from underlying structures, it is apparently only very slightly pilose. The presternal area is slightly sculptured. The anterior margin of the sternal shield is well defined and strongly convex, while the posterior margin is markedly concave although the concavity does not reach the line connecting the second sternal setae. The anterior part of the shield is highly sculptured and more heavily sclerotized than the posterior part. The sternal shield is 32 μ long (at mid-line) and 102 μ wide (at the level of the second setae). The sternal and the metasternal setae are about the same length (approximately 30 μ). The endopodal shields are narrow but well developed and distinct.

The genital shield is the most diagnostic feature of this mite. The anterior part of the shield is shaped like a dome supported by 8 pillars, the posterior part being narrower and bearing the genital setae. About 14 pairs of setae lie on the ventral membrane. The anal shield is pear-shaped and has a rounded anterior margin, it is 86–92 μ long and 60 μ wide. The paranal setae, which are in line with the mid-point of the anus, are slightly shorter than the postanal seta. The peritreme reaches to the middle of coxa I.

The legs are rather slender, their respective lengths (excluding pulvilli) being as follows: I—300 μ; II—240 μ; III—240 μ; IV—315 μ. Coxa I bears a large spur antero-dorsally and a blunter spur postero-ventrally. Two postero-ventral spurs are located on coxa III, while coxa IV carries a small spur postero-ventrally on the coxal rim. The chelicerae are edentate and narrow, the distal end of the fixed digit being



FIGS. 90–93. *Hirstionyssus craticulatus* Keegan. Fig. 90, dorsum of female. Fig. 91, venter of female. Fig. 92, venter of male. Fig. 93, coxae II–IV of male.

hook-shaped. The deutosternal teeth (about 14), are arranged in irregular rows of single teeth on both sides of the median line.

MALE (Text-figs. 92, 93). The dorsal shield is 360–375 μ long and 210–230 μ wide. The shield is ovoid with a rounded posterior margin and it bears 34 pairs of setae (the number of dorsal setae may be variable as some setae lie on the membrane immediately adjacent to the shield). The surface of the shield is ornamented as in the female. The presternal area is highly ornamented and the holoventral shield bears 19 setae (including anal setae). This shield is slightly constricted in front of the anus. About 14 pairs of setae are located on the ventral membrane. The arrangement of the coxal spurs is similar to that of the female. The male of this species has hitherto not been described.

HOSTS AND LOCALITIES. All the specimens were taken from *Gerbillus pyramidum* at Holon, 12.vii.1954. The counts of mites found on four individuals were: 4 ♂, 12 ♀; 2 ♂, 6 ♀; 1 ♂, 7 ♀; 6 ♀.

NOTES. Although Keegan (1956) recorded this species from *Gerbillus gerbillus* and *Jaculus jaculus* it was not found on these rodents in the area of the present study.

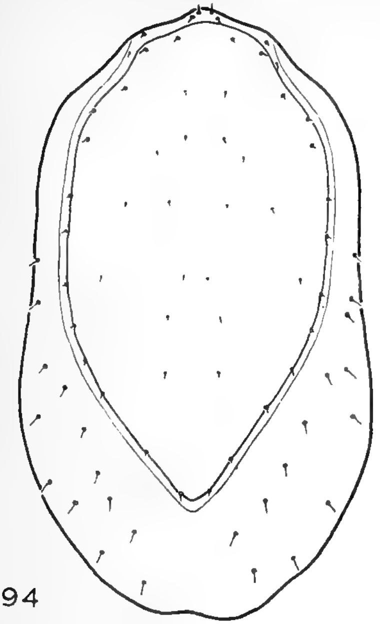
Hirstionyssus ellobii spalacis ssp. nov.

FEMALE (Text-figs. 94, 95, 96). The dorsal shield is 600–630 μ long and 300–345 μ wide, it has well-pronounced shoulders and is attenuated posteriorly. The shield bears 26 pairs of setae of which only the anterior and marginal ones are prominent although very short, the other setae require high magnification for their definition.

The tritosternum has a broad base and long laciniae, the latter being feathered distally with very short hairs. The presternal area is not ornamented. The sternal shield is 86–94 μ long (at mid-line) and 160–170 μ wide. The shield has an almost straight anterior margin, the posterior margin being convex. The setae of the first pair do not reach the posterior margin of the shield. The sternal and metasternal setae are of approximately the same length. The anterior membraneous part of the genital shield overlaps the sternal shield. The anal shield is 110 μ long and 64 μ wide, it is elongated with a rounded anterior margin. The paranal setae are inserted near the anterior margin of the anus, and their length is about the same as that of the postanal seta. About 19 pairs of setae lie on the ventral membrane. The peritreme reaches to the middle of coxa I.

The respective lengths of the legs (excluding pulvilli) are as follows: I—465 μ; II—420 μ; III—420 μ; IV—540 μ. Coxa II bears the usual antero-dorsal spine, this is rather long and sharp, on the ventral side there is only a small wart-like projection but no spur. Coxa III carries two large spurs on the postero-ventral surface, the proximal spur being much bigger than the distal. The hind rim of coxa IV is serrated. Seventeen to nineteen deutosternal teeth are irregularly arranged in alternating rows of single teeth on both sides of the median line. The chelicerae are

FIGS. 94–98. *Hirstionyssus ellobii spalacis* ssp. nov. Fig. 94, dorsum of female. Fig. 95, venter of female. Fig. 96, venter of male. Fig. 97, coxae II–IV of male. Fig. 98, coxae I–IV of female.



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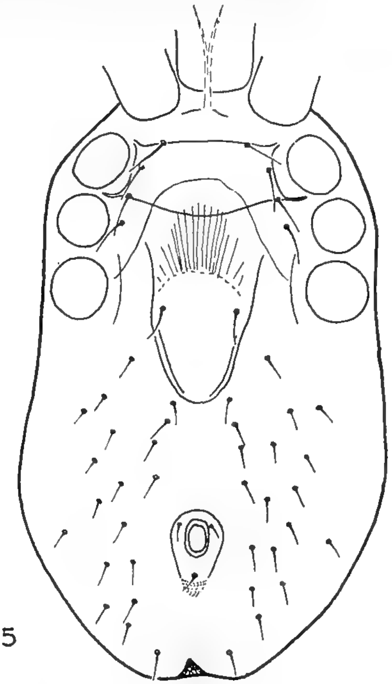

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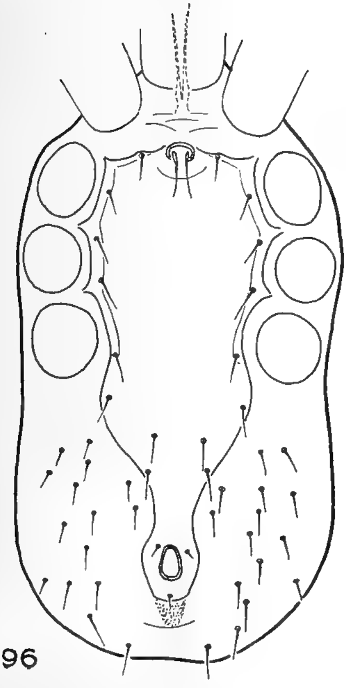

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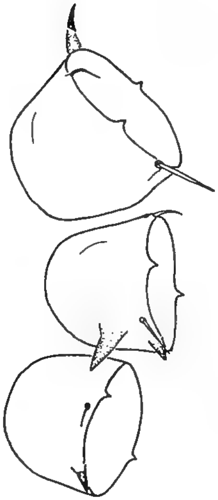

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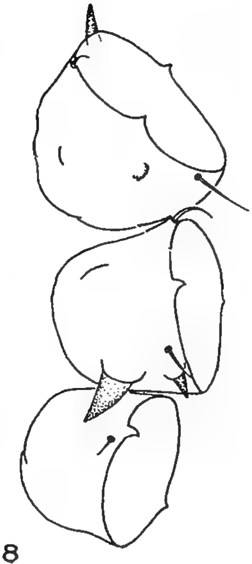

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long and edentate. The rostral setae are short, the anterior rostral seta being the longest of all gnathosomal setae.

MALE (Text-figs. 96, 97). The dorsal shield is 480–495 μ long and 255–270 μ wide. It has well-pronounced shoulders and parallel sides, the posterior part of the shield ends in an obtuse angle. The chaetotaxy of the shield is essentially the same as in the female. The surface of the shield is granulated and the anterior setae are longer and stouter than the marginal setae on the posterior half. The holoventral shield bears 19 setae (including anal setae). This shield which has a granulated surface is violin-shaped. There is a slight constriction at the level of coxae IV and a second, much more marked constriction just in front of the anus. The arrangement of spurs on coxae II and III is similar to that in the female, but the serrated rim of coxa IV bears an additional spur postero-ventrally.

HOSTS AND LOCALITIES. 4 ♂, 10 ♀—*Spalax ehrenbergi*, Zikhron Ya'aqov, 8.v.1954; 31 ♀—*S. ehrenbergi* (no locality), 22.iv.1954; 1 ♀—*Mus musculus*, Tivon, 22.ii.1956.

NOTES. The Israel specimens have been compared with specimens recovered from *Ellobius talpinus* in U.S.S.R., determined by Dr. N. Bregetova, and were found to differ as follows: The proximal spur of coxa II in the Israel material measures about 45 μ in length, whereas the length of the spur in specimens from *E. talpinus* is only 20 μ in length. The shape of the shield is more elongated and less ovoid in the material from Israel, and the posterior margins of the shield form a much more acute angle. It is therefore considered that the Israel material belongs to a new subspecies. The subspecific name *spalacis* has been chosen as this mite is very common on the mole-rat (*Spalax*).

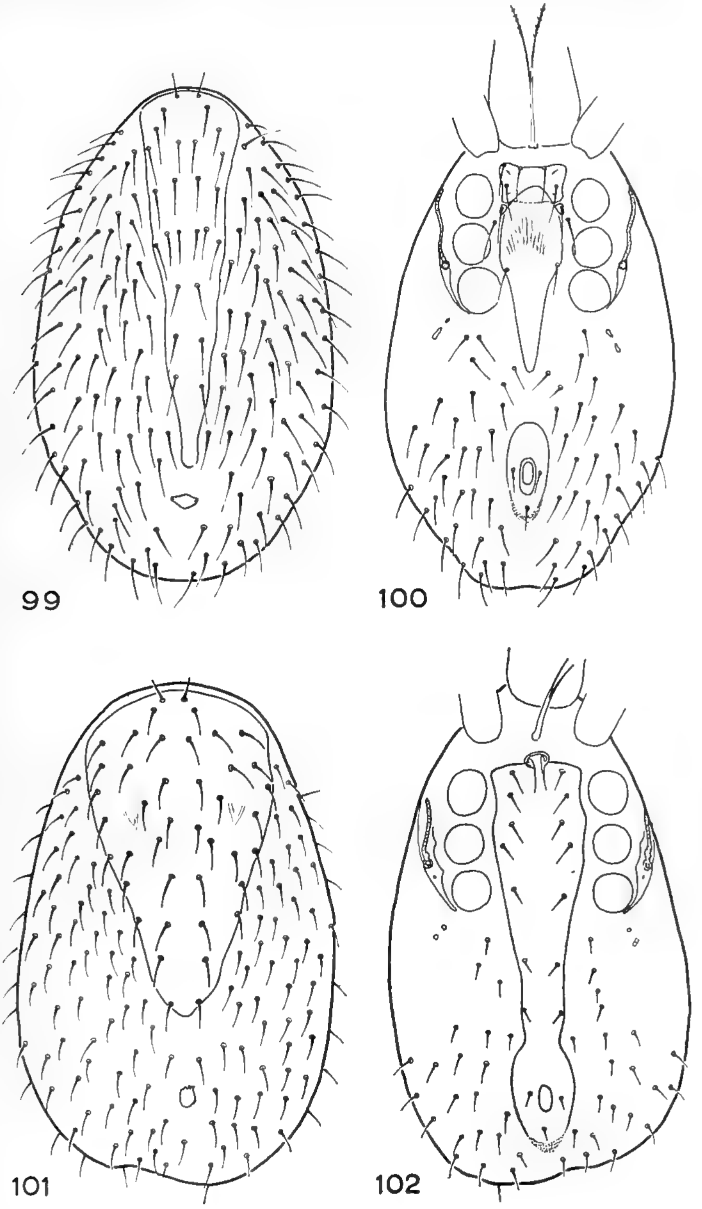
This mite has been recovered in large numbers from sucklings of *Spalax ehrenbergi* taken fron the nests. On these suckling mole-rats *Hirstionyssus ellobii spalacis* can be regularly found clustered in the axial and inguinal cavities, although this circumstantial evidence does not prove that *H. ellobii spalacis* is an active blood-feeder.

Allodermanyssus aegyptius (Hirst)

Dermanyssus (*Liponyssoides*) *aegyptius* Hirst, 1913.
Dermanyssus aegyptius Hirst, 1914.
Allodermanyssus aegyptius, Keegan, 1956.

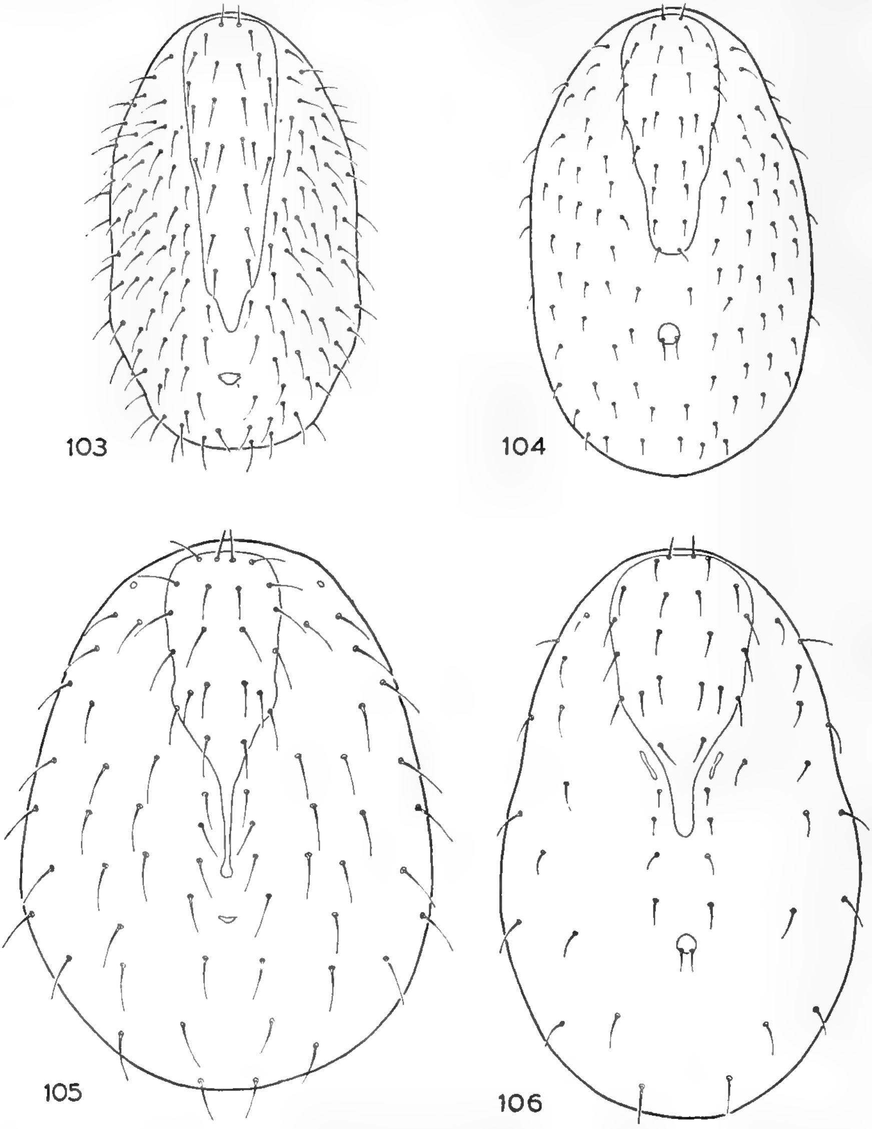
FEMALE (Text-figs. 99, 100). The dorsal surface of the female is covered by two shields, a seta bearing anterior dorsal shield and a small, rudimentary pygidial shield without setae. The anterior dorsal shield (860 μ in length) is elongated and very narrow posteriorly. The shield bears 13 pairs of setae, similar in character to those on the adjacent membrane. The antero-lateral setae of the dorsal membrane are slightly pilose. The pygidial shield which is rather irregular in shape, is 42 μ long and 67 μ wide.

The translucent tritosternum is long and slender, its laciniae are pilose. The sternal shield is divided into the sternal shield proper which bears two pairs of sternal setae, and two small triangular platelets which bear the third sternal setae. The sternal shield proper is about rectangular in shape, 90 μ long (at mid-line) and 145 μ wide (at the level of the second setae). The anterior margin of the sternal shield is slightly concave, and the posterior margin is slightly convex.



99 100 101 102

FIGS. 99–102. *Allodermanyssus aegyptius* (Hirst). Fig. 99, dorsum of female. Fig. 100, venter of remale. Fig. 101, dorsum of male. Fig. 102, venter of male.



FIGS. 103–106. Fig. 103, *Allodermanyssus aegyptius* (Hirst), dorsum of deutonymph. Fig. 104, *Allodermanyssys sanguineus* (Hirst), dorsum of deutonymph. Fig. 105, *A. aegyptius*, dorsum of protonymph. Fig. 106, *A. sanguineus*, dorsum of protonymph.

The genital shield is broad anteriorly and overlaps the sternal shield considerably. Posteriorly the shield is very narrow and projects considerably beyond coxa IV.

The anal shield is very elongated, it is 225 μ long and 150 μ wide, its anterior margin is rounded. The anal setae are all of approximately the smae length (approximately 58 μ). The peritreme reaches to the middle of coxa II.

The legs are very slender and long, their respective lengths (excluding pulvilli) being as follows: I—1,070 μ; II—870 μ; III—880 μ; IV—1,260 μ. Only very few (4–5 ?) deutosternal teeth are present and these are arranged in a single file. The capitular setae are the longest of all gnathosomal setae (approximately 90 μ).

MALE (Text-figs. 101, 102). The anterior dorsal shield (495–540 μ in length) is almost triangular and broadest at the level of the second pair of legs. The shield bears 21 pairs of simple setae. The pygidial shield is irregularly shaped, it is 38 μ long and 38 μ wide. The holoventral shield of the male is very narrow and constricted in front of the anal portion, it bears 17 setae, including the anal setae. The paranal setae are inserted slightly anterior to the mid-line of the anus. Two pairs of small metapodal shields lie posteriorly to coxa II. The legs are very elongated and slender, as in the female. The peritreme is short and does not reach the middle of coxa II.

DEUTONYMPH (Text-fig. 103). The anterior dorsal shield is narrow and elongated, tapering abruptly behind the last pair of setae and ending in a broader knob. The shield bears 13 pairs of simple setae. The pygidial shield is like that of the female. The wedge-shaped sternal shield bears only 3 pairs of setae, but 2 additional pairs flank the sides of the shield posteriorly. The shield projects only slightly beyond the posterior margin of coxa IV. The anal shield is elongated as in the female. The peritreme is short, scarcely projecting beyond the posterior margin of coxa II.

PROTONYMPH (Text-fig. 105). The anterior dorsal shield has a very narrow handle-like projection posteriorly, the end of the handle being slightly broader and knob-like. The shield bears 11 pairs of simple setae (which are considerably longer and stouter than in the protonymph of *L. sanguineus*). The pygidial shield is short as in the female. The sternal shield does not project beyond the posterior margin of coxa IV, it bears 3 pairs of setae. The anal shield is elongated, with the anus situated at the posterior end of the shield. The peritreme is rudimentary.

HOSTS AND LOCALITIES. All specimens were recovered from *Acomys cahirinus*, localities and dates being as follows: 1 pn, 1 dn, 1 ♀—Yotrata, 1.ii.1953; 1 dn—ditto; 1 ♂—Eyn Gedi, 15.iii.1953; 1 dn—ditto; 1 pn—ditto; 3 pn, 1 dn, 1 ♂—ditto; 2 pn, 1 dn—ditto; 11 pn, 2 dn—ditto; 1 pn—ditto; 3 pn, 1 ♂—ditto; 1 dn, 1 ♂, 1 ♀—ditto; 2 pn, 2 dn—Wadi Seyal, 5.iii.1954.

NOTES. See notes of *A. sanguineus*. Keegan (1956) gives *Rattus rattus* and *Rattus norvegicus* as additional hosts of these species in Egypt. These two rodents are not found in the wild state in the southern desert of Israel to which the two *Allodermanyssus* species appear to be confined.

Allodermanyssus sanguineus (Hirst)

Dermanyssus (Liponyssoides) sanguineus Hirst, 1913.
Dermanyssus sanguineus Hirst, 1915.
Allodermanyssus sanguineus, Ewing, 1922.

FEMALE (Text-figs. 107, 108, 109). The dorsum is partially covered by two shields, a main elongated anterior dorsal shield and a small rounded pygidial shield. The anterior dorsal shield is 600–630 μ in length, very narrow and wedgr-shaped. The shield bears 15 (rarely 16) pairs of long setae. Setae *i*1 are shorter than the other setae on the shield and some of the antero-lateral setae are slightly pilose. The pygidial shield is ovoid, 77 μ long and 54 μ wide and bears 2 setae.

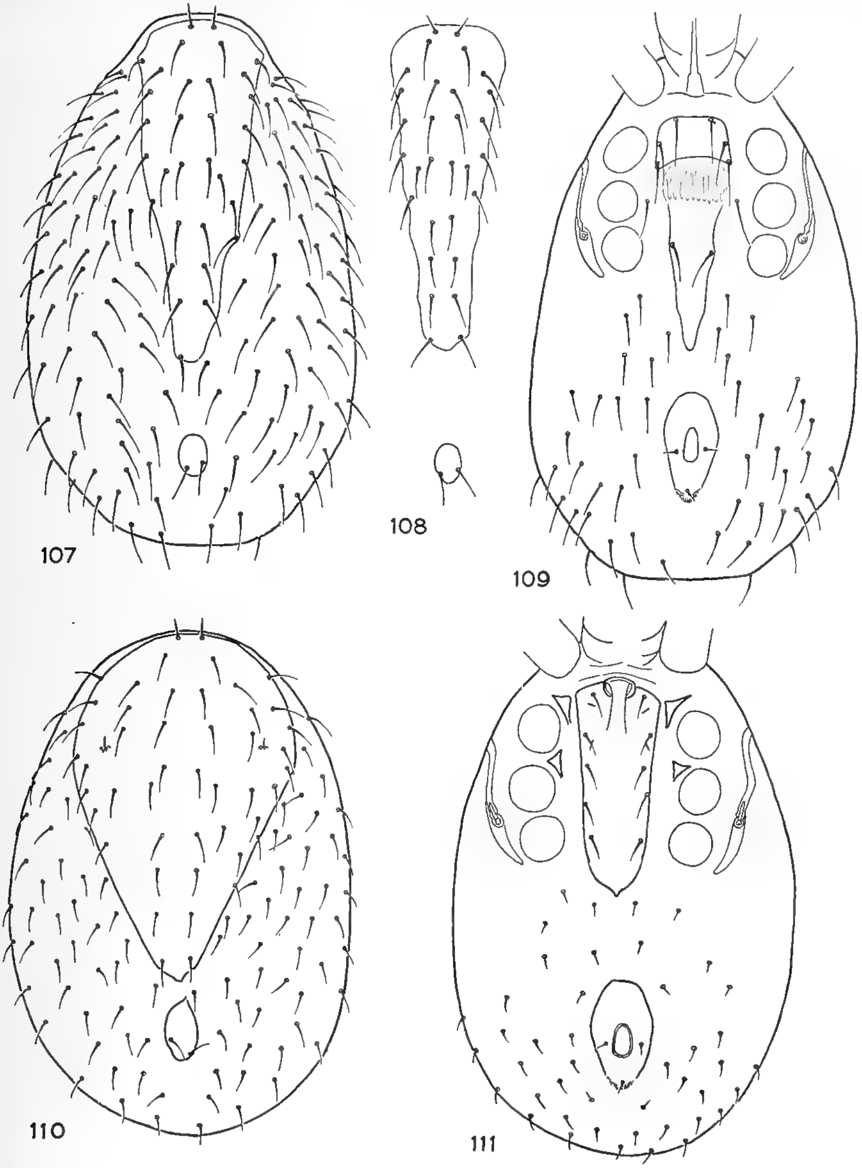
The tritosternum has a broad base and its narrow laciniae are sparsely feathered with short hairs. The sternal shield is 70–85 μ long (at mid-line) and 112–128 μ wide. The anterior margin of the shield is almost straight, with rounded corners,the posterior margin being slightly concave. The pores are very elongated ; the anterior pores are parallel to the anterior margin of the sternal shield while the posterior pores have a pronounced outward slant. The sternal setae are slender and elongated, and the setae of the first pair barely reach beyond the posterior margin of the shield. All the sternal setae and metasternal setae are of about the same length.

The genital shield is wedge-shaped, elongated and projecting backwards well beyond coxa IV. The genital setae are of about the same length as the metasternal setae. The anal shield is elongated and its anterior margin is round. The shield is 210 μ long and 100 μ wide. The paranal setae are generally inserted slightly below the mid-line of the anus, but sometimes at mid-line, these setae are slightly longer than the postanal setae. The peritreme extends to about the middle of coxa II.

The legs are very long and slender, and their respective lengths (excluding pulvilli) are as follows : I—975 μ ; II–795 μ ; III—825 μ ; IV—1,035 μ. Approximately 14 deutosternal teeth are arranged in a single file. The internal posterior rostral setae are the longest of all the gnathosomal setae (approximately 65 μ).

Male (Text-figs. 110, 111). The male of this species has been hitherto unknown (see notes). The dorsal surface is partially covered by 2 dorsal shields as in the female. The anterior dorsal shield which is much broader than in the female is broadest just behind the level of coxa II. Consequently the number of setae on the shield (22 pairs) is higher than in the female. The pygidial shield is elongated and less regularly shaped than in the female, it is 64–77 μ long and 26–42 μ wide in the two specimens examined. The sternito-ventral shield which is separate from the anal shield, is elongated and almost parallel-sided, it projects only slightly beyond the hind margin of coxa IV. The shield bears 5 pairs of setae and these are only slightly longer than the setae on the ventral membrane. Anteriorly the shield is flanked on each side by two small triangular shields. The anal shield is similar to that of the female. The legs are very long and slender, their respective lengths (excluding pulvilli) being as follows : I—700 μ ; II—570 μ ; III—560 μ ; IV—795 μ. The peritreme is very short and apparently reaches only to the middle of coxa III. The accompanying peritrematal shield appears to extend to the middle of coxa II. The chelicerae are elongated and very narrow and the very small deutosternal teeth are arranged in a single file.

Deutonymph (Text-fig. 104). The dorsal surface is partially covered by an anterior dorsal shield and by a pygidial shield. Fifteen pairs of simple setae are inserted on the anterior dorsal shield which is 400–500 μ long. The pygidial shield bears two setae (it is 38–51 μ long and 32–38 μ wide). The sternal shield is wedge-shaped and its pointed end projects slightly beyond coxa IV. The shield bears 4 pairs of setae. The peritreme is very short and scarcely reaches the middle of coxa III.



FIGS. 107–111. *Allodermanyssus sanguineus* (Hirst). Fig. 107, female, showing asymmetrical dorsal shield. Fig. 108, female, normal dorsal shield. Fig. 109, venter of female. Fig. 110, dorsum of male. Fig. 111, venter of male.

PROTONYMPH (Text-fig. 106). The dorsal surface is partially covered by the anterior dorsal shield and by the pygidial shield. The anterior dorsal shield is different in shape from that of the female and the deutonymph. It is rather broad in its main part, but behind the last pair of setae it tapers off into a narrow, handle-like part which does not bear setae. The anterior dorsal shield bears 11 pairs of simple setae. The length of the shield is approximately 285 μ. The small pygidial shield is similar to that of the deutonymph. The sternal shield bears 3 pairs of setae. It is wedge-shaped, broadest at the second pair of setae and tapering off into a pointed end behind the third pair of setae. Three pairs of setae are inserted on the ventral membrane anterior to the anal shield. The beginnings of a short peritreme are discernible.

HOSTS AND LOCALITIES. 8 pn, 17 dn, 1 ♂, 4 ♀—*Acomys cahirinus* (six specimens), Wadi Seyal, 5.iii.1954 ; 2 dn, 1 ♂, 4 ♀—*Acomys russatus*, Mezada, 4.iii.1955.

NOTES. In Hirst's paper (1914) describing some species of *Dermanyssus*, a description of what he thought to be the male of *D. sanguineus* is given, whereas the male of *D. aegyptius* is considered unknown. In the present study, males of both species have been found and compared. It has been found that the male described by Hirst as the male of *D. sanguineus* is actually the male of *D. aegyptius*. A comparison of the males of the two species shows that they differ distinctly in the characters of the dorsal and ventral surfaces.

Ornithonyssus bacoti (Hirst)

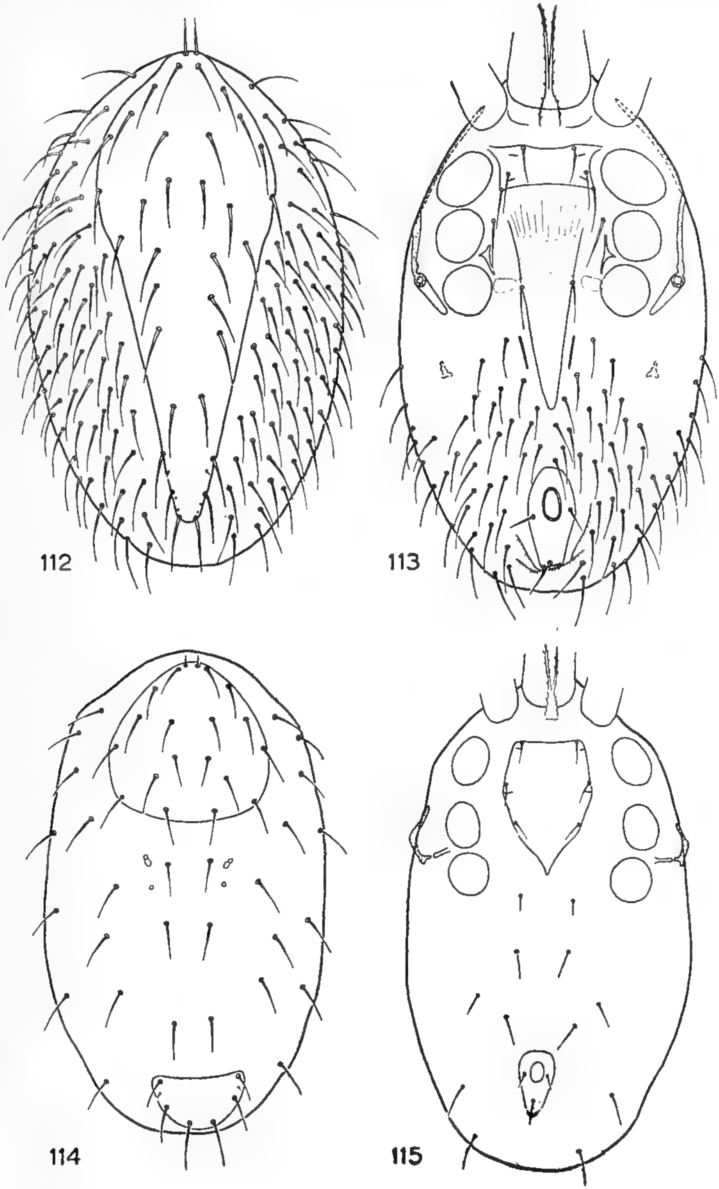
Leiognathus bacoti Hirst, 1913.
Liponyssus bacoti Hirst, 1920.
Bdellonyssus bacoti, Fonseca, 1941.
Macronyssus bacoti, Buitendijk, 1945.

FEMALE (Text-figs. 112, 113). The dorsal shield is narrow and elongated, covering only a small part of the dorsal surface. The shield is 555–660 μ long and 225–240 μ wide at its widest part. It bears 17 pairs of simple elongated setae in addition to one pair of very small setae which are on the posterior margin.

The tritosternum is long, translucent with a feathered base and long, feathered laciniae. The sternal shield is 45 μ long (at mid-line) and 102 μ wide (at the level of the second setae). This shield is almost rectangular, but slightly wider at the anterior than at the posterior margin. The setae of the first pair which scarcely reach beyond the hind margin of the sternal shield, are slightly shorter than the other sternal setae and the metasternal setae.

The genital shield is narrow and pointed. A very narrow elongated shield lies on each side of the posterior part of the genital shield. Numerous setae are inserted on the ventral membrane. The anal shield is elongated, it is approximately 125 μ long and 65 μ wide, it is widest at the level of the paranal setae. The paranal setae are slightly shorter than the postanal seta, they are inserted posteriorly to the middle of the anus. The peritreme reaches to the middle of coxa I, and a narrow peritrematal shield is present.

The legs are slender and long, their respective lengths (excluding pulvilli) being as follows : I—510 μ ; II—380 μ ; III—360 μ ; IV—510 μ. The chelicerae are



Figs. 112–115. *Ornithonyssus bacoti* (Hirst). Fig. 112, dorsum of female. Fig. 113, venter of female. Fig. 114, dorsum of protonymph. Fig. 115, venter of protonymph.

elongated. A single file of 9 deutosternal teeth is present. The internal posterior rostral setae are the longest of the gnathosomal setae.

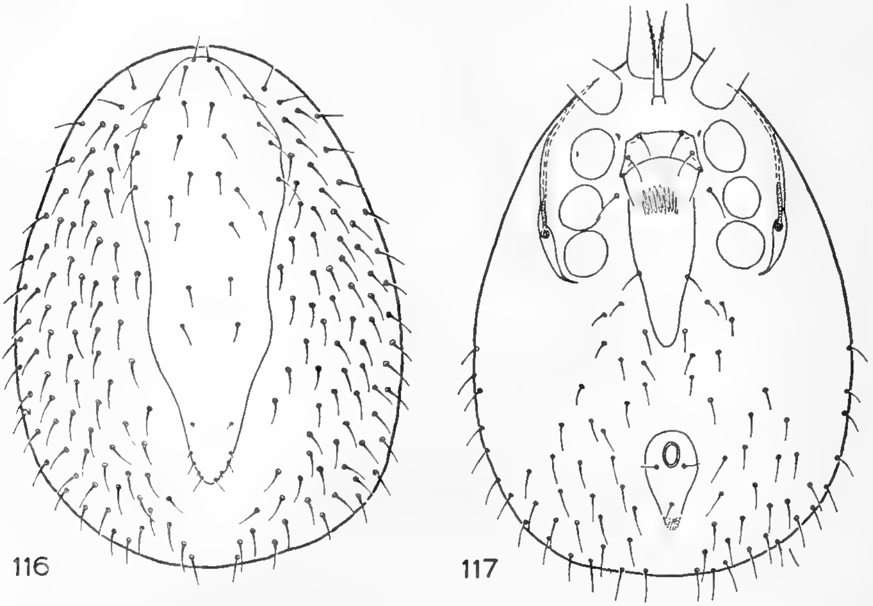
Protonymph (Text-figs. 115, 116). The anterior dorsal shield is approximately 175 μ long and 175 μ wide, its posterior margin is convex. The shield bears 10 pairs of simple long setae, setae *i*1 being shorter than the other setae. The pygidial shield bears 3 pairs of simple elongated setae and one pair of very small setae. The sternal shield, which bears the usual 3 pairs of setae, is pointed at its posterior end and does not project beyond coxa IV. Four pairs of setae lie on the membrane between the sternal and the anal shields.

Hosts and localities. 1 ♀—*Rattus rattus*, Akko (Dunes), 8.iv.1954; 1 ♀—*Acomys cahirinus*, Mishmar Ha'emeq, 28.x.1955; 2 pn—ditto; 8 pn, 2 ♀—Mishmar Ha'emeq, 28.ix.1956; 4 pn—*R. rattus*, Qishon, 16.vii.1957; 2 pn—*Apodemus mystacinus*, Barkai, 16.vii.1957; 1 ♀—ditto, Me'arat Karmel, 25.vii.1957.

Notes. No deutonymphs have been found of this species, which is in agreement with the fact that in *O. bacoti* the deutonymph is non-feeding and moults within 24–36 hours (Baker *et al.*, 1956).

Ornithonyssus nitedulae sp. nov.

Female (Text-figs. 116, 117). The dorsal shield is 615–660 μ long. The shield which is narrow and elongated is constricted in the middle. Nineteen pairs of setae are inserted on the shield, the setae on the posterior part being very short. The setae on the dorsal membrane are narrowly lanceolate.



Figs. 116–117. *Ornithonyssus nitedulae* sp. nov., female. Fig. 116, dorsum. Fig. 117, venter.

The tritosternum is very delicate and translucent, the laciniae being apparently unfeathered. The sternal shield is 35 μ long (at mid-line) and 112 μ wide (at the level of the second pair of setae). Between the setae of the first pair the anterior margin of the shield is straight, but it slopes off at the corners. The posterior margin of the shield is concave. The anterior pores are horizontal, the posterior pores have an outward slant. The sternal setae increase in length from the first to the third pair. The metasternal setae are as long as the third sternal setae (approximately 65 μ).

The narrow genital shield, which bears one pair of setae, projects beyond coxa IV. The anal shield is elongated, it is 160 μ long and 85 μ wide with the anus near the anterior margin. The paranal setae are inserted near the posterior end of the anus, they are of the same length as the postanal seta. Numerous setae are inserted on the ventral membrane. The tubular portion of the peritreme apparently reaches only to the middle of coxa III, it is accompanied by a peritrematal shield which anteriorly reaches to the middle of coxa I, and posteriorly it approaches coxa IV. Coxa II has a strong sharp spur on its antero-dorsal side, it is not marginal.

The legs are fairly short and stumpy, their respective lengths being as follows: I—585 μ; II—465 μ; III—465 μ; IV—585 μ. The chelicerae are elongated, narrow and edentate. The ventral spur on the palpal coxa is prominent and the deutosternal teeth are arranged in a single file.

HOSTS AND LOCALITIES. 6 ♀—*Dryomys nitedula,* Wadi Keren, 20.x.1957.

NOTES. This species is obviously very near *Ornithonyssus dogieli* Breg. which was recorded from the same host (in Tadzhikistan). It can be easily separated from it by the shape and the chaetotaxy of the dorsal shield.

TABLE I. *The Host-parasite Relationships*

Rodents Acari	*Jaculus jaculus*	*Dryomys nitedula*	*Spalax ehrenbergi*	*Apodemus mystacinus*	*Apodemus sylvaticus*	*Rattus rattus*	*Mus musculus*	*Acomys cahirinus*	*Acomys russatus*	*Nesokia indica*	*Gerbillus dasyurus*	*Gerbillus gerbillus*	*Gerbillus allenbyi*	*Gerbillus pyramidum*	*Meriones tristrami*	*Metiones crassus*	*Meriones sacramenti*	*Sekeetamys calurus*	*Cricetulus migratorius*	*Microtus guentheri*
Haemolaelaps androgynus											●									
H. androgynus caluri																		●		
Haemolaelaps glasgowi																				●
Haemolaelaps hirsti													●							
Haemolaelaps hirstionyssoides			●				★													
Haemolaelaps insculptus													●	●			●			
Haemolaelaps longipes										○	○					●				
Haemolaelaps ovalis															●					
Haemolaelaps centrocarpus												●	●	●			●			
Laelaps acomydis								●							★			★		
Laelaps agilis longispinosus					●															
Laelaps algericus							●													
Laelaps ekstremi																			●	
Laelaps pachypus																				●
Androlaelaps marshalli	●												●	●			●			
Eulaelaps stabularis				●	●		●								●					●
Haemogamasus horridus				●																
Hirstionyssus arcuatus						●					○									○
Hirstionyssus craticulatus														●						
Hirstionyssus ellobii spalacis			●				○													
Allodermanussys aegyptius								●												
Allodermanyssus sanguineus								●	●											
Ornithonyssus bacoti				●		●		●												
Ornithonyssus nitedulae		●																		

● = common host. ○ = rare host. ★ = accidental host

SUMMARY

This paper deals with 24 species and subspecies of Laelaptid mites associated with rodents in Israel. The following new species and subspecies are described: *Haemolaelaps hirstionyssoides, Haemolaelaps ovalis, Laelaps acomydis, Ornithonyssus nitedulae, Haemolaelaps androgynus caluri, Laelaps agilis longispinosus*, and *Hirstionyssus ellobii spalacis*.

Descriptions of the hitherto unknown males of *Hirstionyssus craticulatus* Keegan, 1956, and of *Allodermanyssus aegyptius* (Hirst) 1913, are included.

Laelaps ekstremi Zachv., 1948, synonymized with *Laelaps jettmari* Vitzthum, 1930 by Bregetova (1956), is considered a valid species. *Haemolaelaps aegyptius* Keegan, 1956, is synonymized with *Haemolaelaps longipes* Breg., 1952, and *Laelaps arvalis* Zachv., 1948, is synonymized with *Laelaps pachypus* C. L. Koch, 1839.

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University of Khartoum

Pp. 71–107 ; 13 *Text-figures*

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OBSERVATIONS ON THE HEART IN THE FAMILY TRIONYCHIDAE

By SABET GIRGIS, Ph.D. (Lond.)

SYNOPSIS

In the family Trionychidae the heart is asymmetrically situated in the right side of the body cavity, lateral to the base of the neck, and is tilted so that its mid-longitudinal axis forms an an acute angle (approximately 45°) with the sagittal axis of the body. This hitherto unrecorded characteristic of the family has been shown by dissection of specimens representing its different genera. The position of the heart is due to two combined factors: (*a*) the retractility of the head and neck within the carapace, and (*b*) the reduction of the dorso-ventral axis of the body so that the carapace and plastron lie near each other, the former being only slightly convex. The tilting of the heart occurs later in life as it is not seen in new hatches, and it may be due to a pulling force exerted by the left arterial arches.

The anatomical structure of the heart of *Trionyx triunguis* is given. Comparison with *Cyclanorbis oligotylus* shows in the latter a prominent dorso-ventral *secondary septum* which divides the posterior part of the cavum magnum (dorsale) of the ventricle into right and left parts, while the septum in *Trionyx* is quite short.

Distribution of blood into the arterial arches, based purely on anatomical features, is as follows: (*a*) oxygenated blood into the right aorta, (*b*) mixed blood into the left aorta and (c) deoxygenated blood into the pulmonary arch. Blood analysis in the three vessels and in the right and left auricles, agrees with the anatomical findings.

INTRODUCTION

(a) *General*

The heart of the Trionychidae is in many respects similar to that of other Chelonians as described by several authors including Bojanus (1819–21), Rathke (1848), Fritsch (1869), Huxley (1871), Hoffmann (1882), Greil (1903), Burne (1905), O'Donoghue (1918), Goodrich (1919), Thomson (1932), Hyman (1939), Ashley (1955) and others.

Contraction of the heart received the attention of many workers, especially as regards the nerve elements, the cardiac muscles and the route of the contraction wave. A comprehensive review on heart contraction in poikilothermal and homiothermal vertebrates is given by Davies & Francis (1945).

The double circulation through the heart of Chelonians and other reptiles was tackled by practically all the workers who described the anatomy, and most of them have reasoned from the anatomic relations of the cardiac cavities and vessels rather than from experimental evidence. The following papers on circulation are of special interest: Foxon (1955); von Hofsten (1941); Ewer (1950); Foxon, Griffith & Price (1953); Stephen (1954); and Steggerda & Essex (1957).

(b) *Position of Heart*

The peculiar asymmetric position of the heart in the antero-right side of the body cavity, and the tilting of the heart so that its mid-longitudinal axis forms an acute angle with that of the body as a whole are interesting, common characteristics of all members of the Trionychidae, hitherto unrecorded except for one of its members, the Indian mud turtle *Lissemys punctata* Kaushiva (1940), Mathur (1946), Ahsan Al-Islam & Iftikhar Hamid (1951) and Dhillon (1938).

During the course of this work the striking position and tilting of the heart were noticed in the common Nile turtle *Trionyx triunguis* and *Cyclanorbis oligotilus*, which is rather rare in the vicinity of Khartoum (but quite common in the Southern Sudan). It was then interesting to find out whether these characteristics were also shared by other members of the family Trionychidae. The answer was only made possible by the extreme kindness and co-operation of the Keeper of Zoology and of the Staff of the Herpetology Section of the British Museum (Natural History) London. As a guest of the Department during May and June, 1960, the writer was allowed to examine a fairly large number of alcohol-preserved specimens collected from various parts of the world, one and all of which had their hearts at the right side of the base of the neck and tilted to a degree which showed some variation in different species.

Based mainly on the Museum material examined, the two species of the Nile, the work published on the Indian mud turtle and two new hatches of *Amyda ferox spinifera* presented to the author by a friend in America, an important conclusion regarding the position of the heart in the Trionychidae could be arrived at and the relationship between this anatomical feature to the aquatic life of its members discussed.

(c) *Anatomy of Heart*

Trionyx triunguis being available in any required number, was chosen for a study of the anatomy of the heart, the great veins, the arterial arches, the heart beat and the double circulation. A comparative study of the heart of *Cyclanorbis oligotylus* followed.

(d) *Experimental*

Steggerda & Essex (1957) in *Chelydra serpentina*, state that " the saturation levels of the blood leaving the heart via the right and left aortas are the same while pulmonary artery blood is distinctly more venous ". This statement disagrees with the findings of the present work (based merely on anatomical features), where the right aorta carries blood with a distinctly higher oxygen saturation than the left, and it was therefore found necessary to perform a series of blood analysis tests of samples taken from the two aortae and the pulmonary artery, as well as from the left and right auricles, to verify this point.

(e) *Materials and Methods*

Specimens were caught by local fishermen from both the Blue Nile and the White Nile, as well as from Gebel Auleia Dam on the White Nile (25 miles south of Khartoum).

Animals were killed by injecting 5 c.c. of chloroform intramuscularly and setting them free to run vigorously and die in 10 15 minutes. For blood-analysis, specimens of exceptionally large sizes were chosen as 25 c.c. of blood had to be drawn from each ; 3 c.c. of chloroform were injected in each specimen and it took 30–40 minutes, and occasionally longer, for an animal to lie unconscious.

ASYMMETRICAL POSITION OF THE TRIONYCHID HEART

The following examples are meant to cover all the known genera of the family Trionychidae. Numbers 2, 4, 5, 6, 7, 8 and 10 are alcohol-preserved specimens from the British Museum (Natural History), London.

In each case the plastron is removed to expose the ventral body wall and the two great triangular masses of pectoral muscles. The heart lies for the most part dorsal to the right mass, and to expose it the muscular and fibrous tissues which extend between the pectoral muscles on the one hand and the neck and ventral wall of the abdomen on the other hand, have to be carefully severed. The ventral wall of the pericardium is now cut off and the pericardial cavity, the heart (in ventral view) and the arterial arches are exposed (Text-fig. 1).

The pericardial cavity containing the heart lies roughly dorsal to the right mass of the pectoral muscles, ventral to the concave antero-lateral surface of the right liver lobe, anterior to the bulk of the right liver lobe and posterior to the postero-right part of the base of the neck (Text-fig. 1).

1. ***Trionyx triunguis.*** Locality Khartoum, Sudan.

Six specimens were chosen, the smallest weighed 1,370 g. and the dimensions of its carapace were 26 × 23 cm. ; and the largest weight 14,320 g. and its carapace was 50 × 46 cm.

The heart lies at the anterior part of the body cavity, some distance to the right of the mid-longitudinal axis of the body. The mid-longitudinal axis of the heart, taken as the line perpendicular on the transverse axis of the ventricle at its medial point, forms an acute angle with the mid-longitudinal axis of the body. The angle averaged 45° in the six specimens.

2. ***Trionyx triunguis.*** (B.M. 87.3.2.8–12, 13 ; from the Lower Congo.)

A very young specimen, much smaller than any examples in our local (Khartoum) collection.

Weight of specimen = 11·2 g.
Dimensions of carapace = 5·2 × 4·4 cm.

The heart was in the same position as in the older specimens and tilted to the same degree.

3. ***Cyclanorbis oligotylus.*** Locality Khartoum, Sudan.

Six specimens of a fairly large size were examined. The smallest weighed 4,150 g. and the dimensions of its carapace were 24 × 22·5 cm.

The heart was in every case at the antero-right side of the body cavity but nearer to the sagittal plane than in any other Trionychid. The mid-longitudinal axis

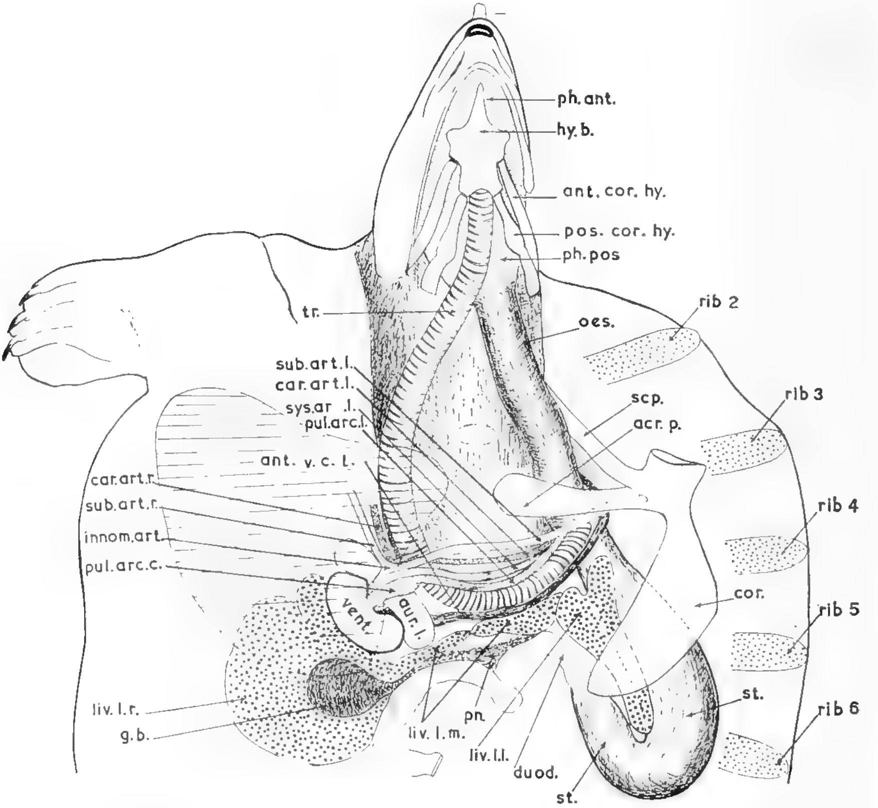

Fig. 1. *T. triunguis.* Dissection to show the position of the heart in relation to other parts of the body.

acr. p., acromal process; ant. cor. hy., anterior cornu of hyoid; ant. v. c. l., left anterior vena cava; car. art. l., left carotid artery; car. art. r., right carotid artery; cor., coracoid bone; duod., duodenum; g. b., gall bladder; hy. b., hyoid body; innom. art., innominate artery; liv. l. l., left liver lobe; liv. l. m., medial liver lobe; liv. l. r., right liver lobe; oes., oesophagus; ph. ant., anterior pharynx; ph. post., posterior pharynx; pn., pancreas; pos. cor. hy., posterior cornu of hyoid; pul. arc. c., common pulmonary arch; pul. arc. l., left pulmonary arch; pyl. sp., pyloric sphincter; scp., scapula; st., stomach; sub. art. l., left subclavian artery; sub. art. r., right subclavian artery; sys. arc. l., left systemic arch; tr., trachea.

of the body passed through the left side of the left auricle. The tilting of the heart was comparable to *Trionyx*.

4. ***Cycloderma frenatum.*** (B.M. 1945.1.1.1–5; from Fort Johnson, Nyasaland.)

Weight of specimen = 14·7 g.
Dimensions of carapace = 4·8 × 3·6 cm.

The heart was in the same position as in *Trionyx*, but tilted to a lesser extent. Its mid-longitudinal axis formed an angle of approximately 35° with the mid-longitudinal axis of the body.

5. ***Pelochelys bibroni.*** (B.M. 1921.11.11.4; from Wangar River, Dutch New Guinea.)

Weight of specimen = 122·7 g.
Dimensions of carapace = 10·6 × 10·2 cm.

The heart was in the same position as in *Trionyx*, and the amount of tilting as in the previous specimen of *Cycloderma*.

6. ***Dogania subplana.*** (B.M. 93.3.6.9–11, from Sarawak, Borneo.)

Weight of specimen = 66·3 g.
Dimensions of carapace = 9·2 × 7·3 cm.

The heart was exactly as in *Trionyx* as regards position and tilting.

7. ***Lissemys punctata.*** (B.M. 84.3.25.3; from unknown locality, somewhere in India.)

A very young specimen.

Weight of specimen = 8·2 g.
Dimensions of carapace = 3·3 × 2·7 cm.

The position of the heart was as in *Trionyx*, but very little tilting was exhibited, the longitudinal axis of the heart being practically parallel to that of the body.

8. ***Amyda ferox spinifera (Trionyx spiniferus).*** (B.M. 59.9.20: 26; from the United States.)

Weight of specimen = 248·3 g.
Dimensions of carapace = 14·5 × 12·1 cm.

The heart was similar to *Trionyx* as regards position and tilting.

9. ***Amyda ferox spinifera.*** Locality United States (presented by Dr. E. Malek, Tulane University Medical School, Lousiana). Two very young specimens.

Weight of one of the specimens = 8·3 g.
Dimensions of its carapace = 4·4 × 3·9 cm.

The heart of both specimens was definitely at the right side of the animal, its left border being just tangential to the mid-longitudinal axis, but no tilting whatsoever was exhibited.

10. ***Chitra indica.*** (B.M. 1921.4.1.197 from Ban Pong, C. Siam.)

The only alcohol-preserved specimen in the Museum and because of its large size it had to be cut into parts. It was not practicable to weigh or measure it. All the same the heart was in the same position as in *Trionyx.*

From the above data it may be deduced that the heart lies at the antero-right side of the body-cavity in all the known genera of the family Trionychidae. This fact, hitherto unrecorded, may be regarded as a general characteristic of the family.

The tilting of the heart seems to be a later development since in the new hatches (Nos. 7 and 9), the heart lies with its mid-longitudinal axis parallel to that of the body. This tilting may well be due to the pulling forces exhibited by the arterial arches on the left side of the body. These arteries extend from the heart in a roughly horizontal direction across the base of the neck to the left side of the body (Text-fig. 1, sub. art. l., car. art. l. and sys. art. l.). They run ventral to the huge central mass of muscles which causes retraction of the head and neck within the shell, namely the *retrachens capitis collique* of George & Shah (1955). The rapid growth of this muscle would cause some pressure on the arteries which, in their turn, would pull the antero-right part of the ventricle where they are attached. There is no counteracting pulling force from the right arterial arches since they do not run in the opposite direction, i.e. horizontally towards the right side, but extend anteriorly (Text-fig. 1, car. art. r. and sub. art. r.).

Except for the Trionychidae, all Chelonians have symmetrically situated hearts in the sagittal axis of the body. This is shown in drawings and descriptions by many early and recent writers, e.g. Bojanus (1819–21) in *Testudinia* ; Martin & Moale (1805) in *Pseudemys* ; Hoffmann (1890) in *Clemmys* and *Chelydra* ; Burne (1905) and O'Donoghue (1918) in *Dermochelys* ; Thomson (1932) in *Testudo* and Ashley (1955) in *Chelydra, Chrysemys* and *Pseudemys.* A sagittaly-situated heart was also found by the writer in *Chelys fimbriata* (B.M. 97.5.15.1 ; from Trinidad) and in *Pelomedusa galeata* (from Khartoum, Sudan).

Presence of an asymmetrically-situated heart in all genera of the family Trionychidae is very striking, and it is almost certain that it could not be incidental but a character that enables members of this family to live under certain conditions common to all of them.

In an effort to explain the relationship of the one-sided position of the heart and the life of these animals, two of their habits are noted :

(*a*) Soft-shelled turtles are expert swimmers as noticed by Agassiz (1857) who described their swimming movements ; Garman (1892) who reported that the turtle can pursue and catch the quickest of fish and can swim against swift currents or dash away in danger, and Cahn (1937) who emphasized their swimming habits. A flat or low convex carapace gives them a great advantage as swimmers since it makes them more stream-lined and lessens water resistance.

(*b*) The flash-like way in which the head protracts to catch food, or retracts when the animal is frightened. As described by Boulenger (1889) " the neck is more perfectly adapted for complete and rapid retraction than in any other Chelonian ".

Retraction of the head and neck in the Trionychids and in all the subclass CRYPTODIRA (where the neck withdraws in a sigmoid way) is effected by huge muscles situated in the sagittal axis of the body, the retrachens capitis collique.

Presence of the central mass of muscles in the CRYPTODIRA does not prevent these animals—the Trionychidae excepted—from having a perfectly symmetrical heart, but then they also have a highly convex or dome-shaped carapace to provide enough room to accommodate both. Such a carapace would certainly be a handicap to a good swimmer.

The shifting of the heart enables the Trionychids to have a shorter dorso-ventral axis and a more or less flat carapace which gives them a great advantage as swimmers, while still retaining the blessing of complete and flash-like retraction of the head.

It is quite possible that the shifting occurred as a result of the carapace and plastron having come nearer to each other. This possibility seems to be further confirmed by the fact that in *Cylanorbis*, where the dorso-ventral axis is deeper than in other members of the family owing to higher convexity of the carapace, the heart lies nearer to the mid-longitudinal axis of the body.

THE HEART OF *TRIONYX TRIUNGUIS*

To save unnecessary complications in describing the heart and blood vessels attached to it, the mid-longitudinal axis of the heart, *and not of the animal as a whole*, will be considered to indicate the antero-posterior direction ; and terms such as " medial " and " lateral " refer to the mid-axis of the heart and not of the animal.

(a) *Pericardium*

The pericardium is a rather thin, white serous membrane which surrounds the heart and the base of the arteries which extend from it. It is reflected to adhere to the outer surface of the collection of arteries, covering them completely within the pericardial cavity. The cavity is quite large, and it contains a faintly-yellowish watery fluid ; 11·5 c.c. of liquid were extracted from a medium-sized specimen (length of carapace 22 cm.).

The postero-dorsal wall of the pericardium is free and lies ventral to the anterior part of the right liver lobe. Here the surface of the liver is curved dorsally to make room for the heart. The antero-dorsal pericardial wall is firmly attached to the following parts (Text-figs. 2 and 3) :

(i) The sinus venosus which lies dorsal to the pericardium, outside the pericardial cavity (sin. v.).

(ii) The dorsal wall of the auricles, except for their short caudal ends which pass into the ventricles, and their anterior ends which are free.

(iii) The left anterior vena cava passes through the pericardium on its anterior left side and runs postero-medially around the edge of the left auricle (ant. v.c. l.). It penetrates the dorsal wall of the pericardium again and passes into the sinus venosus.

(iv) The right anterior vena cava (ant. v.c. r.) runs on the dorsal side of the pericardium, dorsal to the anterior border of the right auricle, and passes into the sinus.

(v) The left hepatic vein runs dorsal to the pericardium directly into the sinus (hep. v. l.). The terminal parts of the left anterior vena cava and left hepatic vein run on top of one another on opposite sides of the pericardium.

(vi) The proximal end of the posterior vena cava on its way to the sinus (post v.c.).

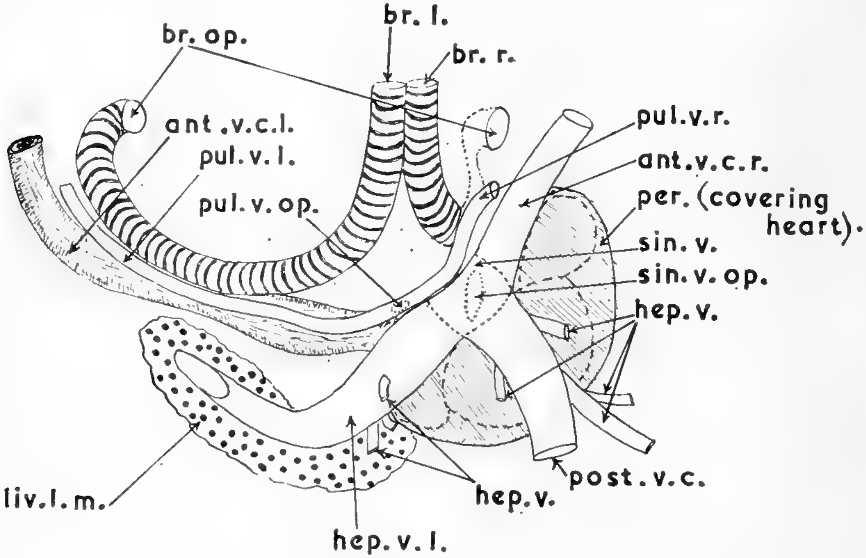

FIG. 2. *T. triunguis.* Dorsal dissection to show relative position of heart, veins and terminal bronchi. (Parts not seen are drawn in dotted lines.)

ant. v. c. l., left anterior vena cava; ant. v. c. r., right anterior vena cava; br. l., left bronchus; br. op., bronchial opening into lung; br. r., right bronchus; hep. v., hepatic vein; hep. v. l., left hepatic vein; liv. l. m., medial liver lobe; per., pericardium; post. v. c., posterior vena cava; pul. v. l., left pulmonary vein; pul. v. op., opening of pulmonary veins; pul. v. r., right pulmonary vein; sin. v., sinus venosus; sin. v. op., opening of sinus venosus.

(vii) The pulmonary veins. The right pulmonary vein (pul. v. r.) runs horizontally anterior and adjacent to the right anterior vena cava, the sinus venosus, and the terminal parts of the left hepatic vein where it runs into its fellow of the other side (pul. v. l.). Their common opening into the left auricle may be seen by making a longitudinal incision in the walls of the vessels (pul. v. op.).

(viii) The coronary vein (Text-fig. 4, cr. v. dor.) runs from the antero-dorsal point at the right side of the medial axis of the ventricle, in a left and dorsal direction, and penetrates the pericardium to the sinus venosus. A shorter fibrous cord attaches the ventricle and the base of the coronary vein to the pericardium and may be termed ventriculo-pericardial ligament (Text-fig. 4, ven. per. lig.).

(b) *Chambers of the Heart*

1. *Sinus Venosus* (Text-figs. 2 and 3, sin. v.)

A dorsal dissection of the heart should be done by severing the heart and associated parts from the body, or alternatively by removal of the carapace and lungs.

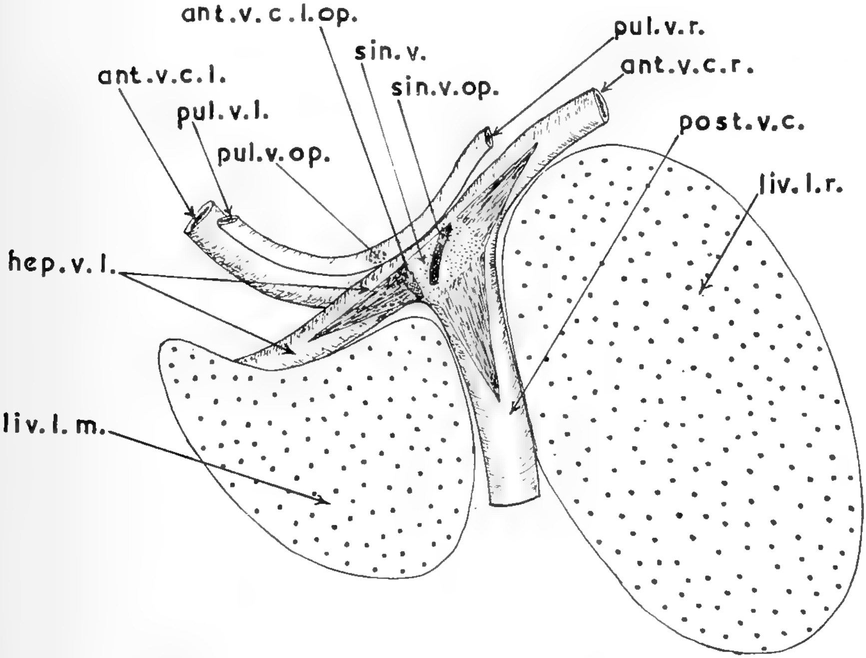

FIG. 3. *T. triunguis.* Dorsal wall of sinus venosus and veins removed to show the borders of the sinus and the oblique sinu-auricular opening. The openings of the left anterior vena cava (ventral) and of the left hepatic vein (dorsal) lie on top of one another.

ant. v. c. l., left anterior vena cava; ant. v. c. l. op., opening of left anterior vena cava; ant. v. c. r., right anterior vena cava; hep. v. l., left hepatic vein; liv. l. m., medial liver lobe; liv. l. r., right liver lobe; post. v. c., posterior vena cava; pul v. l., left pulmonary vein; pul. v. op., opening of pulmonary veins; pul. v. r., right pulmonary vein; sin. v., sinus venosus; sin. v. op., opening of sinus venosus.

The sinus lies on the dorsal side of the pericardial wall on top of the medial part of the auricles, slightly nearer to the right side.

It can be seen dorsally as the part where the *left hepatic* vein, the *posterior vena cava* and the *right anterior vena cava* meet, but its actual borders may only be determined by making longitudinal incisions in the terminal parts of these veins (Text-fig. 3). A shallow ridge marks the border between the *posterior vena cava* and the sinus.

The *left hepatic* and the *left precaval* veins terminate on top of one another on the left side of the sinus, the formal being dorsal and the latter ventral (Text-fig. 3). The *right anterior vena cava* opens in the right aspect of the sinus, and the border is marked by a slight depression of the floor of the sinus which lies more ventrally. The anterior border of the sinus is adjacent to the terminal part of the *right pulmonary* vein.

The middle part of the floor contains the sinu-auricular opening which is spindle-shaped (oval in some specimens) and its long axis runs obliquely (Text-fig. 3, sin. v. op.).

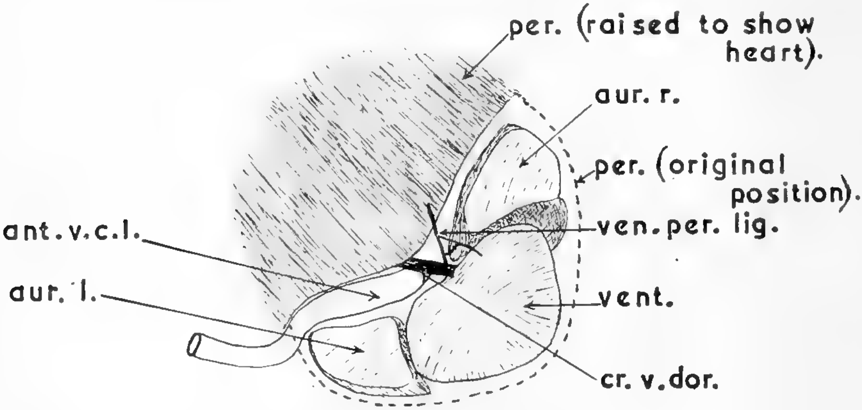

FIG. 4. *T. triunguis.* Dorsal aspect of heart. (Auricles are expanded and ventricle contracted.)

ant. v. c. l., left anterior vena cava; aur. l., left auricle; aur. r., right auricle; cr. v. dor., dorsal coronary vein; per., pericardium; vent., ventricle; ven. per. lig., ventriculo-pericardial ligament.

2. *Left Auricle*

The left auricle (Text-fig. 4, aur. l.) occupies roughly one-third of the anterior border of the two auricles and extends posteriorly for some distance dorsal to the ventricle. Its wall is comparatively thin. The common pulmonary opening (Text-fig. 2, pul. v. op.) is in the dorso-medial wall which is firmly attached to the pericardium and is very near the inter-auricular septum. It is an oval depression not guarded by valves.

The left auricular cavity extends as a narrow passage between the auricular wall externally, and the inter-auricular septum (Text-fig. 11, int. aur. sep.) internally. It ends in the left auriculo-ventricular opening at the left side of the dorsal base of the ventricle. The inner side of its wall and particularly on its dorsal aspect has a number of well-marked muscle strands, the " musculi pectinate " of O'Donoghue (1918).

3. *Right Auricle*

The cavity of the right auricle is the larger of the two. Not only is its anterior border about twice as long as that of the left auricle (Text-figs. 4 and 11), but also the wide passage which connects the auricles to the ventricle is almost completely a part of the right auricular cavity.

The walls are thicker than those of the left auricle especially at the right side where they show some depressions and bulgings comparable to some extent to those of the ventricular wall.

The sinu-auricular aperture lies in a dorso-medial position to the right side of the inter-auricular septum. It is guarded by a valve composed of two membranous semicircular flaps of tissue which overlap one another when closed.

The right auriculo-ventricular opening lies adjacent to the left one, the two openings being separated only by the thickness of the inter-auricular septum (Text-fig. 11, int. aur. sep.). Although nearer to the medial axis of the heart, the right opening is still on its left side. Mathur (1946) states that the left auricle opens into the left part of the cavum dorsale and the right opens into the right. This is not the case in *Trionyx triunguis* (and *Cyclanorbis oligotylus*).

4. *Ventricle*

Examining the heart from the ventral aspect (Text-fig. 8), the ventricle appears as a flat body with a bluntly rounded apex. The horizontal axis in the dilated condition is two and a half times as long as the antero-posterior axis. The right side is rather shorter than the left and they both taper towards the concave anterior base where the arterial arches originate. The roots of the arches occupy approximately the right two-thirds of the base.

Dorsally, the ventricle may be roughly described as deeply convex, with a larger posterior portion which ends in the round apex, and a smaller anterior one which slopes antero-ventrally to join the two sides of the ventricle.

No ligamentous attachment, "gubernaculum cordis", as described by Ashley (1955) in painted turtles, by Mathur (1946) in *Lissemys punctata* and by O'Donoghue (1918) in *Dermochelys coriacea*, exists between the apex of the heart and the pericardium. During contraction of the heart, the ventricle shortens considerably towards its anterior base, and any ligamentous attachment of its apex to the pericardium, unless sufficiently long, would hinder its movements. The ventriculo-pericardial attachments here, are one or more short fibrous ligaments which extend from the antero-dorsal aspect of the ventricle to the dorsal wall of the pericardium (Text-fig. 4, ven. per. lig.), and the fibrous outer sheath of the coronary vein (Text-fig. 10B, ligament).

INTERNAL STRUCTURE OF THE VENTRICLE

The internal structure and the ventricular cavity may be studied by cutting the organ transversely through the round apex and side wall, and opening it (Text-fig. 5), and also by making a number of dorso-ventral sections from apex to near base

(Text-fig. 6, Nos. 1–10). The terminal section which shows the auriculo-ventricular openings and their valves, and the three openings of the arterial arches (Text-fig. 7) is worthy of some special attention.

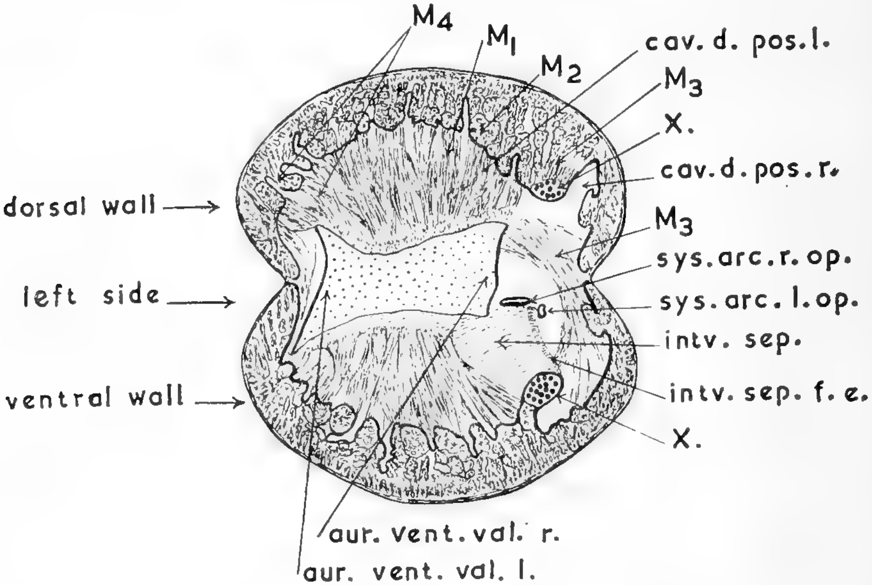

FIG. 5. *T. triunguis.* The ventricle opened horizontally from apex and sides. Internal view. The posterior part of the cavum magnum (c. dorsale) is divided by a short secondary septum into right and left parts. The cavum parvum (c. pulmonale) lies ventral to the inter-ventricular septum and is not in view.

aur. vent. val. l., left auriculo-ventricular valve ; aur. vent. val. r., right auriculo-ventricular valve ; cav. d. pos. l., posterior part of cavum dorsale, left cavity ; cav. d. pos. r., posterior part of cavum dorsale, right cavity ; intv. sep., inter-ventricular septum ; intv. sep. f. e., free edge of inter-ventricular septum ; M1, antero-posterior muscle fibres ; M2, continuation of antero-posterior muscle fibres around apex ; M3, right posterior to antero-medial muscle fibres ; M4, left posterior to antero-medial fibres ; sys. arc. l. op., opening of left systemic arch ; sys. arc. r. op., opening of right systemic arch ; x, secondary inter-ventricular septum.

(a) *Walls of the Ventricle* (Text-figs. 5, 6 and 7)

The wall is quite thick especially at the apex. The muscular tissue which forms the main thickness is composed of a network of bands of cardiac muscle fibres similar in structure to mammalian fibres. In the interstices of the muscle bundles there is a considerable amount of connective tissue. Numerous irregular cavities of variable sizes lie between the muscle bands so that the whole structure forms a rather loose spongy mass. Externally the wall is covered by a smooth serous membrane which, as in mammals, is composed mainly of connective tissue rich in elastic fibre. Internally the anterior part of the ventricular cavity is lined by a rather thick, white fibrous membrane which extends for some distance behind the auriculo-ventricular valves, and extends further to cover both surfaces of the inter-ventricular septum. The rest of the cavity is lined by a thin transparent continuation of the internal membrane.

Most of the muscle fibres are attached to dense fibrous membranes which lie round (i) the auriculo-ventricular openings, and (ii) the edge of the white membranous septum which lines the anterior part of the cavity. An account of the larger bands of muscle fibres follows :

(i) *Muscles of the Left Side* (Text-fig. 5, M.4)

The deeper bands are roughly " U "-shaped. They take origin from the left part of the anterior fibrous lining and run in a postero-left direction, with one limb in the dorsal wall and the other in the ventral wall, the two limbs running into each other around the left side of the apex. The bands nearer to the surface behave in a similar way, but their ends are attached to the fibrous skeleton of the heart around the left auriculo-ventricular junction. The main bands give branches which may either join other bands or are inserted into the outer coat, so that they are firmly attached to each other and to the outer coat.

(ii) *Muscles of the Middle Part*

The muscle bands in the middle part (Text-fig. 5, M1 and M2) behave likewise, but their direction is mainly antero-posterior.

(iii) *Muscles of the Right Part* (Text-fig. 5, M.3 and x)

The muscle bands which form the inter-ventricular septum (Text-fig. 5, intv. sep.) take origin from the right dorsal corner of the apex and run in an antero-medial and slightly ventral direction. They spread fan-wise as they proceed forward to terminate in the fibrous anterior wall. Some bands run dorso-ventrally into, or slightly to the left side of, the caudal end of the inter-ventricular septum (Text-fig. 5x) forming a short secondary septum which extends vertically between the dorsal, ventral and posterior walls and partly divides the posterior part of the ventricular cavity into a larger left and a smaller right portion (Text-fig. 6, Nos. 6 and 7).

The bands of the muscle fibres which form the floor of the right side of the ventricular cavity extend around the right wall of the ventricle and proceed anteriorly (Text-fig. 5, M.3). These are joined by other bands from the right wall, and the large resulting band runs medially and is inserted into the fibrous tissue (skeleton of heart), outside the right auriculo-ventricular junction.

(b) *The Auriculo-ventricular Openings and Valves*

The two openings (Text-fig. 7) lie side by side on the left dorsal base of the ventricle separated by a short septum, an extension of the inter-auricular septum (Text-fig. 11, int. aur. sep.). A transverse flap of fibrous tissue extends on either side of

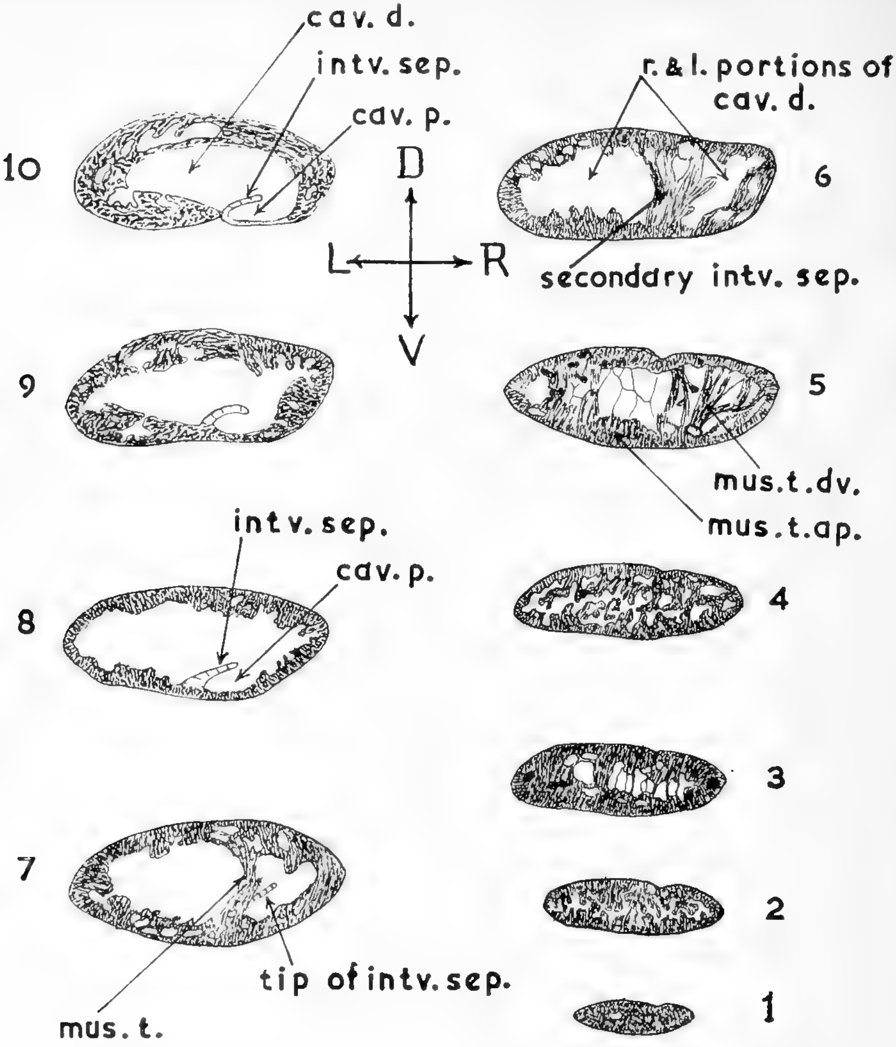

FIG. 6. *T. triunguis.* A series of dorso-ventral sections in the ventricle, parallel to the transverse axis. (Apex to near the anterior border.)

1–4. Spongy wall, with small irregular cavities. Muscle trabeculae run mainly antero-posteriorly and dorso-ventrally.

5. Muscle trabeculae are less in number and the cavities are larger.

6–7. Bands of muscle fibres cross the ventricular cavity in a dorso-ventral direction. They form a secondary inter-ventricular septum which divides the cavity into a larger left and a smaller right portion. The free edge of the inter-ventricular septum appears at the right side of the secondary septum.

8–10. Anterior ventricular cavity divided by the inter-ventricular septum into cavum dorsale (preferably magnum) and cavum pulmonale (preferably parvum).

cav. d., cavum dorsale; cav. p., cavum pulmonale; int. sep., inter-ventricular septum; mus. t., muscle trabecule; mus. t. ap., antero-posterior muscle trabecule; mus. t. dv., dorso-ventral muscle trabecules.

the septum to form the two auriculo-ventricular valves (Text-figs. 5 and 7, aur. vent val.). The valves are attached to the dorsal and ventral walls of the ventricle cutting off an anterior passage from the ventricular cavity. The left valve is comparatively short and its funnel-like opening is adjacent to the left ventricular wall. The right valve is longer and its opening lies at some distance from the right wall of the ventricle.

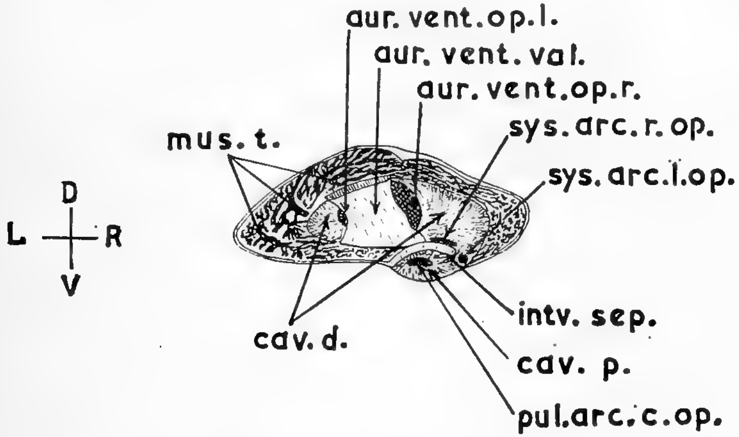

FIG. 7. *T. triunguis.* Anterior part of ventricle cut dorso-ventrally parallel to the transverse axis. Posterior view to show internal structure.

aur. vent. op. l., left auriculo-ventricular opening ; aur. vent. op. r., right auriculo-ventricular opening ; aur. vent. val., auriculo-ventricular valve ; cav. d., cavum dorsale ; cav. p., cavum pulmonale ; intv. sep., inter-ventricular septum ; mus. t., muscle trabecule ; pul. arc. c. op., opening of common pulmonary arch ; sys. arc. l. op., opening of left systemic arch ; sys. arc. r. op., opening of right systemic arch.

(c) *Cavities of the Ventricle*

The ventricle contains mainly two cavities connected with each other (Text-fig. 6, No. 10 and Text-fig. 7). The larger cavity is dorsal and extends from one side of the ventricle to the other, and is termed the " cavum dorsale " (cav. d.). The smaller cavity occupies the ventral and right position, and has been called the " cavum pulmonale " or " cavum ventrale " (cav. p.). The terms are common and have been used by most authors, e.g. O'Donoghue (1918), Goodrich (1919), Mathur (1946), Thomson (1932), Foxon (1955) and others. It is suggested, however, that the terms " cavum magnum " and " cavum parvum " would give a more accurate naming for the cavities which are not strictly dorsal and ventral to each other.

The two cavities are separated by an inter-ventricular septum (intv. sep.) which takes origin from the ventral wall, its line of attachment being roughly from a postero-medial point to an antero-right one (Text-fig. 11, intv. sep. b.). The septum extends towards the right side, sloping slightly dorsally to end in a free edge (Text-fig. 5, intv. sep. f.e.) near, and to some extent parallel to the right wall of the ventricle. The white membranous lining of the ventricular cavity extends on both surfaces of the septum.

Towards the posterior end, the cavum magnum (dorsale) is partially divided into right and left cavities by a secondary septum (Text-fig. 6, Nos. 6 and 7, and Text-fig. 11, x) which, however, is very short and is not effective in dividing the dorsal ventricular cavity.

More posteriorly (Text-fig. 6, No. 5—1) the muscle bands and trabecules increase more and more in number breaking the ventricle into intercommunicating small cavities. Finally we come to the thick outer serous membrane.

(d) *Internal Openings of the Arterial Arches* (Text-fig. 7)

The three arches open near one another at the antero-right side of the ventricle. The pulmonary opening is the largest, the left systemic the smallest, and the right systemic intermediate.

The pulmonary opening (pul. arc. c. op.) lies at the anterior end of the cavum parvum (pulmonale) in the ventral wall of the ventricle near its base. The left systemic opening (sys. arc. l. op.) also lies at the ventral wall, at the right side of the free edge of the inter-ventricular septum. It is quite near the right wall of the ventricle. The opening may be described as situated just outside the entrance of the cavum parvum (pulmonale). The right systemic opens at the base of the dorsal wall of the ventricle, close but somewhat to the left side of the left systemic (sys. arc. r. op.). The two systemics do not open immediately behind the auriculo-ventricular apertures as in the species described by Mathur (1946).

Each of the openings of the arterial arches is guarded by two semi-lunar valves similar in structure to those of mammals. They proved to be equally efficient as it was not possible to inject the ventricle through any of these arches.

(c) *Arterial Arches* (Text-figs. 8 and 9)

The *common pulmonary arch* (pul. arc. c.) to the left, and the *left systemic arch* (sys. arc. l.) to the right, run from the base of the ventricle in an antero-left direction. The *right systemic arch* lies dorsal to them and cannot be seen in a ventral view, but its main branch, the *innominate* artery (innom. art.) is partly visible. A semi-transparent membranous sheath reflected from the pericardium envelopes all the arteries, and several ligamentous processes connect their walls together. Very careful dissection is necessary to separate the arteries without injury and excessive bleeding. It is advisable to inject the circulatory system with formalin and leave the animal for some time in formalin before attempting to dissect the heart and blood vessels attached to it. The vessels would then be dilated and better demonstrated.

The *common pulmonary arch* proceeds forwards for a short distance and then bifurcates into the *right* and *left pulmonary arches*. The former (Text-fig. 9, No. 2, pul. arc. r.) takes a sharp curve to the right side, practically at right angles to the *common pulmonary arch*, and dorsal to the collection of arteries, so that it is not in view in a ventral dissection. It leaves the pericardial cavity opposite the antero-ventral border of the right auricle.

The *left pulmonary arch* (pul. arc. l.), the *left systemic arch* (sys. arc. l.), the *left subclavian* (sub. arc. l.) and the *left carotid* arteries (car. art. l.)—the carotid and subclavian having just emerged from the innominate—take a straight antero-left course and pass through the pericardium (Text-fig. 9, Nos. 2 and 3). Before penetrating the pericardium, the *left carotid* is hidden from view in the ventral dissection, as it lies dorsal to the *left subclavian* (Text-fig. 8).

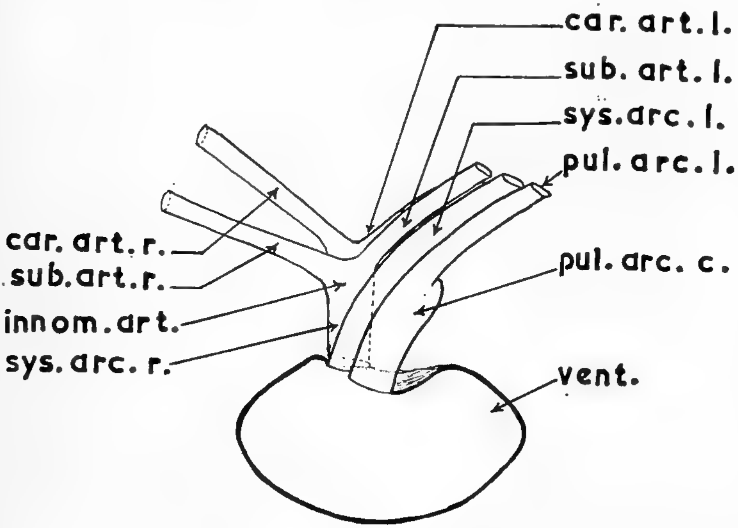

FIG. 8. *T. triunguis.* Arterial arches and their branches as seen in a ventral view.

car. art. l., left carotid artery; car. art. r., right carotid artery; innom. art., innominate artery; pul. arc. c., common pulmonary arch; pul. arc. l., left pulmonary arch; sub. art. l., left subclavian artery; sub. art. r., right subclavian artery; sus. arc. l., left systemic arch; sys. arc. r., right systemic arch; vent., ventricle.

The *right systemic arch* shortly after its origin from the ventricle, gives off the *innominate* artery which is as wide as the arch itself, so that it is difficult to distinguish at a glance which is the origin and which is the branch (Text-fig. 9, Nos. 2 and 3). A longitudinal dorsal incision gives the answer as it shows the inner orifice of the *innominate* in the ventral wall of the *right systemic*. As soon as it gives off its great *innominate* branch, the *right systemic* bends sharply to the right, forming a loop (Text-fig. 9—2) and penetrates the pericardium very near to the exit of the *right pulmonary arch*. The *innominate* artery starts branching while still in the pericardial cavity. A longitudinal dorsal incision (Text-fig. 9—4) helps considerably in following its branches which are extremely close to each other and quite confusing. After a short straight course, the dorsal wall of the *innominate* artery terminates by bifurcating into a wider *right carotid* artery and a narrow *left carotid* artery. The *right subclavian* starts from an orifice (Text-fig. 9, No. 4, sub. art. r. op.) in the ventral wall of the innominate at a short but quite distinguishable distance behind the *right carotid*. The *left subclavian* artery likewise originates from the ventral wall of the *innominate* but its orifice (sub. art. l. op.) is almost ventral to that of the

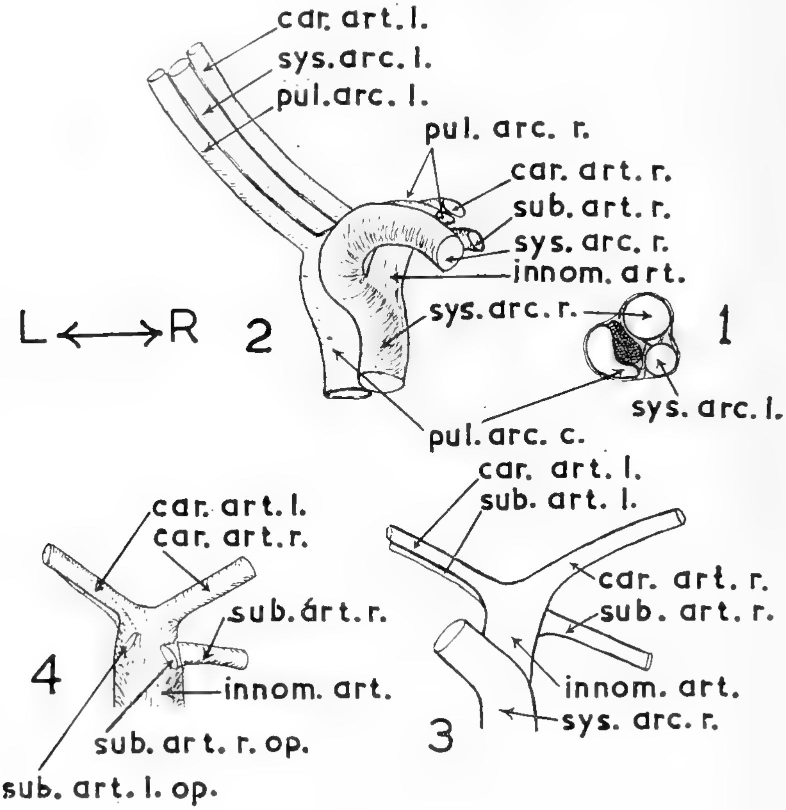

FIG. 9. *T. triunguis.* Arterial arches and their branches from the dorsal aspect.

1. T.S. at exit of arches from ventricle.
2. Arterial arches and their branches.
3. Innominate artery; its four branches seen after removal of part of the right systemic arch (which loops to the right side and covers them).
4. Innominate artery opened by a longitudinal incision to show exit of its four branches.

car. art. l., left carotid artery; car. art. r., right carotid artery; innom. art., innominate artery; pul. arc. c., common pulmonary arch; pul. arc. l., left pulmonary arch; pul. arc. r., right pulmonary arch; sub. art. l. op., opening of left subclavian artery; sub. art. r. op., opening of right subclavian artery; sys. art. l., left systemic arch; sys. arc. r., right systemic arch.

left carotid so that the two arteries run on top of each other until shortly after passing through the pericardium. The *right carotid* and *right subclavian* arteries proceed through the antero-right pericardial wall, the *right carotid* being medial and the *right subclavian* lateral to each other.

The *carotid* is usually described as a branch of the *subclavian* artery of the corresponding side, or both arteries as branches of a *branchiocephalic* artery. Ashley (1955) considers the *branchiocephalic* artery (innominate) as bifurcating to form two large branches each of which gives off two branches in close succession. In *T. triunguis*, however, the four arteries are quite separate and each has its own origin from the *innominate* artery.

(d) *Coronary Circulation* (Text-fig. 10, A and B)

1. *Arteries*

The *coronary* artery (cr. art.) may originate from the base of the *right subclavian* artery (sub. art. r.), or from the adjacent *innominate* artery. It runs in the fibrous sheath which surrounds the arterial arches, along their right side to the anterior border of the ventricle. The artery then bifurcates into a *ventral coronary* (cr. art. vent. b.) and a *dorsal coronary* artery (cr. art. dor. b.). The *ventral coronary* artery runs along the ventral side of the anterior border of the ventricle, and gives smaller branches which run down the ventral wall towards the apex. The *dorsal coronary* artery runs along the dorsal side of the anterior ventricular border and gives some branches to the dorsal wall of the ventricle, as well as right and left *auricular* branches to the posterior walls of the right and left auricles respectively (aur. l. cr. art.).

2. *Veins*

(*a*) Veins from the ventral wall of the ventricle run into a *ventral coronary vein* (cr. v. vent.) which runs at the ventral side of the anterior border of the ventricle adjacent to the corresponding coronary artery, and proceeds along the side of the main coronary artery to terminate in the *right anterior vena cava.*

(*b*) Three veins collect the blood from the right, the middle and the left parts of the dorsal wall of the ventricle. The left vein receives a *branch* from the posterior wall of the left auricle (aur. l. cr. v.) and the right from the right auricle. The three veins join together to form the *dorsal coronary veins* (cr. v. dor.) which passes through the pericardium and terminates in the *sinus venosus*. The dorsal coronary vein is protected by a strong fibrous sheath which also helps to fix the antero-dorsal border of the ventricle to the pericardium (Text-fig. 10, ligament).

(e) *Heart Beat*

In specimens freshly killed by chloroform, the heart continues to beat for a considerable length of time after the apparent death of the animal. Hearts removed from the body and placed in saline solution behaved in a similar manner. Johnson, Clinton & Stevens (1957) report a turtle heart beating 5 days after death.

The number of heart beats in several anaesthetized specimens (weight 4–26·5 kg.), varied between 16 and 29 per minute in different individuals.

The dorsal position of the sinus makes it very difficult to observe in the living animal. It may be reached by inserting a finger gently above the ventricle, but contractions of the sinus could not be felt by finger touch. Yet when the heart, together with the attached blood vessels and adjacent part of liver, had been removed from the animal and put in saline, the rhythmic contractions of the sinus were seen. The contractions were quite feeble, compared to the other chambers of the heart.

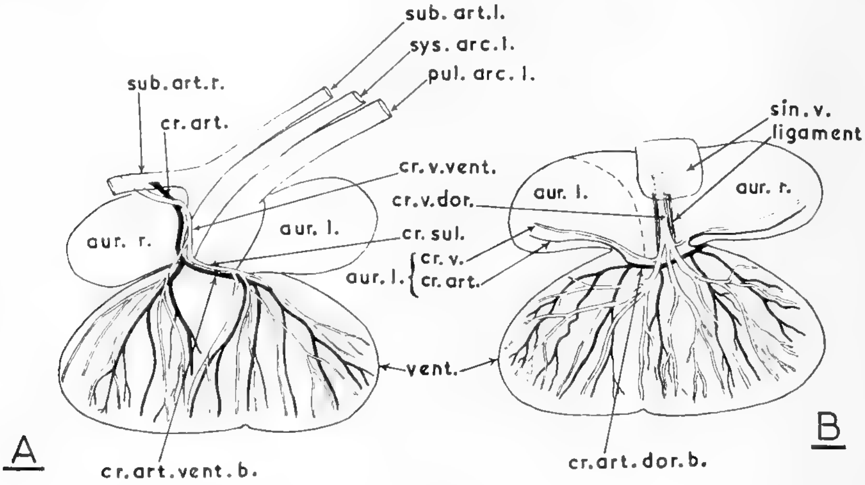

FIG. 10. *Cyclanorbis oligotylis.* Coronary circulation.

A. Ventral view.

B. Dorsal view.

aur. l., left auricle ; aur. r., right auricle ; aur. l. cr. art., left auricular coronary artery ; aur. l. cr. v., left auricular coronary vein ; cr. art., coronary artery ; cr. art. dor. b., dorsal branch of coronary artery ; cr. art. vent. b., ventral branch of coronary artery ; cr. sul., coronary sulcus ; cr. v. dor., dorsal coronary vein ; cr. v. vent., ventral coronary vein ; pul. arc. l., left pulmonary arch ; sin. v., sinus venosus ; sub. art. l., left subclavian artery ; sub. art. r., right subclavian artery ; sys. arc. l., left systemic arch ; vent., ventricle.

The two auricles beat simultaneously, and the ventricle follows immediately. Watching the movement from a ventral view, the auricles were seen to contract strongly at their antero-medial tip. Their middle and postero-lateral parts followed in quick succession, and simultaneously the dorso-ventral diameter shortened considerably, bringing the ventral wall nearer to the dorsal one. The ventricle contracted in a peculiar way. Its left side started the movements by an abrupt shortening of both longitudinal and vertical diameters, bringing the left part of the round apex forwards and slightly medial. The wave of contraction passed towards the right side which terminated the movements by a noticeably strong contraction. The ventricle remained in the contracted condition for a short while, its right side being slightly shorter than the left, and its deep red colour fading to a much paler shade. Beats succeeded one another regularly, a short pause following each ventricular systole.

While most workers agree that the rhythmic contraction of the heart is a specific immanent property of the cardiac muscle itself, there is some difference as to whether the muscle connecting the cardiac chambers has special histological characters which differentiate it from the general myocardium. Davies & Francis (1945) made a comprehensive review on heart contraction in poikilothermal and homiothermal vertebrates and showed that so far as the anatomical studies are concerned the more recent workers are in a reasonable agreement that there is no histological specialization of any part of the cardiac musculature in poikilothermal animals.

As regards the route of the contraction wave, the following work in the Chelonian heart is of special importance. Meek & Eyster (1912) used electrocardiographic methods and found that the wave passes over the heart from the sinus, right auricle, left auricle, base of the ventricle and apex of ventricle. Lowman & Laurens (1924) found that the right and left parts of the auriculo-ventricular funnel are more efficient than the dorsal and ventral for conducting the impulse to the ventricle. Ishihama (1927), by cutting parts of the auriculo-ventricular junction observed that the right and left lateral parts conduct the impulse most readily, the ventral part less easily, and the dorsal part and the atrial septum not at all. Lewis (1916), and Holzlöhner (1930) determined electrocardiographically in fish, amphibia and reptiles that the middle level of the ventricle is the first part to receive the stimulus from the atria, and that the wave of contraction proceeds thence towards the apex and base. Scholomovitz & Chase (1916) observed the effects of the localized warming, cooling, or electric stimulation and showed that the primary pacemaker is a definitely localized portion of the sinus wall, on the right side of the sinus-auricular junction.

(f) *Double Circulation in the Heart* (Text-fig. 11)

Oxygenated blood pours continuously into the left auricle and deoxygenated blood into the sinus venosus. The openings of the veins into these parts are not guarded by valves, contraction of the sinus drives the blood into the right auricle.

The sinu-auricular opening is guarded by a valve made of two flaps of tissue which, when the auricle becomes full, overlap and close the opening.

Contraction of the auricles drives the blood into an empty ventricle. The *auriculo-ventricular valves* play an important part in directing the course of the blood. Oxygenated blood passes through a short passage between the anterior border of the ventricle and the flap of tissue which forms the left part of the valve, and is directed to the extreme left aspect of the ventricle. The right side passage is longer but it does not take the blood all the way to the right end as its stops about half-way through the transverse diameter of the-ventricle. Nevertheless, its opening points to the right, and blood coming in jerks under pressure of contractions of the right auricle is pushed into the right side of the ventricle, dorsal to the inter-ventricular septum and around its free edge, into its goal, the cavum parvum (pulmonale) It was pointed out that the wall of the right auricle contained strong muscle fibres comparable with those of the ventricle. These muscles should provide the necessary force required to push the blood all the way through.

The cavum parvum (pulmonale) will thus be filled with nothing but deoxygenated blood. Its small volume as compared with that of the right auricle suggests that it cannot possibly accommodate all the deoxygenated blood received at each auricular systole. Therefore, some deoxygenated blood remains in the right side of the ventricle both in the ventral part outside the entrance of the cavum parvum (pulmonale) and in the dorsal part which is continuous with the cavum magnum (dorsale).

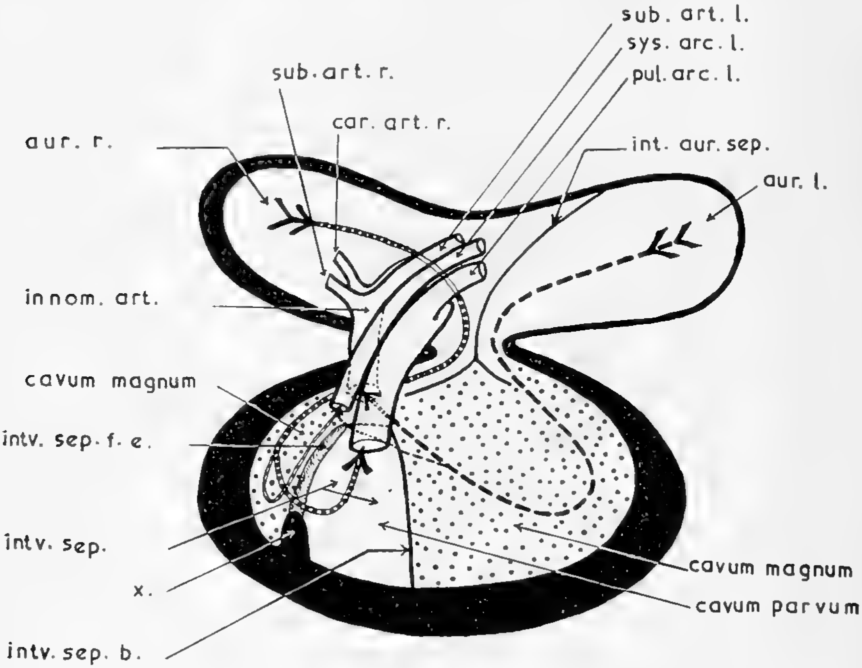

FIG. 11. *T. triunguis.* Diagram of heart and circulation, ventral aspect. Part of the cavum magnum lies under (dorsal to) the cavum parvum.

aur. l., left auricle ; aur. r., right auricle ; car. art. r., right carotid artery ; innom. art., innominate artery ; int. aur.sep., inter-auricular septum ; intv. sep., inter-ventricular septum ; intv. sep. b., base of inter-ventricular septum ; intv. sep. f. e., free edge of inter-ventricular septum ; pul. arc. l., left pulmonary arch ; sub. art. l., left subclavian artery ; sub. art. r., right subclavian artery ; sys. arc. l., left systemic arch ; x., secondary inter-ventricular septum.

Oxygenated blood is now at the left part of the cavum magnum and a considerable proportion of it finds its way to the numerous little cavities in the spongy wall of the ventricle. Mixing of the blood in the middle part of the cavum magnum is unavoidable.

The ventricle having been filled with blood, starts to contract :

1. The left part of the ventricle contracts first, driving its blood towards the right side. Consequently, blood in the right side is forced out of the ventricle into the arterial arches.

(*a*) Deoxygenated blood in the cavum parvum passes into the pulmonary arch, and is replaced by deoxygenated blood from just outside the cavum parvum.

(*b*) Deoxygenated and mixed blood pass into the left systemic arch.

(*c*) Maybe some mixed blood from the middle part, and for the most part oxygenated blood from the left part of the cavum dorsale, pass into the right systemic arch.

2. The right side of the ventricle contracts strongly, while the left side remains in the contracted position until the blood is expelled. Judging by the colour of the ventricle in this condition, very little, if any blood remains trapped in the spongy cavities of its wall.

(*a*) Deoxygenated blood in the cavum parvum passes out through the pulmonary arch. The wall of the ventricle comes in contact with the edge of the inter-ventricular septum cutting off the cavum parvum from the rest of the ventricle.

(*b*) Mixed and maybe some oxygenated blood pass through the left systemic.

(*c*) Oxygenated blood passes through the right systemic. The oxygenated blood in the cavities of the left side of the spongy wall has little chance to mix with deoxygenated blood and is the last blood to leave the ventricle.

To summarize :

The pulmonary arch receives deoxygenated blood, the left systemic receives mixed blood ; and the right systemic receives some mixed and for the main part, oxygenated blood.

THE HEART OF *CYCLANORBIS OLIGOTYLUS*

The heart is similar in its main features to the heart of *T. triunguis* but the following differences were noticed :

1. *Position of the Heart*

The heart lies nearer to the sagittal axis of the body which passes through the left side of the left auricle.

2. *Pericardial Cavity*

The cavity is much larger in *Trionyx*. The carapace in *Cyclanorbis* is more convex and therefore the dorso-ventral axis at the site of the heart is deeper in *Cyclanorbis* and allows for a deeper cavity. In a medium-sized specimen (length of carapace 23 cm.) 25 c.c. of pericardial fluid were extracted from the cavity, while 11·5 c.c. only were obtained from a comparable specimen of *Trionyx*.

3. *External Appearance*

The apex of the ventricle is not bluntly rounded especially during systole, but has a flat appearance with an obvious notch which lies slightly to the right side of the medial axis (Text-fig. 12). The hearts of the two species are, therefore, quite easily differentiated from one another.

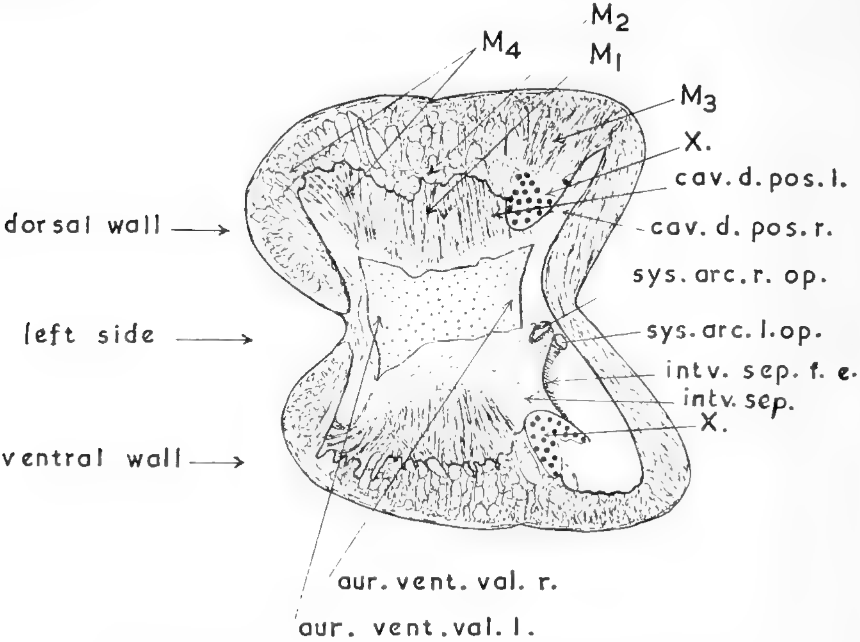

FIG. 12. *C. oligotylis.* Ventricle opened horizontally from apex and sides, internal view. The secondary inter-ventricular septum divides the posterior part of the cavum magnun (c. dorsale) into right and left cavities. The cavum parvum (c. pulmonale) lies ventral to the inter-ventricular septum and is not in view. Most of the antero-posterior muscle fibres are continuous around the apex where they are intermingled with some dorso-ventral muscle fibres and some white fibres inserted in the outer coat.

aur. vent. val. l., left auriculo-ventricular valve; aur. vent. val. r., right auriculo-ventricular valve; cav. d. pos. l., posterior part of cavum dorsale, left cavity; cav. d. pos. r., posterior part of cavum dorsale, right cavity; intv. sep., inter-ventricular septum; intv. sep. f. e., free edge of inter-ventricular septum; M1, antero-posterior muscle fibres; M2, continuation of antero-posterior muscle fibres around apex; M3, right posterior to antero-medial muscle fibres; M4, left posterior to antero-medial fibres; sys. arc. l. op., opening of left systemic arch; sys. arc. r. op., opening of right systemic arch; x, secondary inter-ventricular septum.

4. *Internal Structure* (Text-fig. 12)

A prominent muscular secondary septum (x) divides the posterior part of the cavum magnum (dorsale) into a larger left portion (cav. d. pos. l.), the *cavum sinistrum*, and a much smaller right one (cav. d. pos. r.), the *cavum dextrum.* The septum starts as a few bands of muscular and fibrous tissue which originate from the posterior wall near the dorsal right corner of the apex of the ventricle and run antero-medially and ventrally towards the posterior end of the free edge of the interventricular septum. Here the fibres aggregate to form a fairly thick band which is further enlarged by additional bands which run in a dorso-ventral direction and join the main bulk at its left side. A secondary septum is thus formed which extends between the dorsal, ventral and posterior walls.

From the edge of the secondary septum the fibres spread fanwise as they proceed anteriorly in the ventral wall of the ventricle to terminate in the anterior border of its base. The spreading out of the fibres reduces their depth and leaves a clear anterior passage between the left and right sides of the ventricular cavity.

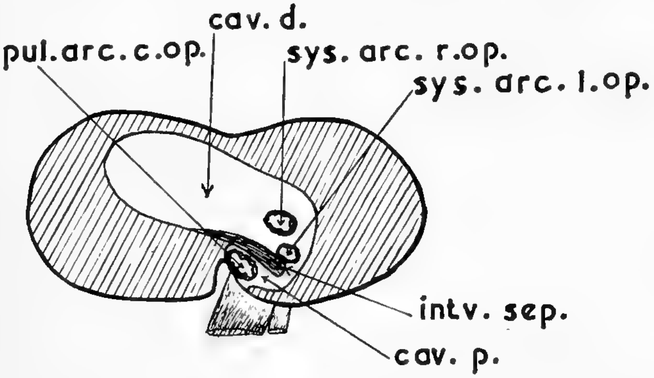

FIG. 13. *C. oligotylis.* Posterior view of a dorso-ventral section in the anterior part of the ventricle to show the openings of the arterial arches in the ventricular cavities.

cav. d., cavum dorsale; cav. p., cavum pulmonale; intv. sep., inter-ventricular septum; pul. arc. c. op., opening of common pulmonary arch; sys. arc. l. op., opening of left systemic arch; sys. arc. r. op., opening of right systemic arch.

The secondary septum in *T. triunguis* is less prominent and is nearer to the posterior wall, so that the division of the cavum magnum posteriorly into two cavities is not as sharp and clear as in *C. oligotylus.*

The position of the openings of the arterial arches (Text-fig. 13) shows no difference from *T. triunguis.*

5. *Heart Beat*

The two auricles contract in the same way as in *T. triunguis* driving the blood to the ventricle, which enlarges considerably. Ventricular systole follows; the left side of the ventricle contracts first and the right side immediately afterwards, the whole ventricle remaining in the contracted condition for an interval during which its wall changes colour from dark red to pale pink as blood drains out. Heart beats succeed one another in the same way. The number of beats varied between 19 and 21 per minute in five specimens but in each case the animal was injected with 5 c.c. of chloroform and opened after its apparent death. The counting, therefore, was not done under normal conditions.

The main difference from *T. triunguis* is the noticeable separate contraction of each of the two sides of the ventricle, while in *Trionyx* there is one long wave of contraction which starts at the left side and terminates at the extreme right.

6. *Circulation*

Separation of the oxygenated and deoxygenated blood seems to be more effective than in *T. triunguis*. In addition to the numerous little cavities in the muscular wall of the ventricle which accommodate a certain proportion of blood, a round opening near the left auriculo-ventricular opening leads to an irregular cavity within the ventral wall of the ventricle, and, judging by the position and size of this cavity it holds a fairly large quantity of oxygenated blood. Blood within the cavities in the wall has no chance to mix until it passes out into the main ventricular cavity on its way to the arterial arches.

The *secondary interventricular septum*, by dividing the posterior part of the cavum magnum into right and left cavities, is another factor in minimizing the mixing of the two types of blood. The deoxygenated blood pushed into the ventricular cavity passes to the right side of the secondary septum into the right cavity as well as around the free edge of the original septum into the cavum parvum (pulmonale). Blood in the right cavity has free access to the cavum parvum (pulmonale). However, as the secondary septum does not extend to the anterior border of the ventricle, some mixing of blood is bound to happen.

6. *Abnormalities*

Some individual differences were noticed in a number of specimens, for example :

(*a*) A thread-like fibrous ligament (gubernaculum cordis) extended between the dorsal side of the ventricle near its apex to the antero-dorsal part of the pericardium. Its length was over double the length of the heart.

(*b*) The dorsal coronary vein in a specimen had its three main branches running separately, only joining each other just before entry of the vein into the sinus venosus. These branches normally combine before the vein leaves the ventricle.

(*c*) The fibrous ligaments which join the antero-dorsal border of the ventricle to the pericardium vary in number and do not always follow the same pattern. Occasionally, ligaments have been found between the auricle and ventricle.

Oxygen Saturation in the Right and Left Systemic Arches, the Pulmonary Arch and the Two Auricles

Little experimental work has apparently been done on the circulation of reptiles. Prakash (1952) used radiological methods in the lizard *Uromastyx hardwickii* and stated that there is very considerable mixing of arterial and venous blood in the heart. Foxon & Price (1953) state (in a preliminary report) that radiographic experiments indicate, in *Lacerta viridis*, the existence of considerable separation of the arterial and venous streams of blood and that probably there is little difference in the type of blood conveyed by right and left systemic arches. Foxon (1955) states, in an addendum to the paper, that the results of using improved radiographic methods confirm the view that there is considerable separation of arterial and venous blood in the ventricle, but they also show a functional division of the cavum dorsale of the ventricle which results in the right systemic artery conveying more highly oxygenated blood than the left. Yet Steggerda & Essex (1957) in the turtle *Chelydra serpentina* having recorded oxygen saturation, blood-saturation dye curves and pressure measurements in the cardiac chambers and arteries leaving the heart, state that the *saturation levels of the blood leaving the heart via the right and left aortae are the same* while pulmonary artery blood is distinctly more venous.

The description of heart circulation in the previous chapter was based on anatomical features alone, but the conflicting results given by Steggerda & Essex necessitated the addition of a very short " experimental " part to investigate this point.

Method. Experimental animals were of the large size whenever possible as 25 ml. of blood were required to be drawn from each. The animal was subjected to mechanical insufflation at the rate of 15 times a minute. The amount of ventilation was adjusted so that with each cycle there was a noticeable raising and lowering of the ventral body wall and heart. This was allowed to continue for at least 20 minutes before samples of blood were taken.

A lightly oiled, 10 ml. syringe was used and its dead space was filled with oxalate solution made as follows : 4 g. potassium oxalate + 6 g. ammonium oxalate in 100 c.c. water. Heparine solution 1/1,000 as used for blood of mammals was tried but failed as blood was found to clot after some time. Blood was drawn from the three arteries, one at a time, and then from each auricle in the order shown below, but samples from the auricles were not taken when the heart did not contain enough blood to give a slow but steady supply to the syringe. Blood samples were collected in polythene bottles under oil.

> *Sample* 1. The base of the left subclavian was pricked, and the needle driven into the innominate artery (see Text-fig. 9). The sample represents the right systemic.
> *Sample* 2. From the base of the left systemic.
> *Sample* 3. From the common pulmonary arch.
> *Sample* 4. From the right auricle.
> *Sample* 5. From the left auricle.

The samples were analysed in the Department of Physiology, Faculty of Medicine, University of Khartoum, by the electrophotometric method. Results were later reported to the writer, signed by the analyst of the Department (Dr. Nasr El Din)—see Table I.

Conclusion

(1) Oxygen saturation in the right systemic artery is higher than in the left, and in the left systemic artery higher than in the pulmonary.

(2) Oxygen saturation in the pulmonary arch is slightly higher than in the right auricle, which shows that a small quantity of oxygenated blood mixes with venous blood as it passes through the heart.

TABLE I.—*Oxygen Saturation in the Three Aortic Arches and the Two Auricles of* Trionyx triunguis

Experiment No.	Weight in kg.	Number of beats per minute	% oxygen saturation				
			pulm.	l. sys.	r. sys.	r. aur.	l. aur.
1	5·14	16	55	80	95	50	95
2	5·08	16–17	60	85	97	50	97
3	2·19	16	55	78	90	45	—
4	7·55	17	52	70	85	50	86
5	8·65	22–0	—	—	—	—	—
6	26·66	28	55	60	90	50	95
7	5·57	20	33	55	80	—	—
8	11·10	20–21	55	78	85	53	85
9	4·14	29	30	45	70	—	—
10	14·32	22	50	70	82	—	—
11	17·95	23	55	60	85	45	85
Average saturation in 10 experiments			50	68·1	85·9	—	—
Average in 6 experiments where samples from both auricles were taken. Nos. 3, 7, 9 and 10 exlcuded			55·3	72·1	89·5	49·7	90·5

(3) Oxygen saturation in the left auricle is very slightly higher than in the right systemic, which shows that practically all oxygenated blood passes into the right systemic.

These results agree with anatomical findings. The statement of Steggerda & Essex (1957) that saturation levels of the blood leaving the heart via the right and left aortas are the same could *not* be true for *Trionyx*.

DISCUSSION

1. *Position of the Heart*[1]

Kaushiva (1940) points out that he was the first person to note the asymmetric position of the heart and the elongation of the anterior arteries of the left side in the Indian turtle *Lissemys punctata*, but Ahsan Al-Islam & Iftikhar Hamid (1951) gave the credit of this recording to Dhillon (1938), but did not cite the literature. According to Mathur (1946) such a displacement and tilting is probably due to the retractility of the neck into the antero-medial part of the trunk. Ahsan-Al-Islam & Iftikhar Hamid (1951) disagree with Mathur's explanation on the ground that in the common turtle (not named) " whose neck is notoriously contractile ", the heart and anterior blood vessels were perfectly symmetrical. They do not offer an alternative explanation but state that this can be proved only by a study of development and by comparative anatomy of different types of turtles and tortoises.

[1] It is important to emphasize here that this work would not have been satisfactorily done if not for the specimens provided by the British Museum (Natural History) London. Representatives of the family Trionychidae are scattered over vast areas of Temperate and Tropical waters. No worker can possibly collect enough species to study a family characteristic. The Museum provided these as well as a well-equipped laboratory, a rich library and on top of all a nice and friendly atmosphere.

It has been shown in this work that the peculiar asymmetric position and tilting of the heart are found in all genera of the family Trionychidae and should, therefore, be considered a general characteristic of the family.

Retractility of the neck could not be the only reason for the displacement of the heart as suggested by Mathur (1946). It is well known that all the subclass Cryptodira, with the exception of the one family Trionychidae, possesses both contractile necks and symmetrical hearts. It seems reasonable to assume that the shifting of the heart is due to two combined factors—the absence of either of which would result in a symmetrical heart. These factors are :

(1) The retractility of the neck which necessitates the presence of bulky muscular tissue at the mid-longitudinal axis of the body.

(2) The reduction of the dorso-ventral axis of the body at the sagittal plane, the carapace being flat or slightly convex, and as near the plastron as possible. The animal is thus provided with a streamlined body which is essential for a good swimmer. The medial part of the body-cavity would not have enough room for both muscle and heart, and the latter has to find accommodation somewhere else. The choice is very limited since the cavity on the left side of the base of the neck is occupied by a dilated portion of the oesophagus and the only possibility is at the right side of the base of the neck.

The following examples show that the two factors combined are necessary for the shifting of the heart :

(a) *Testudo graeca* Thomson (1932). The neck is quite retractile. The missing factor is the carapace which is dome-shaped and forms a high roof at the medial part of the body. The heart here is perfectly symmetrical.

(b) *Chelys fimbriata* (B.M. 97.5.15.1, from Trinidad). A freshwater turtle with a carapace slightly convex and a dorso-ventral diameter comparable to that of *Trionyx*. The missing factor is the neck, which is not retractile. Dissection of the specimen showed a symmetrical heart.

To emphasize the above-mentioned theory, it has been shown that in *Cyclanorbis*—the only *Trionychid* with a comparatively more convex carapace—the heart lies nearer to the sagittal axis of the body, which actually passes through the left auricle.

Explanation of the tilting of the heart has not been attempted before. It occurs later in life since the new hatches examined had the mid-longitudinal axis of the heart parallel to that of the body. Owing to the position of the heart at the right side, arteries running to the left side of the body extent horizontally ventral to the base of the neck, while those of the right side proceed roughly in an anterior direction (Text-fig. 1). It is quite possible that the rapid growth of the muscles at the base of the neck exert a pushing pressure on the left arteries, and the latter in their turn would pull at the antero-left side of the ventricle where they are attached and cause the tilting. The right side arteries extend anteriorly and are not in a position to give an opposite and equal pulling pressure to stop such tilting.

2. *Structure of the Heart*

The division of the cavum grandum (dorsale) into a cavum sinistrum and a cavum dextrum by a complete partition in the posterior part of the ventricle, as stated by

Mathur (1946) in *Lissemys punctata*, agrees with the condition as found in *C. oligotylus*, but is different from that in *T. triunguis*, where the septum is too short to form an effective partition.

O'Donoghue (1918) divides the ventricle into a right ventro-lateral " cavum venosum ", and a left dorso-lateral " cavum arteriosum ", with an almost entirely separate division of the former, " the cavum pulmonale ". Goodrich (1919) and other authors use the same terms but consider them as three, and not two cavities. It was considered preferable to use descriptive terms for naming the cavities, as was done by Foxon (1955), rather than using terms based on their supposed function. The term " cavum pulmonale " used by Huxley (1871) is appropriate because the cavity is closely associated with the pulmonary artery. Huxley (1871) makes the main division of the ventricle that by the auriculo-ventricular valve into cavum venosum and cavum arteriosum. Parker & Haswell (Sixth edition, pp. 413–414), likewise divide " the left-hand portion which is much the larger " imperfectly into the cavum arteriosum on the left and the cavum venosum on the right, " by the two elongated flaps of the auriculo-ventricular valve, which project freely into the cavity of the ventricle ". This division could not be justified as it is obvious that during ventricular systole, the flaps of the valve are pushed forwards and adhere to the auriculo-ventricular openings, and the supposed cavities disappear.

Division of the ventricle according to the incomplete inter-ventricular septum is the only reasonable basis for division. The two cavities resulting are not comparable in size. The terms " cavum magnum " and " cavum parvum " instead of " dorsale " and " ventrale " or " pulmonale " would probably give a more accurate description of these cavities which are in fact neither quite dorsal nor quite ventral.

Thomson (1932) states that the inter-ventricular septum is, to some extent, continuous with the inter-auricular septum. This is definitely not the case in the two species examined by the author, where there is no continuity or relationship between the two septa.

Goodrich (1916 : 271) says that the inter-ventricular septum *in reptiles* divide the chamber into a left cavity leading to the base of the right systemic arch, and a right cavity leading not only to the base of the pulmonary but also to that of the left systemic arch. It is probably better not to generalize reptilian hearts where we have three different types in Lizards, Chelonians, and Crocodiles with major differences between them. As far as Chelonians are concerned, the bases of the pulmonary and left systemic arches do not belong to the same cavity. During systole, the ventricular wall is drawn into the free edge of the inter-ventricular septum blocking the cavum parvum (pulmonale) and pulmonary arch entirely from the rest of the ventricle, but the base of the left systemic lies outside the septum and it draws blood from the main large cavity. Again, the latter cavity does not lead to the base of the right systemic arch alone as in the above statement but also to the base of the left systemic. Karandikar & Kashyap (1956) describe a generalized reptilian heart which differs in shape and in the openings of the arteries from the Chelonian heart.

Ewer (1950) puts forward the view that the left systemic in reptiles persists as a mechanical necessity—a safety valve to take away into the systemic circulation blood which could not be accommodated in the vessels of the lungs. This explanation would assume that the greater part of the blood conveyed in this vessel is deoxygenated.

The diagram of Goodrich (1919) illustrating Chelonia, Lepidosauria and Rhyncocephalia is rather misleading for the Chelonia because :

(*a*) It shows the two auricles opening in both cavities of the ventricle, while actually they open into one (the magnum, dorsale or left cavity).

(*b*) The incomplete inter-ventricular septum is shown as an extension of the inter-auricular septum, which is not the case.

(*c*) The pulmonary does not come out of a special compartment of the ventricle.

Goodrich (1919) also states that " whereas in the Chelonia, as in the Crocodilia, the left arch receives most of its blood from the cavum pulmonale, in the Lacertilia and Ophidia it opens more dorsally so as to receive arterial blood as well ". The writer agrees that the opening is situated in a region of the ventricle which contains deoxygenated blood, but it is not cut off from the main cavity with its mixed and oxygenated blood. It is so close to the opening of the right systemic, although slightly ventral and more to the right, that it inevitably receives some oxygenated blood. This view was confirmed by estimation of the percentage of oxygen saturation in blood samples taken from the right and left systemic arches, the pulmonary artery and the two auricles (Table I).

Von Hofsten (1941) emphasized the importance of the origin of the left systemic arch in relation to the ventricular septum. Whether this arch receives blood from one ventricle or the other, or even a mixture from both, would depend on this relationship. His diagram for the Chelonian type of heart shows the pulmonary and left systemic arches originating from one chamber, which is not strictly correct. The inter-ventricular septum is shown sloping towards the left side instead of the right, and its free margin should be opposite the right and not the left wall, so that blood would pass dorsal to the septum and around its free border into the right (parvum or pulmonale) portion of the ventricle.

From the evolutionary point of view, possibly the Chelonian heart may be an end line in itself which could not have led into the four-chambered avian heart. As Foxon (1955) states, " the completion of the ventricular septum must be achieved not only so that the arterial and venous blood are distributed to the correct arteries, but also so that the left and right divisions of the auricle open into the corresponding ventricle ". There are two possible ways for the complete division of the ventricle in the Chelonian heart :

(*a*) If the inter-ventricular septum extended to the opposite wall, then both auricles would open into one ventricular cavity (the magnum, dorsale or left) and circulation would not be possible.

(*b*) If the secondary septum developed as suggested by Goodrich (1919), " by the growth from behind forwards of a new muscular septum differentiated from the muscular strands which unite the base of the old septum with the dorsal wall of the ventricle ", then the openings of the arterial arches would all be on one side (the right ventricle), and again circulation would not be possible.

There is still the possibility that simultaneously with the development of Goodrich's secondary septum, the right systemic may have changed its position and extended to the left of the new septum. An avian four-chambered heart would thus be developed.

3. *Experimental*

The short experimental part added to find out whether the heart circulation—as predicted by a study of the heart beat, the ventricular cavities and the relation of the arterial arches to the latter —was correct or otherwise, gave some interesting results.

Broadly speaking it may be said that it confirms the well-known and accepted theory that oxygen-saturation is higher in the *right systemic* artery than in the *left*, and in the latter than in the *pulmonary*. It is worth noting that the *pulmonary arch* contains a slightly higher oxygen-saturation than the right auricle, thus some slight mixing takes place in the ventricular cavities during passage of the blood from the right auricle to the *pulmonary arch* as shown by Steggerda & Essex (1957).

Again oxygen-saturation in the *right systemic arch* is only slightly lower than in the left auricle, which shows that in spite of the incomplete division of the ventricle into two chambers, the system is quite efficient in providing the head with highly oxygenated blood. Even in species where a *ductus arteriosus* connects the pulmonary artery on either side with the corresponding systemic artery—Bojanus (1819-21), O'Donoghue (1917) and Mathur (1946)—the ductus arteriosus opens a long way beyond the exit of the *innominate* artery which supplies the anterior arteries.

It is important to record that an open " *ductus arteriosus* " is not a constant feature of turtles. It was found as a vestige of connective tissue by Thomson (1932) in *Testudo*, and by Girgis (1960) in *Trionyx*. An open *ductus arteriosus* would cause mixing of the venous blood with that of the right and left systemics. It is therefore of great importance to note the presence or otherwise of an " open " *ductus arteriosus* in any Chelonian when the question of oxygen saturation in the two systemics is dealt with. It would be interesting to know whether *Chelydra serpentina* possess an " open " *ductus arteriosus* or not as this would throw some light on the oxygen saturation in the two aortae given by Steggerda & Essex (1957).

SUMMARY

1. In the Trionychidae the heart lies at the anterior right part of the abdominal cavity. It is tilted so that its mid-longitudinal axis forms an acute angle with the mid-longitudinal axis of the body.
2. As a result of the situation of the heart, the left anterior arteries and veins are considerably longer than the right.
3. The asymmetrical position of the heart is shown to be a general characteristic of the family Trionychidae and it may have resulted from the retractility of the neck, combined with shortness of the dorso-ventral axis to facilitate swimming. In *C. oligotylus* where the carapace is more convex, the heart lies nearer to the sagittal axis.
4. The sinus venosus lies outside the pericardium on the dorsal side.
5. The right auricle is larger than the left, and both auricles open on the left side

of the ventricle. The openings are guarded by valves which help to direct the course of the blood within the ventricle.

6. The ventricle is incompletely divided by an oblique septum into a dorso-lateral " cavum magnum " and a ventro-lateral " cavum parvum ". The cavum magnum is divided at its posterior part by a secondary septum into left and right cavities. The secondary septum is prominent in *Cyclanorbis oligotylus*, and short and insignificant in *Trionyx triunguis*.

7. The opening of the common pulmonary arch lies in the cavum parvum, that of the left systemic arch in the antero-ventral wall outside the cavum parvum, and that of the right systemic arch in the dorsal wall, anterior and slightly medial to the opening of the left systemic.

8. The pulmonary arch receives deoxygenated blood, the left systemic arch mixed blood and the right systemic oxygenated blood.

9. The arterial arches and their branches are followed until they have passed through the pericardium.

10. The veins entering the sinus venosus and the left auricle are described.

11. Coronary arteries and veins are described.

12. A description of the beating of the heart and the double circulation is given.

13. The hearts of *Trionyx triunguis* and *Cyclanorbis oligotylus* are compared.

14. Analysis of samples of blood in the three arches and in the two auricles confirm anatomical findings.

15. A general discussion follows.

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CHILEAN SPECIES OF THE GENUS *EUPSOPHUS* (ANURA:LEPTODACTYLIDAE)

ALICE G. C. GRANDISON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 8 No. 3
LONDON : 1961

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Pp. 111–149 ; *Plates* 1–7 ; 22 *Text-figures* ; 1 *Map*

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CHILEAN SPECIES OF THE GENUS *EUPSOPHUS* (ANURA : LEPTODACTYLIDAE)

By ALICE G. C. GRANDISON

EUPSOPHUS Fitzinger, 1843, *Syst. Reptilium*, p. 31

Type species *Cystignathus roseus* Duméril & Bibron

THE name *Eupsophus* was pointed out by Parker (1932) to be an available generic name for the species formerly assigned to *Borborocoetes* Bell, the latter name being preoccupied. Boulenger (1882) in his key to the genus *Borborocoetes* divided the component species into two groups according to the presence or absence of a tympanum. Three species, all occurring in Chile, *calcaratus*, *maculatus* and *coppingeri*, were included under the heading of " no tympanum " and he recognized ten Chilean species, one of which was tentatively referred to the genus. As currently classified (Nieden, 1923) the genus is divided into eleven species, six of which occur in Chile. These six species with their ranges are given by Nieden as :

E. grayi (Bell)	Chile.
E. masareyi (Roux) . . .	Coronel (Chile).
E. roseus (Duméril & Bibron) .	Chile to Ecuador.
E. taeniatus (Girard) . . .	Chile.
E. calcaratus (Günther) . .	Chiloé I., Chile.
E. coppingeri (Günther) . .	West coast of Patagonia.

The changes that he proposed involved placing *E. maculatus* (Günther) and *E. bibroni* Bell in the synonymy of *E. grayi* (Bell) and *E. nodosus* (Duméril & Bibron) in the synonymy of *E. roseus* (Duméril & Bibron).

The primary division of the key that he devised for the genus was again based on the " presence " or " absence " of a tympanum but only *calcaratus* and *coppingeri* were said to lack the structure. Although Nieden considered *maculatus* to be conspecific with *grayi* he did not report on the condition of the middle ear in these species nor did he give his reasons for believing them to be synonymous.

Ambiguous and misleading terminology such as tympanum hidden, tympanum invisible and tympanum indistinct were a common fault of early descriptions and keys and led workers to assume that the structure is present beneath the skin and that only externally are the tympanum and tympanic annulus invisible. Even as recently as 1959, Schmidt & Inger remark on the inadequacy of the term " tympanum hidden " and have found by dissection that in species described as having a hidden tympanum some lack the tympanum and associated structures while others possess a complete ear apparatus, although external signs are concealed by a covering of thick skin. Boulenger used the term " no tympanic disk ", which being a more precise statement suggested that the three species of *Eupsophus* mentioned above do in fact lack the structure but an examination of the type specimens concerned revealed that the skin covering the ear region had not at any time been reflected in any of the specimens and it was obvious that Boulenger had not checked this character. It was therefore considered advisable by the writer to investigate the condition of the middle ear of all the Chilean species of *Eupsophus* and to present a comprehensive and critical revision of the group.

ACKNOWLEDGEMENTS

It is a pleasure to express my appreciation to the numerous colleagues at various institutions who have assisted me by supplying information concerning specimens of *Eupsophus* in their care and by lending material. Among these are : Mr. C. M. Bogert, American Museum of Natural History, New York ; Dr. R. F. Inger, Chicago Natural History Museum ; Dr. E. E. Williams, Museum of Comparative Zoology, Harvard ; Monsieur J. Guibé, Muséum National d'Histoire Naturelle, Paris ; Dr. L. Forcart, Naturhistorisches Museum, Basel ; Dr. R. Mertens, Senckenbergische Naturforschende Gesellschaft, Frankfurt a. M. ; Dr. W. Hellmich, Zoologische Sammlung des Bayerischen Staates, München ; Professor H. Brattström, University of Bergen and Dr. Y. Löwegren, Zoologiska Institution, Lunds Universitets. My warmest thanks go to Dr. L. D. Brongersma, Rijksmuseum van Natuurlijke Historie, Leiden, and Mrs. Brongersma for the facilities and hospitality accorded me during my visit to Leiden and to Dr. J. Eiselt, Naturhistorisches Museum, Vienna for his kind and generous assistance and the innumerable favours granted me while working at his institution. It is not possible to express adequately my appreciation of the encouragement and aid given me by Dr. I. Griffiths, who also generously prepared histological sections and alizarine preparations, and by Dr. H. W. Parker. Dr. Parker's criticism of the manuscript is also gratefully acknowledged.

The following abbreviations are used :

A.M.N.H.	American Museum of Natural History, New York.
B.M.	British Museum (Natural History), London.
C.N.H.M.	Chicago Natural History Museum.
M.C.Z.	Museum of Comparative Zoology, Harvard College, Cambridge.
M.H.N.P.	Muséum National d'Histoire Naturelle, Paris.
N.H.M.V.	Naturhistorisches Museum, Vienna.
R.N.H.L.	Rijksmuseum van Natuurlijke Historie, Leiden.
R.S.E.	Royal Society Expedition to Southern Chile.
U.B.	University of Bergen.
Z.I.L.U.	Zoologiska Institution Lunds Universitets.
Z.M.B.	Zoologisches Museum, Berlin.

METHODS AND TERMINOLOGY

During the course of this study 473 alcohol-preserved specimens and one skeleton were examined and for each species young, half-grown and adult examples of both sexes were available. Sexual maturity was determined in males by the presence of secondary sex characters and in females by the presence of a thickened, strongly convoluted oviduct or mature ovarian eggs. In a number of individuals an examination of histological sections of the testis was the means for determining the height of sperm activity and the order in which the secondary sex characters developed and regressed. The drawings of the pectoral girdle were based partly on gross anatomy and partly on stained serial sections of the epicoracoid and sternal region.

Critical measurements were made by dial calipers reading to 0·1 mm. and were as follows :

Length of body (total length) : tip of snout to tip of urostyle.

Head length : the distance from the tip of snout to the posterior rim of the tympanum. In those species having no visible tympanum the head length was taken from the tip of the snout to the jaw articulation.

Head width : the greatest width of the head, usually at the position of the tympani.

Length of tibia : the distance from the convex surface of the knee to the tibio-tarsal joint, the measurement being taken with the leg in the flexed position.

Length of foot : the distance from the tip of the fourth toe to the proximal edge of the inner metatarsal tubercle.

Interorbital space : essentially the width of the frontoparietals between the orbits.

Muscle terminology is that of Gaup (1896).

Eupsophus coppingeri (Günther)

(Text-figs. 1–5 ; Pls. 1 and 6)

Cacotus coppingeri Günther, 1881, p. 19 (type locality, Port Rio Frio, west coast of Patagonia).
Borborocoetes coppingeri Boulenger, 1882, p. 257, pl. 17, fig. 2.

MATERIAL EXAMINED

CHILE :

Llanquihue Province : Casa Pangue, 1,000 ft. (frontier station below the Perez Rosales Pass, wet forest), B.M. 1927.5.7.6–8 ; Peulla, south shore of Lake Todos Los Santos (wet forest), B.M. 1927.5.7.75.

Malleco : Cordilleras de Pemehue, C.N.H.M. 48546–48550 ; Cabreria 800 m., Nahuelbuta, Angol, C.N.H.M. 44210–44214, 44216–44219 ; Nahuelbuta, Angol, C.N.H.M. 40132 (6 exs.).

Magallanes : Termas de Tolhuaca, 3,500 ft., C.N.H.M. 6256 ; Puerto Edèn, east side of Wellington Island, A.M.N.H. 52884 ; Puerto Rio Frio, east side of Wellington Island, west coast of Patagonia, B.M. 80.7.28.14 (1947.2.19.97) (type of *Cacotus coppingeri*) ; Peninsula Munoz Gamero 100 m., R.S.E. (1 ex.) ; plateau below S. Peak, Puerto Edèn, 2,100 ft. R.S.E. (1 ex.).

ARGENTINE :

Rio Negro : Bariloche, south shore of Lake Nahuel Huapi, B.M. 1958.1.3.97–98, A.M.N.H. 23943–4, Z.M.B. 29470, N.H.M.V. 4670.1–8, N.H.M.V. 2278 (skeleton ♀), N.H.M.V. no register number (1 ex.) ; San Martin de Los Andes, N.H.M.V. no register number (3 exs.).

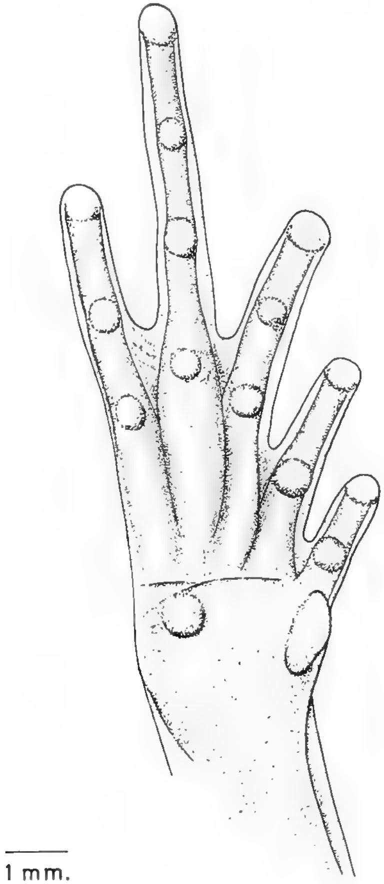

FIG. 1. *E. coppingeri*, C.N.H.M. 48548. Ventral view of the foot. (× 17·5.)

DIAGNOSIS. A large toad-like species (adult females 47–60 mm. ; adult males 42–54 mm.), thick set, stocky build, with short, blunt snout ; head as broad as, or slightly broader than long ; vomerine teeth in two, long, strong, widely separated, posteriorly converging arcs between the choanae ; first finger not longer than second ; toes $\frac{1}{3}$ to $\frac{1}{4}$ webbed, fringed and flattened ; subarticular tubercles prominent and conical; strong tarsal fold; skin of adults pitted, glandular and sometimes with low, glandular swellings; no middle ear; muture males with large nuptial pads on first and second fingers bearing conspicuous horny spines, also round patches of asperities on each side of chest; no vocal sacs.

DESCRIPTION. Adult female, Cabreria 800 m., Nahuelbuta, Angol, C.N.H.M. 44219. Habitus stocky. Tongue broadly rounded, its posterior half free and with only a faint indication of a notch; a very narrow seam forming a frill round the edge of the tongue. Vomerine teeth in two very strong, only slightly oblique groups close to inner edges of anterior borders of the semicircular choanae and widely separated from each other by a distance equal to $1\frac{1}{2}$ times the width of one of the choanae. Snout short, rounded in dorsal view, $\frac{2}{3}$ the horizontal diameter of the eye, rounded rather than truncate in profile, the upper jaw extending a little beyond lower jaw. Nares more lateral than dorsal, slightly projecting, the distance between the middle of the nares equal to the interorbital space which is as broad as the upper eyelid, their distance from the anterior borders of the eyes almost twice their distance from the tip of the snout. Canthus rostralis curved but rather indistinct;

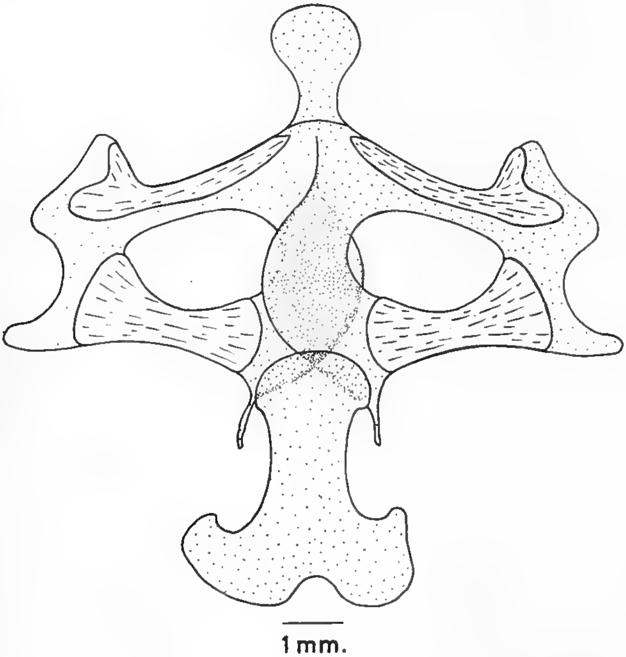

FIG. 2. *E. coppingeri*, B.M. 1958.1.3.97. Ventral elements of the shoulder girdle. (× 17·5.)

loreal region flat and oblique, upper lip flaring out only slightly below ; eye large and prominent, scarcely projecting beyond the jaws in dorsal view. Tympanum, tympanic annulus, cavum tympani and columella stapes absent ; eustachian tubes reduced to minute foramina. Well-developed glandular fold from behind the eye to the insertion of the arm ; at right angles to this fold and continuing laterally and ventrally a pronounced skin fold which passes on to the chest on a level with the clavicles, divided from its fellow by a space equal to the distance between the nares. Omosternum cartilaginous, very short stem and strongly dilated tip ; sternum cartilaginous, 2¼ times the length of the omosternum, of moderate width medially, broadly expanded posteriorly, deeply emarginate, a reversed broad upsilon in shape, only very slightly shorter than epicoracoids. Tibio-tarsal articulation of the adpressed hind limb reaches to the posterior border of the eye. Limbs sturdy, fingers free of web, first finger shorter than second, subarticular tubercles prominent, supernumerary palmar tubercles present. Tips of fingers and toes rounded, with simple terminal phalanges. Length of foot approximately 1⅕ times length of tibia. Toes with reduced webbing, the following number of phalanges on the different toes free from web :

1st toe (external surface)	2
2nd toe (external surface)	2
3rd toe (external surface)	2⅔
4th toe (external surface)	3⅔
5th toe (internal surface)	2

Webbing continued along both edges of the rather flattened toes as a narrow membrane and connecting with a prominent light-coloured tarsal ridge. A large elongate inner, and a small, rounded outer metatarsal tubercle ; supernumerary metatarsal tubercles absent ; subarticular tubercles well developed and conical. Skin on upper parts of body pitted, thick and glandular, with small, glandular tubercles behind the eye and at the corners of the mouth ; ventral surface smooth, except for a granular area around the vent and on the inside of the thighs ; limbs smooth. Dorsum with dark interorbital area, continuing posteriorly in an indistinct hourglass pattern ; vertebral stripe apparent only on posterior third of the body ; hind limbs cross barred ; venter immaculate, dark cream in alcohol.

Measurements :

Length of body .	59·4 mm.
Length of tibia .	27·5 mm.
Length of foot .	31·2 mm.
Length of head .	20·0 mm.
Width of head .	24·3 mm.

AUDITORY REGION. On reflecting the skin covering the temporal region of some of the examples of this species, it was noticed that the underlying soft parts in the area bounded anteriorly by the m. masseter major and posteriorly by the squamosal arm of the m. depressor mandibulae, had been invaded by metacercariae of a strizeid trematode. As is usual with this kind of trematode, which confines itself to one area, the metacercariae were not found elsewhere in the body.

In this species the m. depressor mandibulae is large and firm and has a double origin, the posterior one in the dorsal fasciae overlying the m. dorsalis scapulae and towards the upper edge of the suprascapula, and the anterior arm on the dorsolateral surface of the crista parotica. On severing this muscle from its attachment areas and after removal of the epithelial mass, the large triangular-shaped body of the thymus gland is revealed; it lies in the usual anuran position external to the m. cucullaris and in the space between the inferior arm of the squamosal and the m. dorsalis scapulae. Removal of the m. cucullaris and the underlying muscle bands of the petrohyoideus from their origin on the ventral portion of the crista parotica reveals the oval, cartilaginous operculum which, with the small eustachian tubes, are the only elements of the middle ear that are present in this species. The operculum is partly overlain by the m. levator scapulae superior which has a broad origin of more or less the width of the plug. There is no trace of calcification of the operculum and there is no superior slip to the "opercular" muscle originating on the auditory capsule behind and internal to the operculum.

VARIATION. The vomerine teeth are between the anterior halves of the choanae in all but two individuals, a half-grown male and a sexually mature female, which have the teeth more posteriorly placed and projecting beyond the posterior borders of the choanae. While the groups of teeth are usually separated posteriorly by a space at least as broad as one of the choanae, in one half-grown individual the groups are contiguous.

Ontogenetic change in head proportions occurs, the head of young individuals (total length less than 30 mm.) being as broad as long and becoming distinctly broader than long with increasing age. Foot length as a proportion of body size varies from 0·43–0·57 ($M = 0{\cdot}49$; $N = 41$); length of tibia as a proportion of body size is 0·38–0·48 ($M = 0{\cdot}43$; $N = 40$).

Differences in skin texture do not appear to be correlated with sex or age although there is a tendency for young specimens to have a more warty skin and older examples of both sexes, from throughout the known range of the species, have a thick, glandular, porous skin with many raised pustules, as in the described specimen. Cei (1960) describes this species as having a smooth skin and no glandular tympanic ridge but this error may have been due to his having specimens in a poor state of preservation.

Occasionally a vertebral stripe is present. Four immature specimens and three adults have a well-defined stripe extending from the tip of the snout to the vent.

Although there is extremely little variation in the shape of the sternum in the individuals examined, the specimen from Munoz Gamero is an exception. It has a short, stumpy sternum with no appreciable style but a widely flared out, notched plate which is quite asymmetrical in shape. On the under surface of the skin in the pectoral area, and loosely anchored to the underlying tissue, was found an ovoid capsule of approximately 3 mm. in length. Mr. Prudhoe of this department kindly examined it and on dissecting it found that it contained a young Microfilaria nematode. The irritation to the surrounding tissue produced by the nematode had

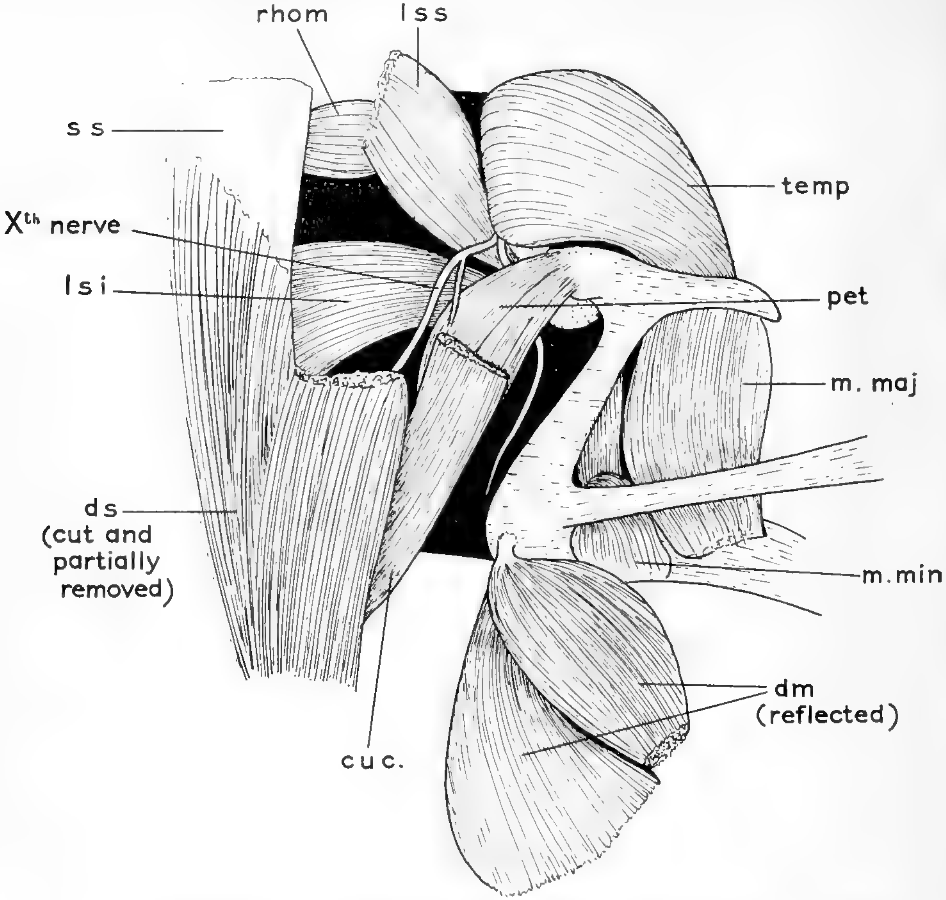

FIG. 3. *E. coppingeri.* Lateral view of the head showing the muscles of the otic region.

Explanation of Reference Letters Used in Figures

col, columella.
cp, crista parotica.
cuc, musculus cucullaris.
dm, musculus depressor mandibulae.
ds, musculus dorsalis scapulae.
lsi, musculus levator scapulae inferior.
lss, musculus levator scapulae superior.
m. maj, musculus masseter major.
m. min, musculus masseter minor.
op, operculum.
pet, musculus petrohyoideus.
rhom, musculus rhomboideus anterior.
sq, squamosal.
ss, suprascapula.
temp, musculus temporalis.

evidently caused the numerous coats to be laid down encompassing the source of the irritation. The pressure of the " capsule ", lying directly ventral to the sternal muscles, may account for the malformation of the sternal cartilage.

SECONDARY SEX CHARACTERS. Conspicuous nuptial pads are present on the mediodorsal surface of the first and second fingers of two males measuring 53·5 mm. and 56·5 mm. The pads extend distally as far as the bases of the terminal phalanges, are unpigmented and bear large, sharp spines which apparently increase in length and acquire heavily pigmented horn as the individuals reach the peak of the breeding season. On the thumb there may be 18–21 such spines but fewer on the second finger (10–12) Text-fig. 5. On each side of the chest, just posterior but close to the folds described for the specimen C.N.H.M. 44219, are well-defined circular asperities consisting of closely set, conical, pigmented tubercles. These pads of excrescences are separated from each other by a distance equal to the length of the inner metatarsal tubercle. From the condition of the gonad in adult males, it appears that the pad on the thumb develops first, then the chest asperities develop at about the same time as the pad on the second finger. Only after the chest pads become differentiated do the spines on the fingers become cornified and acquire melanin. At Bariloche the height of the breeding season occurs late in November. Adult males collected about that time of year have fully developed nuptial pads but by December the spines have regressed. A female collected on 1st December and another taken on the 21st January contain mature ovarian eggs.

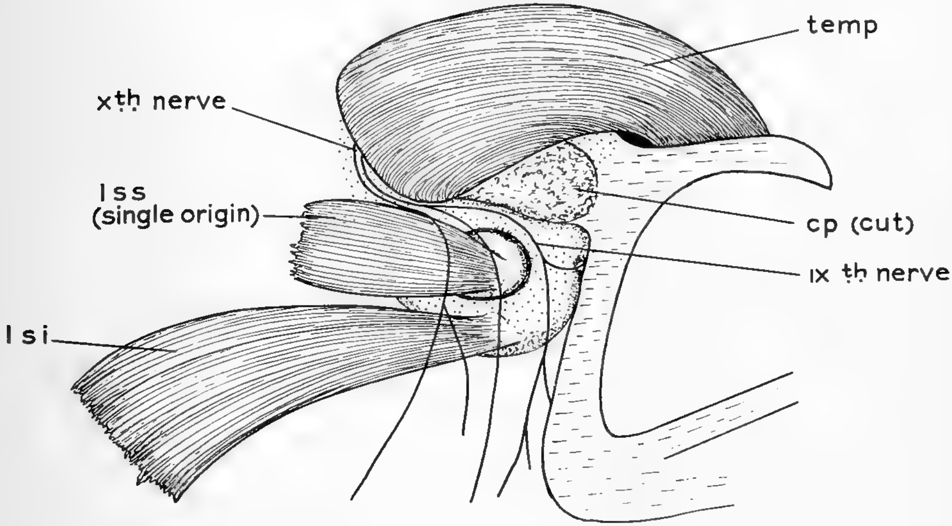

FIG. 4. *E. coppingeri*. The operculum and levator scapulae muscles. (Muscles attached to the crista parotica have been removed.) For abbreviations see Fig. 3.

ECOLOGY. The following is an extract from a personal communication to the author from Dr. Holdgate, zoologist with the Royal Society Expedition to Southern Chile, of the habitats of the examples of *coppingeri* that were taken at Puerto Edèn and on Munoz Gamero :

" 1. ' Plateau below S. Peak, Puerto Edèn. Under stone, 2100′ 7.12.1958'.

FIG. 5. *E. coppingeri*, Z.M.B. 29470. Nuptial asperities on dorso-medial surface of hand of mature male.

" GENERAL

" The country around Puerto Eden, Wellington Island, forms part of the zone described by Godley (1960) as ' Magellanic moorland '. It is mountainous, the peaks on the island itself reaching from 2500 to 4500 ft., and the permanent snow line is at about 3500 ft. There are small glaciers on the highest peaks. The lower country and all the valleys show signs of intense glaciation. The rock is mainly dioritic with some schist etc. The vegetation includes some patches of highly impoverished evergreen rain forest, which is dominated by the evergreen southern beech *Nothofagus betuloides*. This forest is restricted to the coastal strip, the shores of some lakes, gullies, and odd patches on the flanks of the mountains perhaps where the soil is deepest. Between the forest patches there are tracts of bog dominated by the ' carpet ' plants (*Astelia pumila*, *Donatia fascicularis*, *Gaimardia* sp., *Oreobolus* sp. etc.). On steeper slopes there are tracts of ground with grass tussocks and tussocks of *Schoenus laxus*.

" The forest becomes stunted with increasing altitude, and at about 2000 ft. the evergreen beech is replaced by the deciduous *Nothofagus antarctica*. This forms tangled, dwarf thickets. Its upper limit is at about 2500 ft. By 2000 ft. the peat forming carpet plants no longer cover much of the ground surface, and peat accumulation is negligible. Above 2500 ft. there is virtually no bog, except in wet hollows, and above 3000 ft. the vegetation consists of low cushions of *Azorella* sp. and allied upland low-growing species, occasional herbs such as *Senecio* spp., and mosses and liverworts. Stones are scattered everywhere on the uplands and major rock outcrops account for an appreciable part of the land surface. All vegetation stops at about the 3200–3500 ft. level.

" DETAIL

" The specimen of *Eupsophus* was found under a stone, turned in searching for insects. The site lay on open ground above the main evergreen forest which grows fairly thickly on the flanks of this particular mountain. The country was an undulating plateau, with small craggy hills rising about 50 ft. above the general surface, and small valleys of comparable depth. The animal was taken on a low knoll scattered with stones, and the vegetation was here a wet mat of grasses, cyperaceae, and a small amount of the cushion plant *Astelia pumila.* The soil was organic but not a pure peat : lumbricoid oligochaetes were present in it.

" In this site the species therefore was inhabiting open moorland like the other amphibia (*Bufo variegatus*) taken on the expedition at Edèn.

" 2. ' Peninsula Munoz Gamero, under stone at about 100 m. on mountain of 750 m. 27.12.1958.'

" This locality, like Puerto Edèn, lies in the Magellanic moorland zone and has a discontinuous forest, restricted to the lowlands, boggy vegetation of ' carpet plants ' above that, and stony mountainside at a higher level. The extent of forest is smaller in this area which is much farther South than Wellington I. : the peat-forming vegetation on this particular mountain also stopped at a lower level (about 1000 ft.).

" DETAIL

" The specimen was taken in the lowland area, outside the forest, on an open boggy hillside. The vegetation, and also occurrence of the animal under a stone, are closely comparable with the Puerto Edèn record."

At Casa Pangue and at Puella in Llanquihue Province the biotope of *coppingeri* is said to be wet forest. Further ecological details of this region are given in the account of F. W. Edwards' itinerary in Alexander (1929).

DISTRIBUTION. Angol, Malleco Province to Peninsula Munoz Gamero, Magallanes Province. Also in Rio Negro Province, Argentine.

Eupsophus nodosus (Duméril & Bibron)

(Text-figs. 6–10 ; Pls. 2–3)

Cystignathus nodosus Duméril & Bibron, 1841, p. 413 (type locality, Valparaiso).
Cacotus maculatus Günther, 1868, p. 482, pl. 38, fig. 5 (type locality, Chile).
Borborocoetes verrucosus Philippi, 1902, p. 83 (type locality, Province of Cautin)
Borborocoetes kriegi Müller, 1926, p. 195 (type locality, near Valdivia).
Borborocoetes kriegi Müller & Hellmich, 1932, p. 204.

Material examined

Chile :

Valparaiso : M.H.N.P. 763, 763a (types of *C. nodosus*).
Santiago : Cordilleras of Santiago, N.H.M.V. 4661 (2 exs.).
Maule : Ninhue, B.M. 1920.1.20.4050 (2 exs.).
Malleco : Angol, C.N.H.M. 23897.
Valdivia : N.M.B. 1518.
No precise locality : B.M. 60.9.23.4–5 (re-registered 1947.2.19.98–99 ; types of *C. maculatus*) ; Z.M.B. 4484 (2 exs.) ; Z.M.B. 3340 ; R.N.H.L. 2068 (11 exs.) ; N.H.M.V. (no register number, 1 ex.).

Diagnosis. Medium- to large-sized frog, somewhat rectangular in outline. Head flattened, distinctly broader than long ; snout fairly long, broadly rounded. Vomerine teeth in two almost straight groups between the choanae. First finger equal to or longer than second ; toes with only the barest rudiment of web, but flattened along sides and with a slight seam ; subarticular tubercles very prominent and conical ; supernumerary metatarsal tubercles present ; tarsal ridge present. Skin of adults pitted slightly with small, round glandular swellings. Middle ear present but small, diameter of tympanum about $\frac{1}{4}$ the horizontal diameter of the eye, not visible externally. Mature males in the breeding season with spinous nuptial pads covering a prominent bony protuberance on the basal phalanx of the thumb and the inner aspect of the second finger ; two longitudinal crests on the humerus, the ventral crista medialis being visible externally as a curved projection ; patches of asperities on each side of the chest ; no vocal sacs.

Description. Half-grown ♂, Chile, R.N.H.L. 2068. Habitus stocky, toad-like in appearance. Tongue cordiform, the posterior $\frac{1}{3}$ free, feebly notched, occupying $\frac{2}{3}$ of the mouth width. Vomerine teeth in two, small, only slightly oblique groups between the anterior halves of the circular choanae and closer to each other than to the choanae. Snout moderately long, semicircular in dorsal view, $1\frac{1}{3}$ times the horizontal diameter of the eye, rounded in profile, the upper jaw barely extending beyond the lower jaw. Nares dorsolateral, not projecting, the distance between the middle of the nares equal to the interorbital space which is narrower than the upper eyelid, their distance from the anterior borders of the eyes $1\frac{1}{2}$ times greater than from the tip of the snout. Canthus rostralis almost straight but rather indistinct ; loreal region flat and strongly oblique, upper lip flaring out below. Eye large and prominent, not projecting beyond the jaws in dorsal view. Middle ear apparatus present but feebly developed and deeply seated ; annulus tympanicus incomplete dorsally ; extra columellar cartilage very large and pear-shaped, occupying almost the full area of the tympanum ; horizontal diameter of the tympanum $\frac{1}{4}$ that of the eye ; operculum entirely cartilaginous. A glandular fold from behind the eye to the arm insertion. Omosternum cartilaginous with moderately long stem and only very slightly dilated tip ; sternum cartilaginous, twice the length of the omosternum, of moderate width medially, expanded posteriorly, deeply emarginate, only very slightly longer than the epicoracoids. Tibio-tarsal articulation of the adpressed hind limb reaches to the temporal area. Fingers free of web, first finger slightly longer than the second, subarticular tubercles very prominent, supernumerary palmar tubercles present. Tips of toes and fingers rounded with simple terminal phalanges. Toes with the barest rudiment of web; only an indication of toe fringes; a short, somewhat indistinct tarsal ridge present. An oval inner, and a small, rounded outer metatarsal tubercle present, the inner tubercle approximately equal to the distance from the tip of the first toe to the distal edge of the tubercle; supernumerary metatarsal tubercles present, at least one at the base of each digit; subarticular tubercles very pronounced and conical. Skin on the upper parts of the body pitted, with small, round, slightly elevated warts on the dorsum and upper surfaces of the thighs; ventral surface smooth except for a granular area around the vent and on the inside of the thighs; limbs smooth. Dorsum with a light triangular area on the snout, a dark interocular band and obscure dark marblings; the dorsal warts tend to be light coloured in the centre and edged with dark ocelli. A dark band along the canthus and loreal region is continued posteriorly as an oblique bar from behind the eye, across the temporal area to behind the arm insertion. There is also a conspicuous light, transverse line just posterior to the vent. Venter mottled, particularly on the throat. Limbs markedly cross barred.

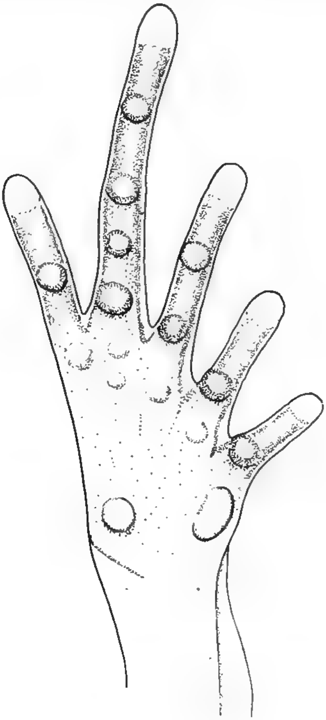

FIG. 6. *E. nodosus*, M.H.N.P. 763a (one of the types). Ventral view of foot. (× 17·5.)

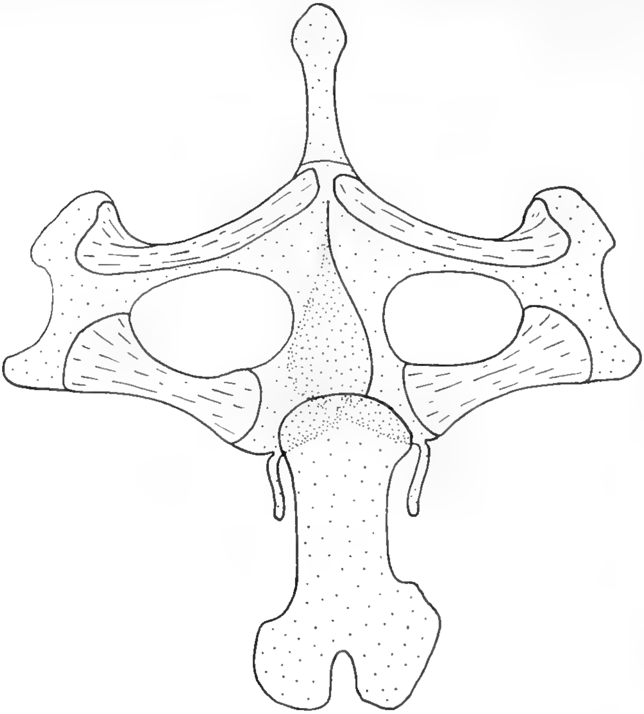

FIG. 7. *E. nodosus*, Z.M.B. 4484. Ventral elements of the shoulder girdle. (×17·5.)

Measurements :

Length of body .	44·2 mm.
Length of tibia .	19·3 mm.
Length of foot .	21·6 mm.
Length of head .	14·7 mm.
Width of head .	16·3 mm.

VARIATION. In its bufonid appearance and thick, pitted, glandular skin bearing numerous warts this species may readily be confused with *coppingeri* but it can be distinguished from it and from all other Chilean species of *Eupsophus* by its webbing, supernumerary tubercles on the foot, male secondary sexual characters and small, deeply seated tympanum. There is little variation in the individuals examined ; all young and immature specimens have similar scattered white tubercles on the dorsum and the position of the vomerine teeth is fairly constant. In the adult males examined, the sternum has become calcified, whereas in younger individuals it is wholly cartilaginous. The length of foot relative to total length varies from

0·43–0·54 ($M = 0·48$; $N = 24$) and the tibia length as a proportion of total length varies from 0·37–0·50 ($M = 0·42$; $N = 24$).

REMARKS. The type specimens of *Cacotus maculatus* Günther were compared with the series of *nodosus*, including the types, and were found to agree well in characters. The figure in Dr. Günther's paper of the under surface of the foot of one of the types illustrates the supernumerary tubercles on the metatarsals which are characteristic of *nodosus* but the tarsal fold which is present in the type specimens is not apparent in the figure. Although Boulenger (1882) stated that *maculatus* lacked a tympanic disk, an examination of the ear region by reflecting the covering skin discloses a complete, although poorly developed middle ear apparatus with a pear-shaped tympanic annulus and a large extra columella cartilage. No other character remains by which *maculatus* can be distinguished from *nodosus* and the two must be considered synonymous.

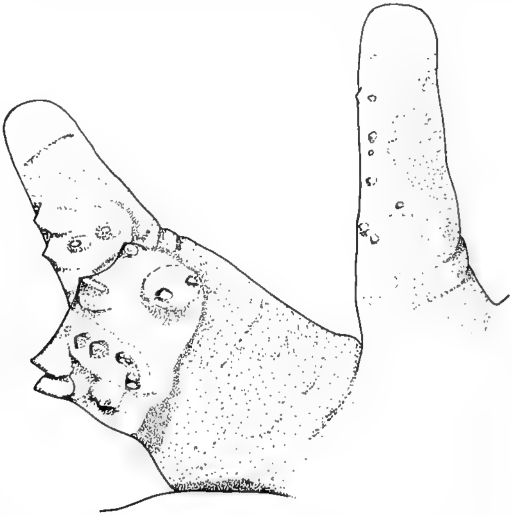

FIG. 8. *E. nodosus*, N.H.M.V. 4661.1. Nuptial asperities on dorso-medial surface of hand of mature male. (×17·5.)

It is unfortunate that the types and other examples of Müller's *Borborocoetes kriegi* which were housed in the Zoologische Sammlung des Bayerischen Staates at Munich were destroyed during the Second World War. However, from the detailed descriptions by Müller (1926) and later by Müller & Hellmich (1932) there is little doubt that *kreigi* too falls into the synonymy of *nodosus*, the only conflicting part in the descriptions being the width of the interorbital space which in *kreigi* is said to be distinctly broader than the upper eyelid. Their detailed description of the breeding male *kriegi* particularly strengthens the probability of the two species being synonyms for all the secondary sex characters described above for *nodosus* were apparently developed in the *kriegi*.

Cei (1960) has included *E. verrucosus* Philippi in the synonymy of *nodosus* but in view of the conflict in the descriptions of the characters of the two species his judgment is open to question. Vellard (1947) re-described *verrucosus* stating that an internal vocal sac is present. No vocal sacs are present in male *nodosus* in full breeding condition. Furthermore, he makes no mention of supernumerary tubercles under the metatarsals nor of the length of the first finger, characters typical of examples of *nodosus* of all age groups. However, the position of the vomerine teeth, the reduced lateral toe fringes, the invisible tympanum and the shape of the head are suggestive of a closer relationship with *nodosus* than with any other Chilean species of *Eupsophus*.

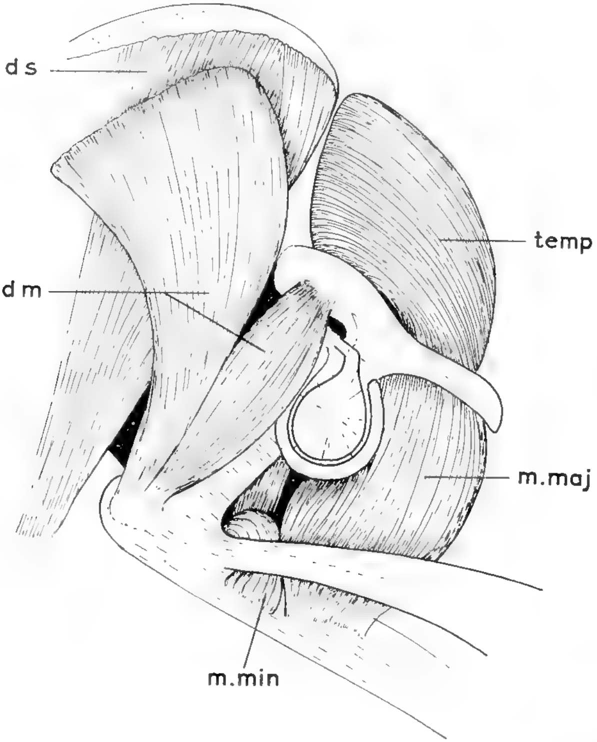

FIG. 9. *E. nodosus*, N.H.M.V. 466.1. Lateral view of head showing tympanic annulus, extra columella and neighbouring muscles. For abbreviations see Fig. 3.

SECONDARY SEX CHARACTERS. At the height of development the base of the thumb of the male *nodosus* is very bulbous and bears clusters of conical tubercles which are tipped with horn. Similar tubercles are present on the proximal half of the penultimate phalanx of the thumb which is not swollen. The median surface of the second finger bears a few scattered, spinous tubercles. The irregularly shaped, glandular, spinous knob on the pollex surmounts a bony protuberance on the distal half of the inner aspect of the metacarpal. The fore limbs of a breeding male are massive with an enormous increase of humeral musculature and an associated increase in their attachment area on the crests on the humerus which have expanded to form two longitudinal flanges, partially enclosing a deep sulcus and of unequal height, the lower one being more prominent and visible externally as a curved projection. The males at maximum development also have round patches of chest asperities consisting of sparsely set, conical warts, somewhat similar in appearance to those on the hand but not as spinous and without pigment. These chest pads are divided by a space equal to the horizontal diameter of the eye.

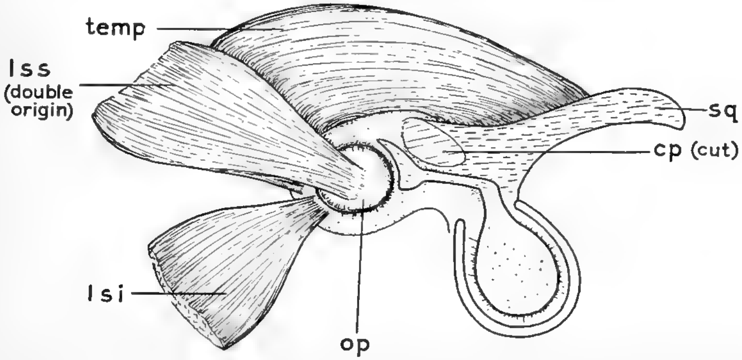

FIG. 10. *E. nodosus*, N.H.M.V. 4661.1. The operculum, elements of the external ear and levator scapulae muscles. (Muscles attached to the crista parotica have been removed.) For abbreviations see Fig. 3.

In addition to the characters described above, the type of *kriegi* was described as having in front of the axilla several warts, some with, some without spines; these axillary warts were absent from the specimen which was collected 5.x.1930 and was described later by Müller & Hellmich. It may be that the *nodosus* males in the series examined were not taken at the very peak of sperm activity but that such spinous warts in the axilla are the last sex character to develop. Unfortunately the reproductive organs have been completely removed from the apparently sexually mature male collected at Valdivia, which was examined (N.M.B. 1518).

SEX DIMORPHISM. On the basis of the series at hand it is impossible to judge whether there is any dimorphism in size between the sexes as none of the females is sexually mature. The largest specimens that were examined, 59·3 mm. and 69·3 mm., are both sexually mature males. The male specimen identified as *kriegi* and described by Müller & Hellmich measured 77 mm. while the type of *kriegi*, also a mature male, had a total length of 75 mm.

ECOLOGY. No ecological data on the series examined is available. The Munich Museum specimens identified as *kriegi* were found at night in a heavily wooded ravine with a permanent stream close by at an altitude of 1,200 m. in the environs of Santiago. The type of *kriegi* was collected in an area rich in virgin rain forest near Valdivia.

As regards the habits of this species, Parker (1940) observed that burrowing forms tend to have a larger extra plectral cartilage, a more deeply seated and smaller tympanum and a thickened skin. *E. nodosus* in possessing all these features may well be a cryptozoic species; its short, robust limbs, bufonid-like foot and conical subarticular and supernumerary tubercles also suggest this mode of life.

DISTRIBUTION. Valparaiso to Valdivia.

Eupsophus roseus (Duméril & Bibron)

(Text-figs. 11–15; Pl. 4, fig. 1)

Cystignathus roseus Duméril & Bibron, 1841, p. 414 (type locality, Chile).
Borborocoetes grayi Bell, 1842, p. 36, pl. 17, fig. 2 (type locality, Valdivia).
Borborocoetes bibroni Bell, 1842, p. 35, pl. 17, fig. 1 (type locality, Valdivia and at Chiloé).
Cyclorhamphus fasciatus Peters, 1869, p. 789 (type locality, Puerto Montt).
Cacotus calcaratus Günther, 1881, p. 19 (type locality, Chiloé).
Borborocoetes calcaratus Boulenger, 1882, p. 256, pl. 17, fig. 1.
Borborocoetes masareyi Roux, 1910, p. 111 (type locality, Coronel, Chile).
Eupsophus maculatus Schmidt, 1954, p. 5.
Eupsophus grayi Capurro, 1957, p. 24.
Eupsophus grayi Cei, 1960, p. 3.

MATERIAL EXAMINED

CHILE:

Santiago: Z.M.B. 5363 (2 exs.).

Concepcion: Tumbes, Z.M.B. 13396 (3 exs.); Pelun, B.M. 1905.5.31.26; Coronel, N.M.B. 2789 (type of *B. masareyi*).

Malleco: Cabreria, 800 m., Nahuelbuta, C.N.H.M. 44181–4, 44215.

Cautin: Maqushue, Temuco, B.M. 1907.1.22.22–29.

Valdivia: Valdivia, Z.M.B. 9826, N.M.B. 1523–1526, N.H.M.V. 4660.3, 4660.5–6, 4660.10, 4660.12, 4663.1, 4663.9–13, 4663.8, 4662.14–16, 4654 (4 exs.), N.H.M.V. (2 exs., no register number), Z.M.B. 5365, B.M. 89.12.16.181–182, 1920.1.20.347, 45.5.25.25 (type of *B. grayi*); Panguipulli, M.C.Z. 8653–8656; Desague, N.H.M.V. (1 ex., no register number); Corral, M.C.Z. 13742, Z.M.B. 13427 (8 exs.).

Llanquihue: Puerto Montt, Z.M.B. 6617 (type of *C. fasciatus*), N.H.M.V. 4654 (2 exs.); Pangue, N.H.M.V. 4654 (1 ex.), N.H.M.V. (2 exs., no register number).

Chiloé: B.M. 1920.1.20.468, 68.9.22.8 (type of *C. calcaratus*); Ancud, B.M. 1927.5.7.10–11; NE. Ancud, 41° 51′ 50″ S., 73° 49′ 20″ W., U.B. 62–63; S. of Lechagua, 41° 53′ 18″ S., 73° 51′ 55″ W., U.B. 26–36, 38–40, 42, 44, 46–52, Z.I.L.U. (4 exs. no register number); C.S. Carlos, N.H.M.V. 4654 (1 ex.).

Chonos: B.M. 45.5.25.43 (type of *B. bibroni*).

No precise locality: Z.M.B. 3132, 3342–3, C.N.H.M. 39994, N.H.M.V. 4658 (3 exs.), 4655 (10 exs.), M.H.N.P. 762, 762a (types of *C. roseus*); C. Chile, Z.M.B. 13918; S. Chile, B.M. 91.8.29.16.

ARGENTINE:

Rio Negro: San Martin de Los Andes, N.H.M.V. (3 exs., no register number); Bariloche B.M. 1932.10.2.64–65, N.H.M.V. (1 ex., no register number), N.H.M.V. 4655 (4 exs.).

DIAGNOSIS. Medium-sized frog, adults 32·0–46·0 mm., plump build with short, blunt snout; head as broad or slightly broader than long; vomerine teeth in two straight or slightly oblique groups well behind the posterior margin of the choanae; first finger shorter than second; toes with only a rudiment of web; subarticular tubercles prominent and conical; usually a heel tubercle; no tarsal ridge; skin of adults shagreened; middle ear present, tympanic annulus usually visible externally; mature males with large nuptial pads on dorsal surface of first and second fingers and with paired internal vocal sacs.

DESCRIPTION. Adult ♀, Panguipulli, M.C.Z. 8653. Plump habitus. Tongue broadly rounded, its posterior ⅓ free and with only a faint indication of a notch; a very narrow, inconspicuous seam forming a frill round the edge of the tongue. Vomerine teeth in two, strong, oblique groups well behind the posterior borders of the semicircular choanae and separated from each other by a distance equal to 1½ times the width of one of the choanae. Snout fairly long, rounded in dorsal view, in profile slanting backwards towards the lip border and distinctly rounded, almost equal to the horizontal diameter of the eye. The upper jaw barely extends beyond the lower jaw. Nares dorsolateral, slightly projecting, the distance between the middle of the nares equal to the width of the interorbital space which is as broad as the upper eyelid, their distance from the anterior borders of the eyes about equal to their distance from the tip of the snout. Canthus rostralis curved and prominent; loreal region concave and oblique with upper lip flaring out below; eye large and prominent, not projecting beyond the jaws in dorsal view. Middle ear apparatus complete; the tympanic annulus conspicuous externally, its diameter ½ the eye width; extra columella baton-shaped; operculum partly calcified. Omosternum cartilaginous, moderately long stem and dilated tip; sternum also cartilaginous, with dumpy style and slightly expanded plate, almost twice the length of the omosternum and 1¼ times the length of the epicoracoids. Tibiotarsal articulation of the adpressed hind limb reaches to the anterior border of the eye. Fingers free of web, first finger shorter than second, subarticular tubercles moderate. Tips of fingers and toes rounded, with simple terminal phalanges. Toes rounded without webbing but metatarsals partially separated by web. A large elongate inner, and a small, rounded outer metatarsal tubercle present; supernumerary metatarsal tubercles absent; subarticular tubercles well developed; a small heel tubercle present. Skin on upper parts of body shagreened with thickened, slightly pitted area in the paratoid region and at the corners of the mouth. A pronounced glandular, dorsolateral fold extends from the posterior edge of the eyelid, passes above the tympanum and posteriorly to midway between the arm and the leg insertion. Ventral surface smooth, except for a granular area around the vent and on the insides of the thighs; limbs smooth. Dorsum with a conspicuous light patch on forehead, a dark triangular mark in post interorbital area and posteriorly an indistinct hour-glass pattern; dark patches on either side of the lumbar region. Hind limbs cross barred; venter immaculate.

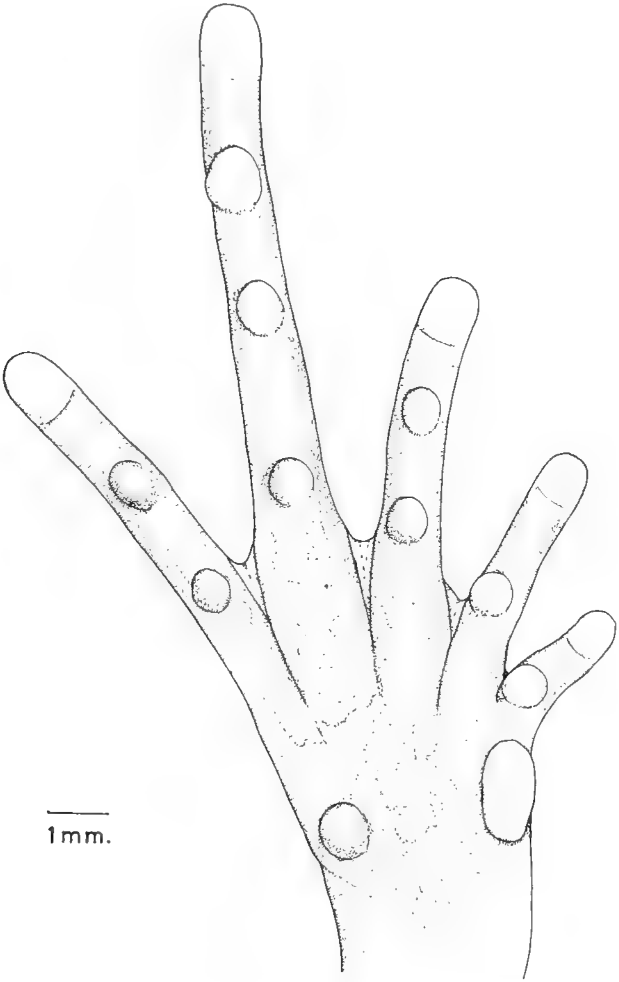

FIG. 11. *E. roseus*, U.B. No. 49. Ventral view of the foot. (×17·5.)

Measurements

Length of body .	39·5 mm.
Length of tibia .	20·7 mm.
Length of foot .	18·0 mm.
Length of head .	14·2 mm.
Width of head .	15·5 mm.

VARIATION. Remarks on sex dimorphism, adult size, percentages of specimens having heel tubercles and two metatarsal tubercles are contained in the following section on "Remarks".

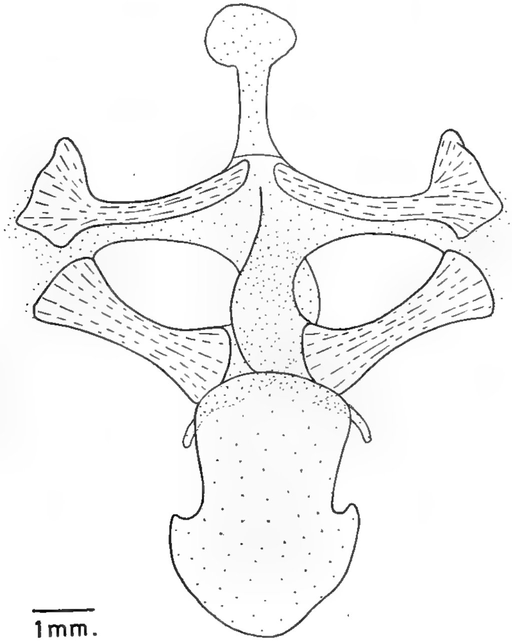

FIG. 12. *E. roseus*, Z.M.B. 13918. Ventral elements of the shoulder girdle. (×17·5).

Notes were made on the position of the vomerine teeth in 119 individuals. There are no exceptions to the rule that in examples of *roseus* the teeth are placed behind the posterior level of the choanaе. Three specimens have contiguous groups and two specimens are aberrant in having only one; otherwise all have two slightly oblique groups separated from each other on the mid-line.

The proportions of the ventral elements of the pectoral girdle vary considerably, although the sternum is consistently longer, even if only slightly, than the epicoracoid cartilages. The length of the omosternum relative to the epicoracoids is especially variable and may be from ½ to ¾ its length. Calcification of the whole of

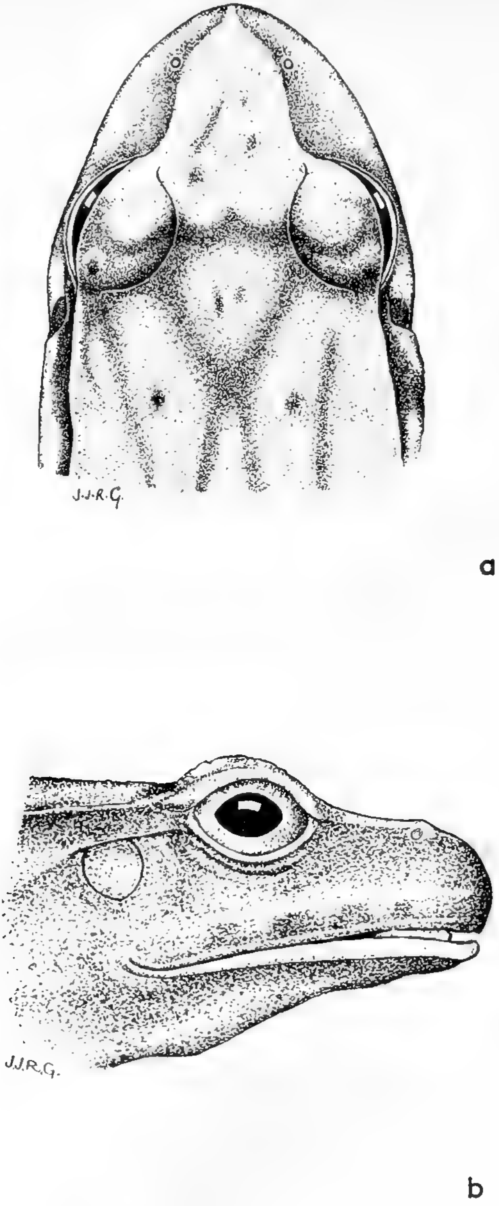

FIG. 13. *E. roseus.* a. Dorsal view of head ; b. Lateral view of head.

the sternal style, or at least the central portion of it takes place in many of the fully-grown specimens but among a collection of adults of approximately similar body size taken from one locality, the numbers of individuals with calcified style about equal those that are wholly cartilaginous.

Foot length/Total length . . 0·46–0·60 ($M = 0{\cdot}52 : N = 91$).
Tibia length/Total length . . 0·45–0·60 ($M = 0{\cdot}52 : N = 88$).

REMARKS. *Cystignathus roseus* was described from two sexually mature individuals, a male and a female. Notwithstanding the fact that their present condition is bleached, soft and flabby, certain diagnostic characters are still manifest, notably the position of the vomerine teeth, which are in slightly oblique groups behind the posterior level of the choanae, the remnants of a dorsolateral fold, the velvety clusters of asperities on both the first and second fingers of the male and an internal vocal sac in the male. In addition, there is in the male a suggestion of a heel tubercle. All these characters are consistent with the chief diagnostic characters of Bell's *grayi*. But apart from morphological considerations, the colour pattern, which was so ably described by Duméril & Bibron, fits exactly a large proportion of specimens that have been identified as *grayi* by previous workers. The only major discrepancy between the types of *roseus* and individuals identified as *grayi* is the size of the female *roseus* type which is 46·5 mm. in total length and is almost 2 mm. greater than the largest female *grayi* that has been measured. The size range of mature females of *grayi* is 32·0–44·7 mm. with a mean of 38·6 mm. ($\text{S.E.}_{\text{m}} = 0{\cdot}50$; $N = 33$). However, too great emphasis need not be placed on this size difference between the species particularly as the types of *roseus* are without a precise locality and it has been noted in the examination of the *grayi* material that there is a cor-

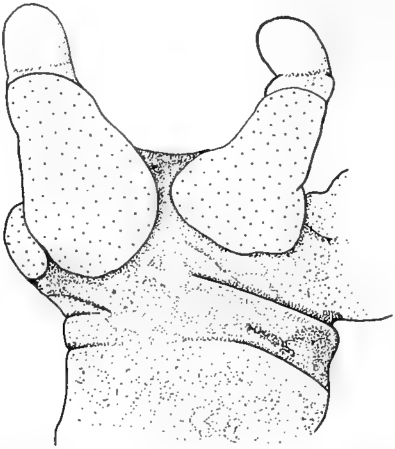

FIG. 14. *E. roseus*, C.N.H.M. 39994. Nuptial pads on hand of mature male. (× 17·5.)

relation between size at sexual maturity and geographical distribution, individuals from the northern part of the range of the species tending to be larger while the population occurring in insular Chiloé in the south tends to be small. An explanation for the extreme size of the *roseus* types could lie in the fact of their having been taken in an area towards the northern limit of the distribution of the species. Certainly there is no justification for maintaining *grayi* as a species distinct from *roseus*.

Nieden (1923) placed *E. bibroni* (Bell) and *E. fasciata* (Peters) in the synonymy of *E. grayi* but he maintained that Roux's *masareyi* could be separated from *grayi* on the basis of skin texture, number of metatarsal tubercles and also skin folds. The type of *masareyi* has been examined by the present author ; its condition is poor and the specimen is hard and brittle but there is no doubt that only one metatarsal tubercle is present and no heel tubercle exists. But only 61% of the individuals studied here possess a heel tubercle although 96% have two metatarsal tubercles. The exceptions are adults of both sexes and from localities throughout the range. In other characters *masareyi* agrees well with the description of *roseus* and with the specimens examined and there seems no reason to suppose that *masareyi* is other than a synonym of *roseus*.

Although up to the present time *E. calcaratus* (Günther) has been considered a valid species and was thought to differ from the *grayi-roseus* group in lacking a tympanum (Boulenger, 1882 and Nieden, 1923), the type of *calcaratus* does possess a tympanum. The degree to which the middle ear structures are developed immediately suggests an immature specimen and this is borne out by an examination of other anatomical structures, notably the shoulder girdle and sex organs. The type has a heel tubercle and the position of the vomerine teeth, body proportions and other external characters leave no doubt that the description of *calcaratus* was based on a young specimen of *roseus*. Also the " V "-shaped mid-body ridge present in the type of *calcaratus* and apparent in the figure in Boulenger's catalogue occurs frequently in young and half-grown examples of *roseus*.

All the Lund University Chile Expedition amphibian material, which was reported on by Schmidt (1954), has been examined and the specimens identified as *E. maculatus* are in fact examples of *roseus*.

The description given by Cei (1960) of the colour, vomerine teeth and size and the figure of specimens determined by him as *roseus* clearly indicate that his series does not belong to *roseus* but should be referred to the new species described below.

A few comments on the notes and photographs relating to the species *roseus* and *grayi* in Capurro's paper (1957) are called for on account of the confusion in identifications and the apparent transposition of the captions to the photographs. Although his description of *E. grayi* suggests that it was based on examples of *E. roseus* (D. & B.) the photograph bearing the caption " *E. grayi* " is not of an example of *roseus* but of the species described in the following section. Likewise, there is confusion with his description and figure of what he terms *E. roseus* and since the frog that is photographed resembles an individual of D. & B.'s *roseus* it is possible that the error has been made by the printer.

Secondary sex characters. Mature males have paired internal vocal sacs opening on the floor of the mouth in wide slits. The nuptial pads present on the first and second fingers consist of clusters of fine brown spinules, are restricted to the dorsal surface and extend to the bases of the distal phalanges. The inner palmar tubercle also bears asperities which like those on the fingers are granular.

Unlike *E. taeniatus*, in which all the adult males have vocal sac openings on the floor of the mouth, the external sex characters of *roseus* appear to regress between the mating seasons and specimens taken at these periods can be sexed only by an examination of the gonads. Seemingly there is no predetermined order of development of the different sex characters for in some cases the sac openings develop prior to the nuptial pads while in other examples the reverse order is the case but the openings are always present by the time the pads acquire spinules and a deposition of pigment.

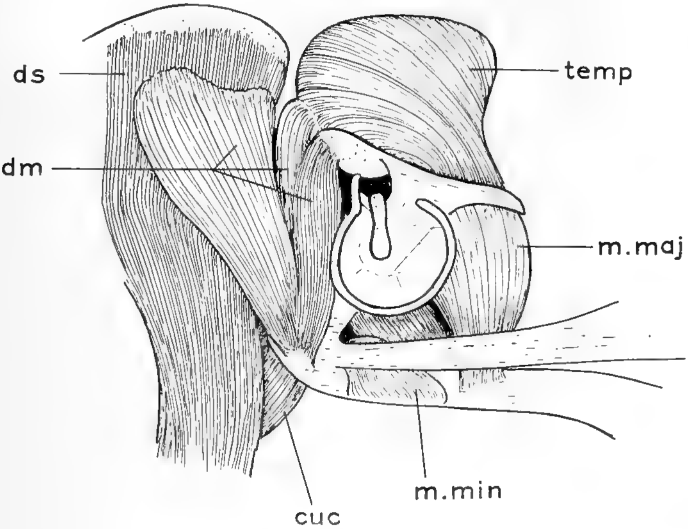

FIG. 15. *E. roseus*, U.B. No. 42. Lateral view of head showing tympanic annulus, extra columella and neighbouring muscles.
For abbreviations see Fig. 3.

Exceedingly few of the examples studied bear any collecting dates and consequently little information on breeding dates is available but females bearing ripe ova were taken at Bariloche during November, at Nahuelbuta on the 1st December and at Lechagua on 18th November as well as on 1st January and 6th March.

COLOUR. The colour in life of some of the *roseus* collected near Ancud was noted by the collector as being mottled yellow-red, red, grey and brown. A few of the specimens that are preserved in the collections of the Vienna Museum still retain their original coloration. The ground colour of these individuals is magenta with a brown band on the canthus, across the tympanum and along the lateral fold. Numerous other brown marks are apparent on the haunches and on the interorbital region ; the cross barring on the limbs and the semicircular shoulder marks are also brown. The venter is cream suffused with rose.

Duméril & Bibron's description of the coloration of the type specimens of *roseus* is reproduced here verbatim since it is so detailed and exact.

" Le dessus de la tête, le dos, la face supérieure des membres et même les flancs offrent une teinte rose ; l'extrémité du museau et les régions frénales sont colorées en brun pâle, ainsi que les tempes et les épaules ; mais non d'une manière uniforme, car on y voit un semis de points blanchâtres. Il y a des dessins bruns, irréguliers sur la nuque, et des bandes de la même couleur en travers des jambes et des tarses. La partie postérieure des cuisses est ponctuée de blanc sur un fond noirâtre. Un mélange de brun fauve et de blanc sale est répandu sur la gorge, et sur la face inférieure des membres. La ventre est d'un blanc grisâtre."

ECOLOGY. Only the Lund University Chile Expedition specimens bear ecological data. Descriptions are given by Brattström & Dahl (1952) and Schmidt (1954).

DISTRIBUTION. *E. roseus* occurs as far north as Santiago de Chile and extends south to the Chonos Archipelago ; it occurs also in the Rio Negro Province of Argentine.

Eupsophus vertebralis sp. nov.

(Text-figs. 16–18 ; Pl. 4, fig. 2)

Borborocoetes roseus Boulenger, 1882, p. 253 (*nec* Duméril & Bibron).
Eupsophus roseus Schmidt, 1954, p. 5.
Eupsophus roseus Capurro, 1957, p. 24.
Eupsophus roseus Cei, 1960, pp. 1–13.

MATERIAL EXAMINED

CHILE :

Holotype : Adult ♀ Valdivia, Chile, N.H.M.V. 4660.1, collected by Steindachner, 1881.

Paratypes :

Valdivia : B.M. 1932.10.2.68–71, A.M.N.H. 23931, N.H.M.V. 4660 (2, 4, 7, 8, 9, 11, 13), 4662.1–13, 4663.2–7, 4657 (6 exs.), 4656, 13331, N.M.B. 1519, Z.M.B. 7082, 9835–6 ; Corral, A.M.N.H. 22106–7, 22150, Z.M.B. 13388, 13431, 13919 ; Desague, N.H.M.V. (4 exs., no register number).

Santiago de Chile : Z.M.B. 7082.

Llanquihue : Frutillar, A.M.N.H. 23989 (1 ex.), B.M. 97.1.25.5 ; Casa Pangue, B.M. 1927.5.7.4–5.

Chiloé : N.H.M.V. 4659 ; S. Lechagua, Ancud, U.B. 4, 5, 37, 41, 43, 45 ; Quellon, C.N.H.M. 3715.

No precise locality : B.M. 45.5.25.22, M.C.Z. 2244, Z.M.B. 14033 (2), Z.M.B. 3338.

DIAGNOSIS. A large species of frog (50–66 mm. when mature) with broadly rounded snout and head broader than long ; vomerine teeth in two, only slightly curved groups between the posterior halves of the choanae, separated medially; first finger not longer than second; toes somewhat flattened along sides with a rudiment of web at bases of digits and between metatarsals; subarticular tubercles prominent; no tarsal fold; skin almost smooth, usually with a vertebral band which may be as broad as the distance between the nares; supratympanic fold present; usually two chevron-shaped ridges between the shoulders; middle ear present and tympanic annulus visible externally; mature males with a white glandular nuptial pad on basal phalanx of thumb and with paired internal vocal sacs.

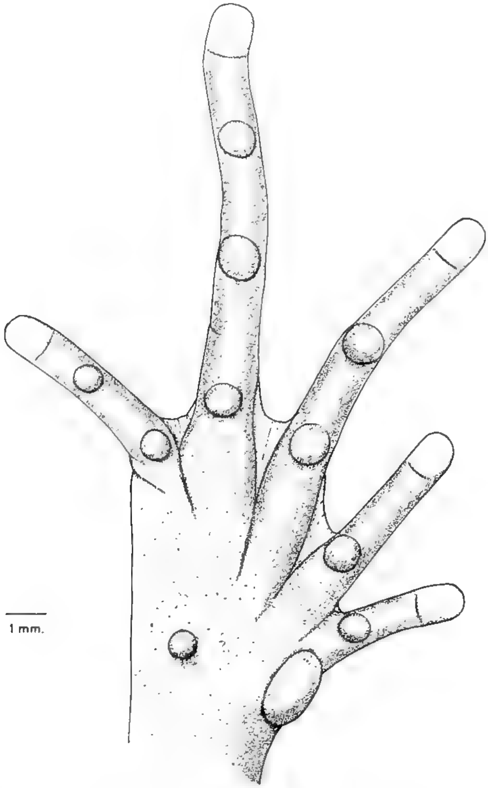

Fig. 16. *E. vertebralis.* Ventral view of foot. (× 17·5.)

Description of holotype. Habitus robust. Tongue broadly rounded, its posterior $\frac{1}{3}$ free and slightly notched. Vomerine teeth in two long, only slightly curved groups between and close to the posterior halves of the choanae, separated from each other by a space equal to $\frac{1}{3}$ the width of one of the choanae. Snout fairly long, broad and rounded in dorsal view, equal in length to the horizontal diameter of the eye, somewhat angular in profile, the upper jaw scarcely extending beyond the lower jaw. Nares superolateral, slightly projecting, the distance between the middle of the nares $1\frac{1}{4}$ times the width of the interorbital space which is narrower than the upper eyelid, equidistant between the anterior borders of the eyes and the tip of the snout. Canthus rostralis rounded and obtuse, not sharply defined; loreal region flat and strongly oblique, upper lip flaring out strongly below; eye large and prominent, not projecting beyond the jaws in dorsal view.

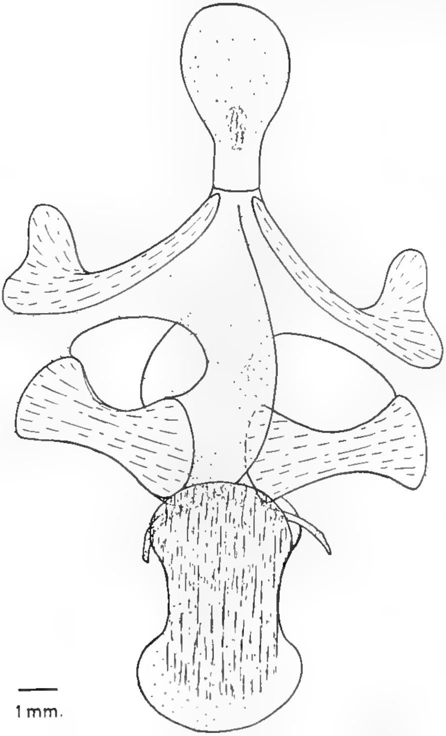

FIG. 17. *E. vertebralis*, N.H.M.V. 4660.1. Ventral elements of the shoulder girdle of the holotype. (Sternum slightly displaced at left side.) (× 11·25.)

Middle ear apparatus complete; the horizontal diameter of the tympanic annulus rather less than half the diameter of the eye and conspicuous externally; columella baton-shaped. Thick, glandular, supratympanic fold present. Omosternum cartilaginous with short broad stem, in the centre of which is a small calcified area, tip strongly dilated; sternum cartilaginous, 1·4 times the length of the omosternum, somewhat rectangular in shape with slight median constriction, almost wholly calcified; epicoracoids 1·25 times the length of the sternum. Tibio-tarsal articulation of the adpressed hind limb reaches to the middle of the eye. Fingers free of web, first finger slightly shorter than second; subarticular tubercles moderate; small

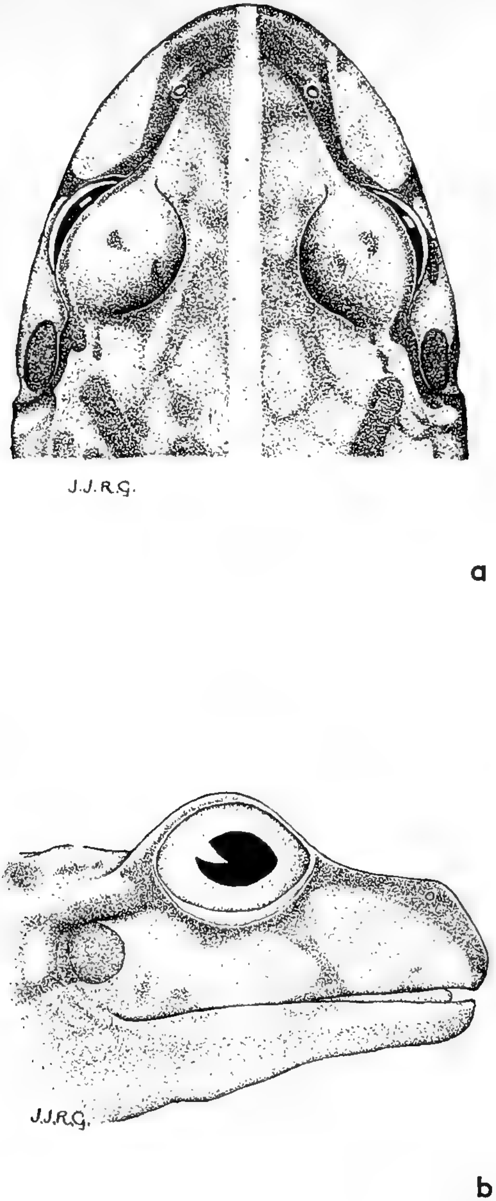

FIG. 18. *E. vertebralis.* a. Dorsal view of head; b. Lateral view of head.

supernumerary palmar tubercles present; two palmar tubercles, the outer one partially divided. Tips of fingers and toes rounded, with simple terminal phalanges. Toes with an inconspicuous ridge along the sides and separated by a rudiment of web; between the third and fourth the web extends to the distal edges of the basal subarticular tubercles but is somewhat less between the other digits. Metatarsals partly separated by web. An elongate inner and a small rather inconspicuous outer metatarsal tubercle present; supernumerary metatarsal tubercles absent; subarticular tubercles rather prominent. Skin on upper parts of body pitted and finely granular with occasional small, elongated tubercles on flanks; between the shoulders on either side of the mid-line are longitudinal crescent-shaped ridges. Venter smooth except for granulations in region of vent and on inside of thighs; limbs smooth. Dorsum mottled, with inconspicuous, light coloured vertebral band from tip of snout to vent; a dark line from tip of snout through nares to anterior border of eye and a dark patch on upper lip just anterior to eye; tympanic area dark; lips not barred. Limbs indistinctly cross barred. Ventral surface cream in alcohol.

Measurements:

Length of body .	59·4 mm.
Length of tibia .	27·9 mm.
Length of foot .	28·3 mm.
Length of head .	21·7 mm.
Width of head .	23·7 mm.

VARIATION. The other adults do not vary much from the described specimen and the proportions of the pectoral girdle elements of the holotype are fairly typical of the series examined. The actual variation in the size of the sternum relative to the omosternum is 1·3–2·1 and the relation of the epicoracoids to the omosternum is the same. While in one individual, an adult ♀ from Valdivia in extremely poor condition, the vomerine teeth are behind the choanae, in all other examples of the species the groups are similar in position to that described, although their degree of development differs in a few individuals, one being devoid of teeth while two juveniles and one adult among the Valdivia examples have only one group. Fifty-seven per cent of the examples studied have a broad vertebral band which either extends the length of the body or is present only in the posterior half.

SECONDARY SEX CHARACTERS. Mature males have a glandular nuptial pad on the basal phalanx of each thumb; none shows any deposit of melanin. The vocal sac apparatus consists of paired subgular sacs communicating with the mouth through long slits which extend forwards from the jaw commissures.

SEX DIMORPHISM. The females are somewhat larger than the males at sexual maturity. Females with ripe ova measure 50·2–66·1 mm. (Mean = 57·6; $\text{S.E.}_{\text{m}} = 1{\cdot}05$; $N = 15$) in body length, whereas males with vocal sacs measure 43·3–65·1 mm. (Mean – 53·5; $\text{S.E.}_{\text{m}} = 2{\cdot}21$; $N = 8$). Also, the insular population from Chiloé appears to attain sexual maturity at a smaller size than the mainland and more northern populations, the males being 43–46 mm. and the females approximately 53 mm.

ECOLOGY. Data on biotopes for the Ancud material (U.B. examples) is described in Brattström & Dahl (1951) and in Schmidt (1954). These specimens were found in association with *E. roseus*.

DISTRIBUTION. Santiago de Chile to Chiloé Island.

Eupsophus taeniatus (Girard)

(Text-figs. 19–22 ; Pl. 5)

Cystignathus taeniatus Girard, 1854, p. 226 (type locality, from the neighbourhoods of Santiago, Chile).

Cystignathus taeniatus Girard, 1855, p. 207, pl. 34, figs. 8–11.

MATERIAL EXAMINED

CHILE :

Santiago : Santiago de Chile, Z.M.B. 5363.

Nuble : Chillan, B.M. 1920.1.20.1061.

Concepcion : Marsh between Concepcion and Talcahuano, N.H.M.V. 4667 (23 exs.) ; Concepcion, B.M. 1905.5.31.27–28 ; 45.5.25.60.

Cautin : Maqushue, Temuco, B.M. 1907.1.22.16–21 ; Ultra Cautin, M.C.Z. 17874.

Malleco : El Vergel, Angol, C.N.H.M. 44185.

Valdivia : L. Ranco, N.H.M.V. 9777 (16 exs.) ; La Union, N.H.M.V. 14664 (6 exs.) ; Valdivia, N.H.M.V. 4668 (15 exs.), (no number, 8 exs.), N.M.B. 1521–2, Z.M.B. 9833 (2 exs.), 5362 (3 exs.), 26120 (4 exs.), 9837, B.M. 89.12.16.174–180, 79.5.6.1–2, 1920.1.20.346 ; Desague, N.H.M.V. 4666 (24 exs.), (no number, 1 ex.) ; Panguipulli M.C.Z. 8646–51.

Llanquihue : Z.M.B. 13420–1 ; Frutillar, Z.M.B. 13406 ; Puerto Montt, Z.M B. 13399–13400, 6619 ; Maullin, B.M. 1940.4.21.1–4 ; Casa Pangue, N.H.M V. 4664.1 ; Puerto Toledo, Rio Maullin, Station T1 41° 30′ S. 73° 20′ W. U.B. No. 3 ; Estero Pichi Pilluco, E. of Puerto Montt, near sea, station L4 41° 27′ S., 72° 55′ W., U.B. Nos. 1–2, 10–11, 25, 60–61, 64–65, 67.

Chiloé : B.M. 1920.1.20.469, 69.5.3.56 ; Castro, B.M. 1927.5.7.9 ; Chepu, R.S.E. (1 ex.) ; NE. Ancud 41° 51′ 50″ S., 73° 49′ 20″ W., Station T6, U.B. (1 ex.).

No precise locality : N.H.M V. 4665 (5 exs.) ; N.H.M.V. (no register number, 7 exs.) ; N.H.M.V. 4664 (Nos. 4–5) ; Z.M.B. 8368, 4711, 27041, 15874 (2 exs.), 16003, 6695 ; R.N.H.L. 4434 ; S. Chile B.M. 91.8.29.11–14.

ARGENTINE :

Rio Negro : Bariloche B.M. 1932.10.2.67 ; N.H.M.V. 4664.3 ; N.H.M.V. (no register number, 8 exs.) ; San Martin de Los Andes N.H.M.V. 4664.2.

DIAGNOSIS. Small-sized frog, slender build with rather long, narrow, flattened snout ; head slightly longer than broad ; vomerine teeth in two small, straight or only slightly oblique groups between the middle of the choanae; first finger shorter than second; toes with a rudiment of web, not fringed but somewhat flattened; metatarsals slightly separated by webbing; proximal subarticular tubercles prominent and conical; no tarsal ridge present; skin of adults smooth or very occasionally with low, longitudinal ridges; middle ear present; mature males with granular, pigmented nuptial pads on inner palmar tubercle and on first and second fingers; single internal vocal sac with paired openings.

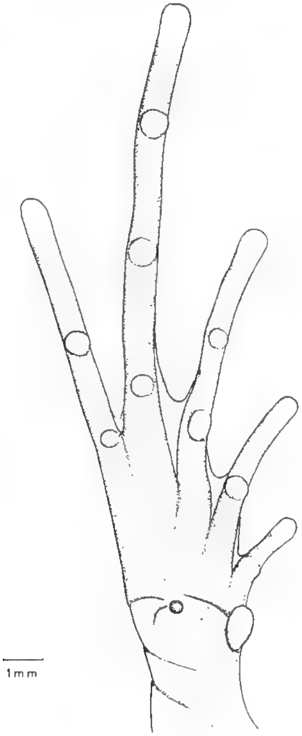

FIG. 19. *E. taeniatus*, U.B. No. 3. Ventral view of foot. (×17·5.)

DESCRIPTION. Adult female, Valdivia, Z.M.B. 9833. Habitus slender Tongue rounded, its posterior half free and notched, ½ the width of the mouth opening. Vomerine teeth in two straight groups between the middle of the circular choanae and separated from each other by a distance equal to the width of one of the choanae. Snout long, oval in dorsal view, the length 1⅓ times the horizontal diameter of the eye, strongly sloping forwards and rounded at tip in profile, the upper jaw barely extending beyond lower jaw. Nares dorsal, slightly projecting, the distance between the middle of the nares less than the interorbital space which is slightly broader than the width of the upper eyelid, their distance from the anterior borders of the eyes 1⅓ times their distance from the tip of the snout. Canthus rostralis obtuse, slightly curved but not well defined; loreal region concave and strongly oblique, upper lip flaring out below; eye large and prominent, not projecting beyond the jaws in dorsal view. Middle ear apparatus fully developed; horizontal diameter of the tympanum ⅓ that of eye. Well-developed, curved, glandular, supratympanic fold from behind eye to arm insertion. Short, cartilaginous omosternum with dilated tip; sternum shaped like a toadstool with pedicel directed anteriorly and calcified and posteriorly a broadly expanded cartilaginous plate without indentation, 1¼ times the length of the epicoracoids and 2⅓ times the length of the omosternum. Tibio-tarsal articulation of adpressed hind limb reaches to the anterior border of the eye. Fingers free of web, first finger shorter than second, subarticular tubercles prominent; two prominent palmar tubercles, the outer round, the inner elongate. Tips of fingers and toes rounded, with simple terminal phalanges. Toes with a rudiment of webbing and some webbing between the metatarsals, notably between the second and third, and third and fourth. An inconspicuous ridge extends along the sides of the toes which are also slightly flattened. A large, elongate, inner metatarsal tubercle with free distal edge and a very small, outer metatarsal tubercle; supernumerary metatarsal tubercles absent; subarticular tubercles well developed and somewhat conical, especially those proximal. Skin on upper parts of body quite smooth; ventral surface smooth, except for a granular area around the vent and

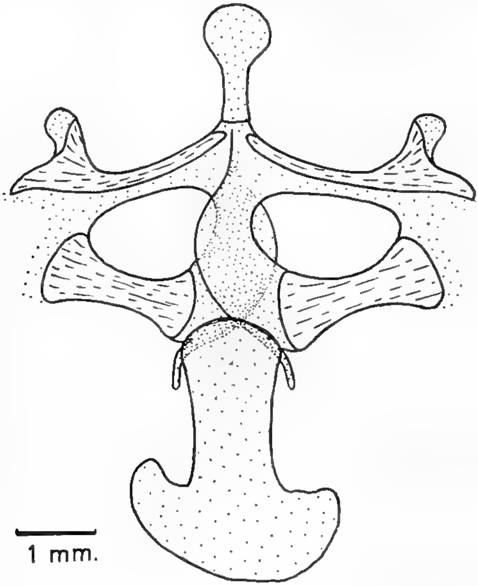

FIG. 20. *E. taeniatus*, U.B. No. 25. Ventral elements of the shoulder girdle. (×17·5.)

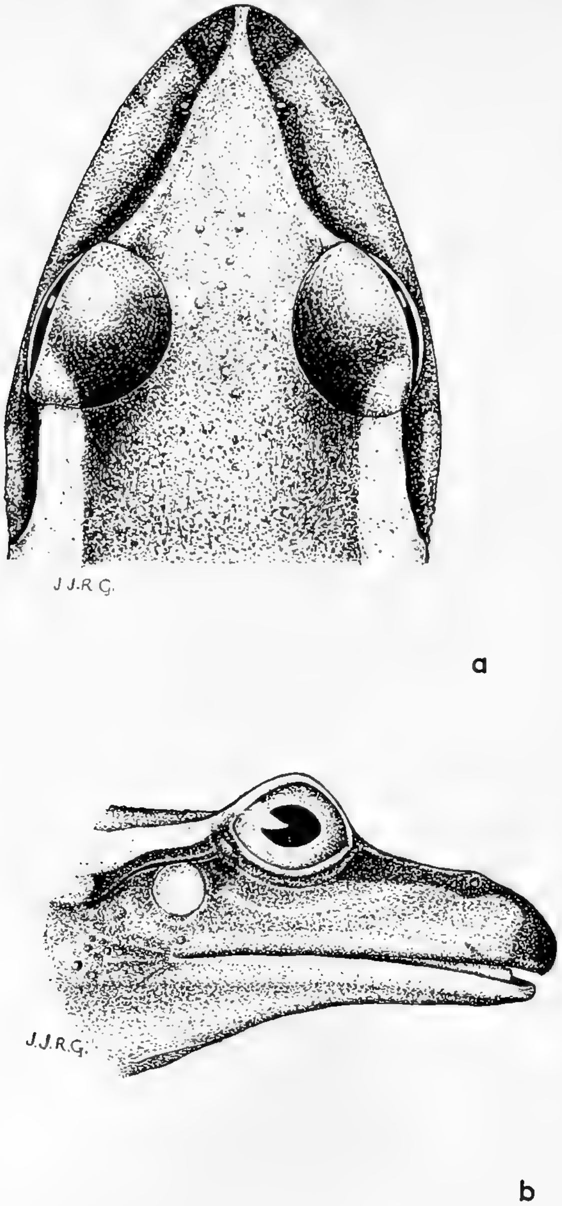

FIG. 21. *E. taeniatus.* a. Dorsal view of head ; b. Lateral view of head.

on the insides of the thighs ; thighs smooth. Dark canthal line continued posteriorly as a well-defined band in the tympanic area and bounded above by a thin, light-coloured line ; longitudinal posteriorly converging dark bands on the dorsum run from behind the upper eyelid to the sacral region ; patch of bold, dark blotches on the posterior surface of the distal half of the femur ; dark spots in the inguinal area ; venter finely speckled ; limbs indistinctly cross barred ; light tarsal line from the inner metatarsal tubercle to the tibio-tarsal joint ; light band present along the upper jaw, bordered by a narrow, dark line.

Measurements :

Length of body .	38·5 mm.
Length of tibia .	19·5 mm.
Length of foot .	21·8 mm.
Length of head .	14·2 mm.
Width of head .	13·3 mm.

VARIATION. Apart from pattern, this species is remarkably constant in its characters, especially in the position of the vomerine teeth. Normally the vomerine teeth are on a level with the middle of the choanae and out of the 174 specimens examined the only exceptions are three examples, all adults from Temuco, Llanquihue and Valdivia, which have the teeth placed farther back and slightly beyond the posterior level of the choanae. Males appear to reach sexual maturity when quite small, the smallest male in full breeding condition that was examined being 21·0 mm. whilst the largest is 35·2 mm. Females are larger than males when mature ; the largest female measures 43·5 mm.

The individuals of this species exhibit a dimorphic pattern, some being striped, as described above, while others are either immaculate or are slightly mottled and with an indication of an hour-glass pattern on the posterior interorbital area. Efforts to correlate geographical distribution, sex and age with the variation in colour pattern were unavailing. In the series examined 51% are of the striped form and 49% are immaculate or mottled. In only 4% is the throat and venter immaculate. The canthal and tympanic band is constant. It was noted that individuals which had groin marks also possessed the spots on the thigh (11 exceptions but four of these may have been due to bleaching of the specimens).

The length of foot relative to total length varies from 0·51–0·67 ($M = 0{\cdot}58$; $N = 117$) and the tibia relative to total length varies from 0·43–0·57 ($M = 0{\cdot}49$; $N = 117$).

SECONDARY SEX CHARACTERS. Males in the breeding condition have nuptial pads consisting of dense clusters of black spinules which cover the medio-dorsal surface of the basal phalanx of the first finger and continue as a narrow band along the median edge of the distal phalanx. Similar spinules are also present on the inner palmar tubercle and, in irregularly shaped patches, on the median edge of the second finger from its base to the proximal edge of the terminal phalanx. A median subgular vocal sac communicating with the mouth by means of paired slits is present in all males, regardless of their sexual condition.

COLORATION IN LIFE. Specimen No. 25 in the University of Bergen collection was described by the collector as having a broad chocolate-brown dorsal stripe with ventral surfaces grey-yellow with small brown spots. Throat yellow-white, without spots.

ECOLOGY. At Chepu, where one example of this species was taken, the forest is very wet and in parts where the canopy is open there is a dense underscrub. Except in the densest parts there is a ground cover of moss. The collector states that the frog was collected from the mosses of the forest floor.

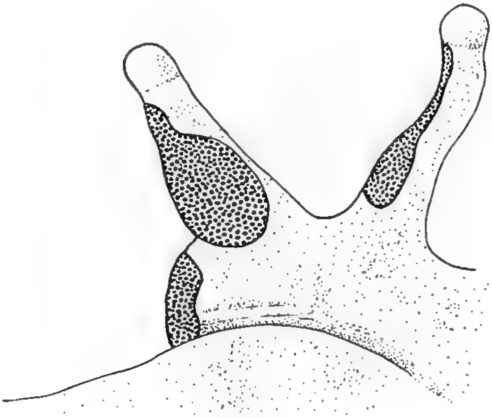

FIG. 22. *E. taeniatus*, R.N.H.L. 4434. Nuptial pads on hand of male. (×17·5.)

The biotopes and substrata relating to the University of Bergen specimens collected in Chiloé and Llanquihue have already been described by Brattström & Dahl (1951) and by Schmidt (1954).

DISTRIBUTION. Santiago to Chiloé. Also in Rio Negro Province in Argentine.

KEY TO CHILEAN SPECIES OF *Eupsophus*

I. Middle ear apparatus absent.
  No supernumerary metatarsal tubercles; tarsal fold present; toes distinctly webbed and fringed . . . . **coppingeri**

II. Middle ear apparatus present.
  1. External signs of typanum concealed by thick, glandular skin; supernumerary metatarsal tubercles present; tarsal fold present; first finger longer, or at least equal to second . . . . **nodosus**
  2. Typanum usually visible externally; tarsal fold absent 3
  3. Vomerine teeth in two straight groups between the choanae; small, slender build, narrow snout in length 1½ times eye diameter . . . . . **taeniatus**
  4. Vomerine teeth in two oblique groups behind the posterior border of the choanae; dorsolateral fold; usually a heel tubercle . . . . **roseus**
  5. Vomerine teeth between the posterior halves of the choanae; no dorsolateral fold; no heel tubercle; usually a vertebral band . . . . **vertebralis**

SUMMARY

The genus *Eupsophus* in Chile is now known to occur between latitudes 32° S. and 53° S. and is represented there by five distinct species (*coppingeri*, *nodosus*, *roseus*, *vertebralis* and *taeniatus*) which are sympatric over a large geographical area within the Valdivian Forest faunistic zone.

An examination of the tympanic cavity of existing types of Chilean *Eupsophus* has helped to clarify the status of the species and especially of *calcaratus*, *maculatus* and *coppingeri*, these three species having been described as having no tympanum ; in fact, only *coppingeri* lacks a middle ear apparatus.

A new key to the component species is presented which employs the tympanum as the chief diagnostic character and each of the valid species is defined, fully described and figured. Secondary sex characters of each of the five species are also described in detail and figured.

The changes in nomenclature adopted in this paper are :

Cacotus calcaratus Günther = *Eupsophus roseus* D. & B.
Borborocoetes masareyi Roux = *Eupsophus roseus* D. & B.
Borborocoetes grayi Bell = *Eupsophus roseus* D. & B.
Cacotus maculatus Günther = *Eupsophus nodosus* D. & B.
Borborocoetes kriegi Müller = *Eupsophus nodosus* D. & B.

It is shown that the name *Eupsophus roseus* has been misapplied to a population of frogs that is sympatric with but distinct from *E. roseus* D. & B. This population is described and is named *Eupsophus vertebralis* sp. nov.

ADDENDUM

The author has been unable to decide whether *Cystignathus hidalgoi* Jiminez de la Espada, 1875, is distinct from the five Chilean species of *Eupsophus* now recognized, although one would have thought that the description of the species being long and exceedingly detailed and the types having come from an area in which all five valid species of *Eupsophus* occur it would have been relatively easy to establish its status.

The possibility of conspecificity with *E. coppingeri* (Günther) or with *E. nodosus* (D. & B.) can be eliminated on the grounds of the presence of a tympanum that is visible externally. *E. roseus* (D. & B.) can also be eliminated on account of the more anterior position of the vomerine teeth which in the *hidalgoi* types were in arched series between the middle of the choanae, separated on the mid-line and with their extremities touching the inner edges of the choanae. In this character *C. hidalgoi* agrees reasonably well with *E. taeniatus* (Girard) and synonymy with *taeniatus* is in fact proposed by Cei (1960). However it is difficult to agree with such a suggestion since there are strongly conflicting differences in the body proportions and skin textures of these two species.

Cystignathus hidalgoi appears to be most closely related to *E. vertebralis*. Each has a plump build, large head and a roughly semicircular contour to the maxillae, also each has a somewhat glandular and porous skin, but on the other hand *vertebralis* differs from *hidalgoi* in lacking dorsolateral bands on the body.

Unfortunately, the types of *Cystignathus hidalgoi* were destroyed during the Spanish Civil War (according to the Curator of the Herpetological Collections at the Madrid Museum).

In view of *Cystignathus hidalgoi* being unidentifiable and the types having been lost and to prevent further taxonomic confusion it might be advisable to submit to the International Commission on Zoological Nomenclature an application for suppression under the Plenary Powers of the specific name *hidalgoi* Jiminez de la Espada, 1875, as published in the combination *Cystignathus hidalgoi*.

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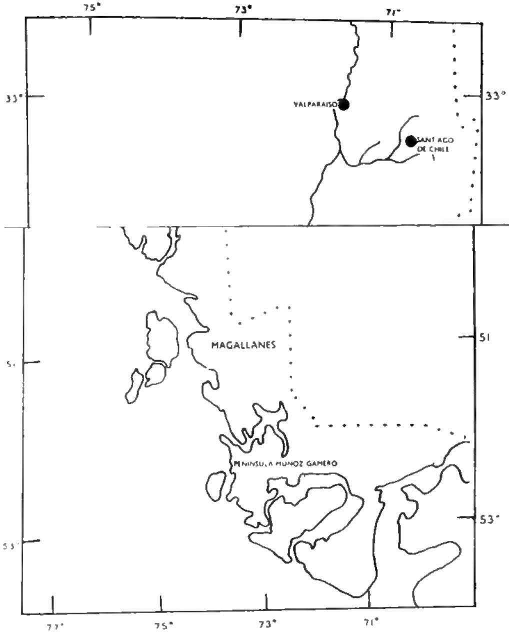
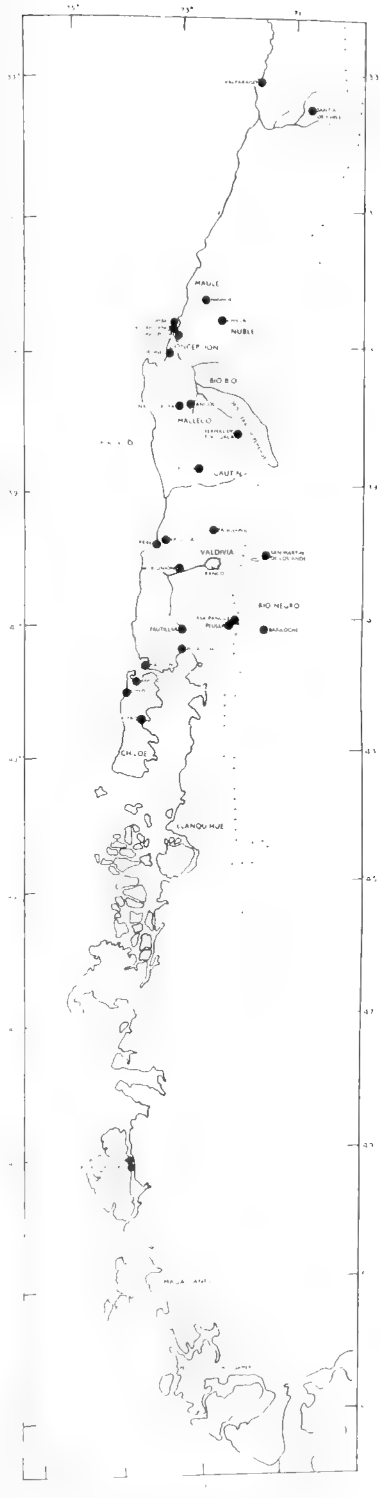


Map Showing Principal Collecting Localities



Map Showing Principal Collecting Localities

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PLATE 1

Eupsophus coppingeri (C.N.H.M. 6256, adult ♀); A, dorsum ×2; B, profile ×3.

PLATE 2

Eupsophus nodosus (N.H.M.V. 4661 : 1, adult ♂) ; A, dorsum 1·3 : B, profile × 3.

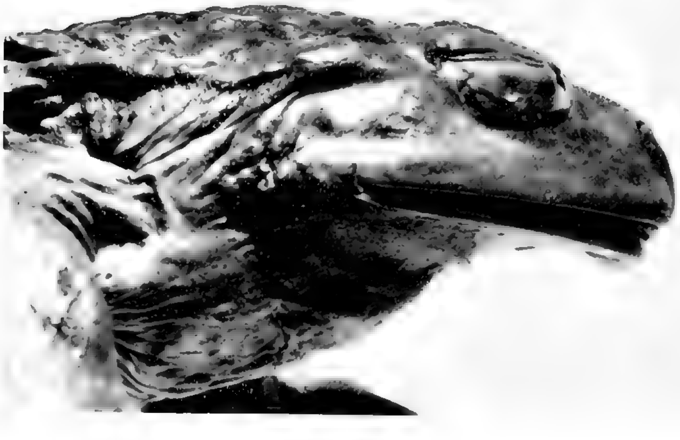

PLATE 3

E. nodosus (N.M.B. 1518, 5); X-ray showing humeral crests and thumb pad.

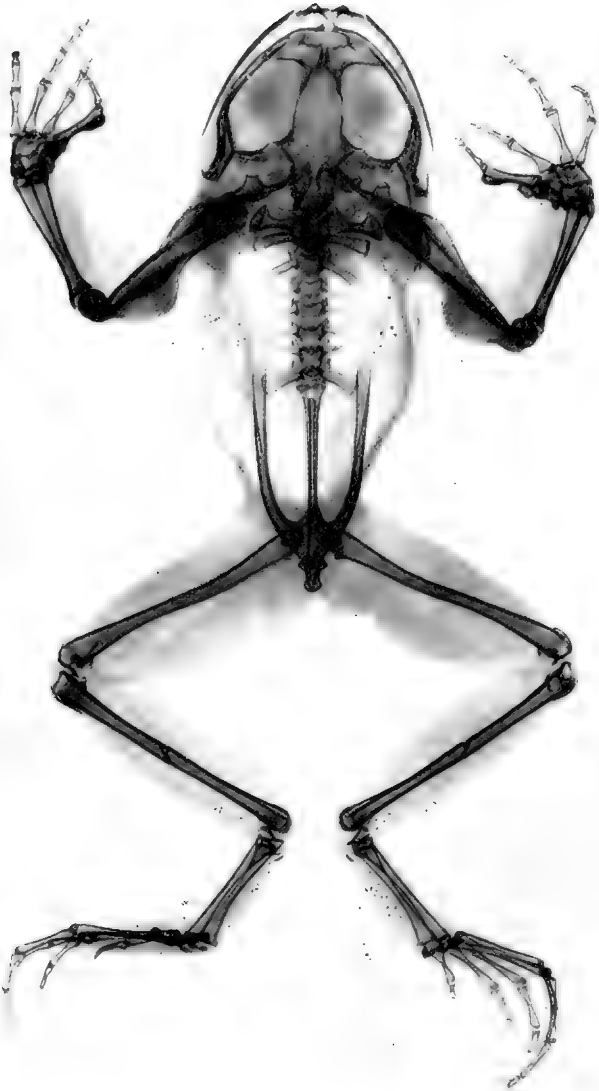

PLATE 4

Fig. 2. *Eupsophus vertebralis* (U.B. 41, adult ♀, × 1·4).
Fig. 1. *Eupsophus roseus* (N.H.M.V. 4060 : 5, adult ♀, × 2·3).

2

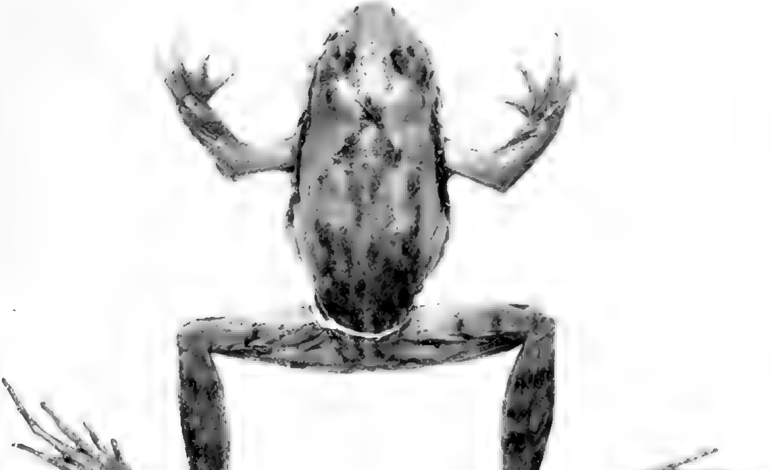

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PLATE 5

Eupsophus taeniatus (Z.M.B. 6619, adult ♀, × 2·4).

PLATE 6

Peninsula Munoz Gamero; taken at 760 m. The stony foreground with a discontinuous plant is not unlike the habitat of *E. coppingeri* at Puerto Eden on Wellington Island.

(Plates 6 and 7 by Professor G. A. Knox. Reproduced by kind permission of the Royal Society Expedition to Southern Chile.)

PLATE 7

Peninsula Munoz Gamero; taken at about 100 m, lower down slope shown in foreground in Fig. 1. The patch of *Nothofagus betuloides* among the slopes of rock and boggy plant is typical of the discontinuous woodlands of this region. A specimen of *E. coppingeri* was found under a stone in open country to the left of this photograph.

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A REVISION OF CERTAIN *BARBUS* (PISCES, CYPRINIDAE) FROM EAST, CENTRAL AND SOUTH AFRICA

P. H. GREENWOOD

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ZOOLOGY Vol. 8 No. 4
LONDON: 1962

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BY

P. H. GREENWOOD

Department of Zoology, British Museum (Natural History)

Pp. 151–208; 15 *Text-figures*

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A REVISION OF CERTAIN *BARBUS* SPECIES (PISCES, CYPRINIDAE) FROM EAST, CENTRAL AND SOUTH AFRICA

By P. H. GREENWOOD

CONTENTS

INTRODUCTION

THIS revision stems from an attempt to check the validity of three supposedly new species found in certain affluent rivers of Lake Victoria (see Whitehead, 1960). It was therefore primarily a revision of the Lake Victoria *Barbus* belonging to the group of species with radiately striate scales (Boulenger, 1911). At the same time, I was identifying a number of newly acquired specimens from Kenya and Tanganyika. The new material increased the range of variability of several species whose limits then had to be checked in relation to other species, apparently similar, but not recorded from East Africa. In this way, three geographical areas were involved and *Barbus* from outside East Africa were drawn into the revision.

Species not closely related to the original species-groups under consideration are not included here. It seems likely that their relationships lie with West African species. Because of these restrictions it is still impossible to draw up a key to all the East African *Barbus*. But, a key to the *Barbus* occurring in the Lake Victoria basin is included since all species from that area are considered in detail.

Two species found in the general area covered by this paper have led to a reappraisal of Herre's genus *Beirabarbus* (Herre, 1936). This genus was created for a *Barbus*-like fish in which the head is covered with raised lines of so-called pit organs. At generic level the systematics of *Barbus* are still unsettled. For this and one other reason, I have decided to consider *Beirabarbus* as an infrageneric category, without any intention of prejudicing future generic divisions. The revision of *Beirabarbus* is also incomplete because the majority of species occur in West Africa and thus lie beyond the geographical (and phyletic) limits of this paper.

Unfortunately, it was impossible to include ecological factors when considering the species, nor was I able to evaluate the significance of coloration (as distinct from the residual black and white colour patterns of preserved material). In this sense, the revision is strictly a museum-worker's concept of the species. It is now left to field-workers as a guide for the preparation of more realistic definitions, in which bionomic factors must perforce play a greater part. I have no doubt that one or two species may eventually prove to be microgeographical variants and I suspect that at least one species here synonymized may have to be resurrected. Likewise, it is apparent that most species are polytypic. Here again, only field-work and more collections will establish the significance of suspected population differences.

From the outset I must express my thanks and gratitude to Dr. Ethelwynn Trewavas who lent me all her unpublished notes on an intended revision of the East African *Barbus* species. To her must go the credit for working out the relationships of the species now referred to *B. amphigramma*, and for establishing the basis on which I have built the synonymy of *B. neumayeri*. Throughout this study Dr. Trewavas has given unstintingly of her time and experience.

Notes on counts and measurements. The standard length (S.L.) and total length (T.L.) are taken in the usual manner. *Interorbital width* is the least distance between the *bony* margins of the interorbital space ; the narrow ledge of skin lateral to the bony margin is not included in this measurement. *Snout length* is measured directly from the anterior orbital margin to the premaxillary symphysis, and the distance *snout to dorsal origin* is also taken directly from the premaxillary union to the first unbranched dorsal ray. *Eye diameter* is measured, horizontally, from anterior to posterior rim of the orbit. All other counts and measurements are in accordance with standard practice.

Barbus apleurogramma Blgr., 1911

(Text-fig. 1)

Barbus apleurogramma Boulenger, 1911, *Cat. Afr. Fish.* **2** : 144, fig. 120.

Barbus mohasicus (part ; 8 of the type specimens). Pappenheim & Blgr., 1914, Fische, *Wissenschaftliche Ergebnisse der Deutschen Zentral-Afrika Expedition*, 1907–1908, **5** : 241.

Barbus rufua (part ; 11 of the types). Pappenheim & Blgr., 1914, *op. cit.*, *tom. cit.*: 243.

Barbus zanzibaricus (part ; one type of *B. z. paucior*), Blgr., 1911, *tom. cit.* : 136.
Barbus (*Agrammobarbus*) *babaulti* Pellegrin, 1935, *Rev. Zool. Bot. Afr.* **27** : 382.
Agrammobarbus babaulti, Poll, 1939, Poissons. *Exploration du Parc National Albert, Mission G. F. de Witte* (1933–1935), fasc. 24 : 29, fig. 10. Poll & Damas, 1939, Poissons. *Explor. Parc. Nat. Albert, Mission H. Damas* (1935–1936), fasc. 6 : 26.
Barbus aphantogramma Regan, 1920, *Ann. Mag. nat. Hist.* (9) **6** : 105.
Barbus schneemanni Klausewitz, 1957, *Senck. biol.* **38** : 279, fig. 1.

Note on synonymy. Except for *B. mohasicus* and *B. rufua* all the species listed above, when first described, were compared with *B. apleurogramma*. Specific differences were based mainly on discrepancies in the number of scales in the longitudinal series and particularly the number of scales bearing lateral-line pores. Some differences in preserved coloration were also noted. *Barbus mohasicus* and *B. rufua* provide a more complicated case because both species were described from multispecific samples.

I have examined type specimens of all the species except *B. babaulti* and *B. schneemanni*, where I have relied on the original and subsequent descriptions and figures. Differences in the number of lateral-line pore scales and scales in the longitudinal series do occur ; but, when all the " species " are compared the variation shows such overlap that these characters can no longer be considered trenchant. Likewise, there are slight differences in the coloration of preserved specimens, but comparable variation is found within samples of *B. apleurogramma* from Lake Victoria (personal observations). No other characters separate the so-called species. When more material is available from the different localities represented by these " species " it may be feasible to recognize morphologically distinct populations, particularly with reference to the number of lateral-line pore scales. For example fishes from Rufua (= *B. rufua* P. & B.) have the highest number of pore scales whilst fishes from Lake Victoria (*B. apleurogramma* Blgr.) have the lowest number.

Description based on twenty-five fishes, 29–45 mm. S.L. (including the types of *B. apleurogramma* and *B. aphantogramma* and some syntypes of *B. rufua* and *B. mohasicus*). All measurements are expressed as percentages of the standard length.

Depth of body 28·4–34·3 (mean (*M*) = 30·5), length of head 25·8–30·7 (*M* = 28·0). Snout length 6·7–10·0 (*M* = 8·0), eye diameter 6·5–8·6 (*M* = 7·0 ; no marked allometry in the sample studied), least interorbital width 11·1–13·3 (*M* = 12·0).

Anterior barbel absent, length of posterior barbel 3·6–6·7 (*M* = 5·1).

Length of last unbranched dorsal ray 13·3–19·8 (*M* = 17·2), length of pectoral fin 16·7–23·4. Distance from snout tip to dorsal origin 49·5–57·0 (*M* = 54·0).

Caudal peduncle length 20·0–25·0 (*M* = 22·6), its depth 11·4–14·9 (*M* = 13·3).

Midlateral longitudinal scale series with 20–25 scales ; lateral-line pores sometimes absent, or present on the first to seventh scales. This character may show some geographical correlation. For example, in Lakes Victoria, Nabugabo and Nakavali no (rarely one) pore scales ; Tanganyika Territory (specimens identified as *B. aphantogramma*) with 0 (f.4), 1 (f.5), 2 (f.6), 3 (f.9) or 4 (f.1) ; Lake Mohasi (*B. mohasicus* in part), 0 (f.2), 2 (f.3), 3 (f.1) ; Lake Rufua (= *B. rufua* in part), 3 (f.2), 4 (f.1), 5 (f.1), 7 (f.1) ; Lake Edward basin (= *B. babaulti*) 2–6 pore scales (no frequencies are available).

Seven and a half to eight and a half (rarely 5 or 7) scales between the dorsal and pelvic fin origins ; 10–12 (mode 10) around the caudal peduncle ; 9–11 in the predorsal row.

Origin of dorsal fin above the last few pelvic rays or even slightly behind the base of the pelvics ; dorsal with 3/7 rays, the last unbranched ray stout and serrated on its posterior face. *Anal fin* with 3/5 rays.

Coloration in preserved material. Ground colour brownish-yellow (greyish in formol-fixed fishes) ; scales (especially the three or four midlateral rows) edged with black, particularly in adult males ; a silver midlateral streak from the opercular margin to the caudal base (often darkening to a thin black stripe) ; a well-defined midlateral black spot at the caudal base, another at the anterior part of the anal base and a third, sometimes more diffuse spot at the base of the anterior dorsal rays. Anal fin colourless basally but often with a broad dark band at its margin ; dorsal hyaline but with a broad, obliquely and downwardly directed band on the upper half of the fin, the distal margin being clear. The base of the dorsal fin membrane is sometimes dark, giving the impression that the pigmentation is continued from the dark spot at the fin base. Caudal often edged with black.

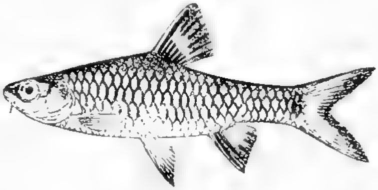

FIG. 1. *Barbus apleurogramma*, holotype, about N.S. (from Boulenger, *Cat. Afr. Fish.*).

Coloration in live fishes (based on specimens from the Lake Victoria basin). Ground colour tarnished silver to golden-silver ; flank scales with dark margins. A dark spot at the base of the anal, caudal and dorsal fins. Dorsal and anal fins black but with an orange-red blotch at the centre. The caudal is outlined in black with the greater part of the membrane orange. Pectoral and pelvic fins orange. The intensity of this orange coloration appears to be related to the level of the fish's sexual activity and is most intense in adult males. Klausewitz's (1957) description of live colours in *B. schneemanni* agrees closely with that for *B. apleurogramma* in Lake Victoria.

Habitat (fishes collected in the Lake Victoria basin). *Barbus apleurogramma* is one of the commonest *Barbus* species in the area, occurring in temporary and permanent streams as well as in the marginal water-lily swamps of the lake. Observations made near Jinja suggest that *B. apleurogramma* spawns in temporary streams when these are flooded during the biannual rainy seasons.

There is no published information from other areas on the habitat preferences of this species.

Distribution. The present records for this species present an interesting pattern. *Barbus apleurogramma* is widely distributed in Uganda (basins of Lakes Victoria and

Edward), in the neighbouring areas of Ruanda Urundi (Lakes Kivu and Mohasi, and associated rivers) and in Tanganyika Territory (various localities including the coastal region near Dar es Salaam, affluent streams of Lake Manyara and from Lake Tanganyika [see Poll, 1953 [under *B. aphantogramma*], who does not record the species from the lake ; however, the B.M. (N.H.) possesses a few specimens, collected by Christy, from " Lake Tanganyika "]). The most northerly limit of the species is Aoué, in the Ennedi plateau region of French Equatorial Africa. (I am most grateful to Dr. Trewavas for allowing me to publish this record, thus partly anticipating the results of her work on the fishes from Ennedi.) These Aoué fishes were found in a small rock pool.

A surprising feature in the distribution of *B. apleurogramma* is its apparent absence from Kenya (excepting, of course, those streams and rivers connected with Lake Victoria). I find this discontinuity rather difficult to explain unless it is due to the lack of extensive collections from areas east of the Rift Valley.

Barbus zanzibaricus Peters, 1868

(Text-fig. 2)

Barbus zanzibaricus Peters, 1868, *Mber. Akad. Wiss. Berl.*: 601.
B. zanzibaricus (part), Blgr., 1911, *Cat. Afr. Fish.* **2** : 136 (excluding *B. z. paucior* Hilgd.).
B. pfefferi Blgr., 1905, *Ann. Mag. nat. Hist.* (7) **16** : 43 (*nom. nov.* for *B. altus* [*non* Günth.], Pfeffer, 1896, *Thierw. O. Afr., Fische* : 43).
B. argyrotaenia Blgr., 1912, *Proc. zool. Soc. Lond.*: 674.

I have not examined Peters' types, but from his original description and from a knowledge of similar species occurring in the type and neighbouring areas (Kenya, near Mombasa), I have no doubt as to the distinctness of *B. zanzibaricus*. Little need be said about the synonymous species. I can find no characters to separate them from *B. zanzibaricus*. Specimens of Hilgendorf's *B. z.* var. *paucior* are excluded from the synonymy since they are referable to *B. kerstenii* and *B. apleurogramma* (see pp. 169 and 155 respectively).

Description based on twenty-two specimens, 39–76 mm. S.L. (including some syntypes of *B. pfefferi* and *B. argyrotaenia*). All measurements are expressed as percentages of the standard length.

Depth of body 28·4–33·5 (M = 31·5), length of head 23·0–29·0 (apparently showing negative allometry). Snout length 6·1–8·7 (M = 7·3) ; eye diameter (showing very slight negative allometry) 6·3–8·8 ; least interorbital width 9·2–12·3 (M = 10·1).

Length of anterior barbel 3·1–7·3 (M = 5·1), of posterior barbel 6·1–10·0 (M = 8·1).

Length of last unbranched dorsal ray 22·5–30·8 (M = 26·0) ; there is some suggestion that this character may show a correlation with locality. Pectoral fin length 17·2–22·5. Distance from snout tip to origin of dorsal fin 48·8–55·5 (M = 52·2).

Caudal peduncle length 17·9–23·9 (M = 20·6), its depth 13·3–17·8 (M = 15·1). The proportions of the caudal peduncle seem to vary from population to population ; fishes from the Sabaki River have the deepest peduncles and those from Dar es Salaam the most slender.

Lateral line with 28 (f.4), 29 (f.17), 30 (f.11), 31 (f.3), 32 (f.2) or 33 (f.1) scales ;

5½ or 6 (less frequently 5 or 6½) between the lateral line and the dorsal origin, 3 or 3½ between the lateral line and the pelvic origin ; 14 (rarely 12, 15 or 16) scales around the caudal peduncle and 10 (f.2), 11 (f.8), 12 (f.11) or 13 (f.1) in the predorsal row.

Dorsal fin origin above the middle of the pelvic fin base. Dorsal with 3/8 rays (one specimen from the Sabaki River with 3/9 rays [Whitehead *in litt.*]) the last unbranched ray ossified, moderately stout and serrated posteriorly. *Anal fin* with 3/5 (rarely 3/6) rays.

Coloration. In *alcohol-fixed* material (types of *B. pfefferi* and *B. argyrotaenia*) ground colour brownish with a silver sheen, especially on the thoracic region ; an intensely silver, relatively broad midlateral stripe. Fins colourless. In *formol-fixed* specimens the ground colour is yellowish becoming darker (greyish-brown) on the dorsal surfaces of the body and head. A dark (brownish-black) and moderately broad midlateral stripe runs from the opercular margin to the caudal fin base. Each lateral line pore scale has, on its posterior border, a small dark blotch above and below the pore. All fins colourless.

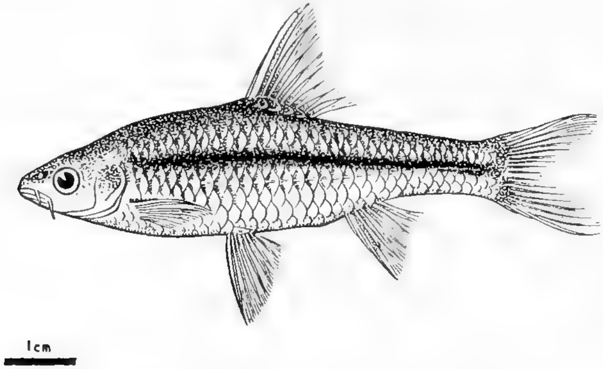

FIG. 2. *Barbus zanzibaricus*, drawn by Lavinia Buswell.

Affinities. Barbus zanzibaricus seems closely related to *B. argenteus* from Angola and the upper Zambezi. The principal interspecific difference lies in the more anterior insertion of the pelvics (relative to the dorsal origin) in *B. zanzibaricus.*

Barbus taitensis Günther, 1894

(Text-fig. 3)

Barbus taitensis Günther, 1894, *Proc. zool. Soc. Lond.*: 91.
B. paludinosus (part) Blgr.; 1916, *Cat. Afr. Fish.* **4** : 251 (specimens from Maji Chumbi, Kenya).

Lectotype. A fish 63 mm. S.L. (B.M. (N.H.) 1890.3.27.12) from Taita.

Description. Measurements and counts are based on the two types and one other specimen (43, 63 and 74 mm. S.L.). Additional data on coloration are derived from ten specimens collected by Mr. P. J. P. Whitehead in the lower Sabaki River. All measurements are expressed as percentages of the standard length.

Depth of body 22·9–23·4, head length 23·0–25·7. Snout length 5·4–7·0, eye diameter 6·3–7·0, least interorbital width 9·5–10·5.

Length of anterior barbel 2·7–3·5; of posterior barbel 5·4–6·6.

Length of last unbranched dorsal ray 21·6–30·0, length of pectoral fin 18·7–21·0. Distance from snout tip to dorsal origin 49·0–54·0. Caudal peduncle length 24·3–25·2, its depth 11·7–14·8.

Lateral line with 33 scales; 6 scales between the dorsal fin origin and the lateral line, 4 between the lateral line and the pelvic origin; 14 scales around the caudal peduncle, 12 in the predorsal row.

Dorsal fin with 3/7 rays, its origin above the middle of the pelvic fin; last unbranched dorsal ray very stout and serrated posteriorly. *Anal fin* with 3/5 rays.

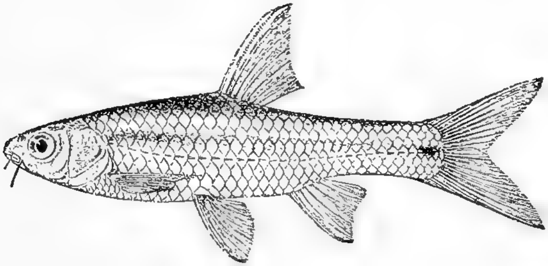

FIG. 3. *Barbus taitensis*, lectotype, about N.S. (from Boulenger, *Cat. Afr. Fish.*).

Coloration. In *alcohol-fixed* specimens, the colour is either brownish with an overall silvery tinge or yellow without any trace of silver. A moderately well-developed silver to blackish midlateral stripe runs from behind the operculum to a point slightly anterior to the caudal fin base. Immediately behind this point there is a small but distinct black spot or blotch. In some fishes the lateral-line pore scales have a small dark spot above and below the tubule. All fins are colourless. In *formol-fixed* fishes the ground colour is yellowish and there is a thin black midlateral band, sometimes overlain by an ill-defined silver tinge. The precaudal spot is intense. All fins colourless.

Distribution. East Africa (*Kenya:* Taita district [type locality]; lower Sabaki River; Maji Chumbi [inland of Mombasa; the collector's notes say from salt water, i.e. probably from a saline pan]. *Tanganyika:* Mangonga River, near Tinde [flows into Lake Kitangiri]).

Affinities. Barbus taitensis is closely related to *B. paludinosus* and cannot easily be separated from that species on morphometric characters alone; it is, however, immediately distinguished by the well-defined spot at the caudal base. Except in one population, no caudal spot has been observed in any specimen of *B. paludinosus*. In the exceptional population, the spot was very weakly developed. The presence of the caudal spot and the slightly larger lateral line scales in *B. taitensis* (33 cf. mode 36 in *B. paludinosus*) are the most obvious characters separating the two species. Another, but somewhat variable diagnostic character is the more anterior position of the pelvic fins in *B. paludinosus* ; usually in this species the greater part of the pelvic fin base is anterior to the perpendicular through the first dorsal ray. In *B. taitensis* this line falls at about the middle of the pelvic fin.

On morphometric characters, *B. taitensis* also closely resembles *B. amphigramma* and there is a further resemblance in the partial pigmentation of the lateral line scales. However, in *B. taitensis* the intensity of the lateral-line pigmentation is less than in *B. amphigramma* and no specimens were found with the entire tubule outlined in black, the usual condition in *B. amphigramma*. Another difference in coloration is the absence in *B. taitensis* of a dark blotch at the base of the anal fin. The two species may also be distinguished by the larger scales of *B. taitensis* (see above). The relative position of the dorsal and pelvic fins in *B. taitensis* and *B. amphigramma* is similar.

On the basis of these characters, *B. taitensis* could represent a fairly well-defined subspecies of either *B. paludinosus* or *B. amphigramma*. The distribution of *B. taitensis* is outside the recorded localities for both these species, yet it is still within their general area of distribution. At present it is impossible to enlarge upon this relationship.

Barbus paludinosus Peters, 1852

(Text-fig. 4)

Barbus paludinosus Peters, 1852, *Mber. Akad. Wiss. Berl.*: 683 ; Boulenger, 1911, *Cat. Afr. Fish.* **2** : 115 (a full synonymy including *B. welwitschii* Günth., *B. vinciguerrai* Pfeff., 1896 ; *B. macropristis* Blgr., 1904 ; but excluding *B. macropristis meruensis* Lönnb., 1907 which is here considered a synonym of *B. amphigramma*) ; Barnard, 1943, *Ann. S. Afr. Museum*, **36** : 171 (including *B. tsotorogensis* Fowler, 1935) ; Ricardo-Bertram, 1943, *J. linn. Soc.* (*Zool.*) **41** : 203 ; Groenewald, 1958, *Ann. Transv. Mus.* **23** : 309, pl. 64, fig. 4.

Barbus gibbosus (*nec* C. & V.), Peters, 1852, *Mber. Akad. Wiss. Berl.* : 683.

Barbus longicauda Blgr., 1905, *Proc. zool. Soc. Lond.* **1** : 63 (*nom. nov.* for *B. gibbosus* Peters, 1852) ; *Idem* (part), 1911, *Cat. Afr. Fish.* **2** : 121, fig. 98 (the Zambezi specimens only).

Barbus akakianus Blgr., 1911, *tom. cit.* : 122, fig. 99.

? *Barbus ivongoensis* Fowler, 1934, *Proc. Acad. Nat. Sci. Philad.* **86** : 428, figs. 17 and 18 ; Crass, 1960, *Ann. Nat. Mus.* **14** : 428.

No further comment is needed on the earlier synonymies published by Boulenger (1911) and Barnard (1943). Where possible I have checked on the material used by Boulenger and, where the specimens were unavailable, on the original descriptions of the synonymous species. Barnard's inclusion of *B. tsotorogensis* Fowler was based on an examination of Fowler's material.

I have examined carefully the material of *B. longicauda* described by Boulenger (1911) and find that all three specimens should be referred to *B. amphigramma* (see p. 165). Unfortunately, Peters' types (originally described as *B. gibbosus*) were not available to me. But, from the original description and from a knowledge of similar *Barbus* in the type region (lower Zambezi) I do not hesitate to refer this species to *B. paludinosus*.

Likewise, our increased knowledge of variation within *B. paludinosus* makes it impossible to distinguish *B. akakianus* from this species. However, I would add this proviso : when further specimens are obtained from Ethiopia, it may be possible to recognize a distinct Ethiopian form of the species.

Fowler's species *B. ivongoensis* (from the south coast of Natal) provides something of a puzzle. On all morphometric characters and on preserved coloration the species cannot be separated from *B. paludinosus*, especially from Natal specimens of the species. Fowler himself noted the relationship of *B. ivongoensis* with *B. longicauda* (now a synonym of *B. paludinosus*). Furthermore, I have secured specimens collected in a neighbouring stream and identified by Mr. R. S. Crass as *B. ivongoensis*. Crass (1960) states that this species differs from *B. paludinosus* in certain morphometric characters (not stated) and in coloration. It is difficult to agree with the first statement if the entire variation of *B. paludinosus* is considered ; nor can I find any difference in preserved coloration. Thus, if there is any difference between the species, it must be in the colours of live fishes. If such a difference exists and if it is at all marked (and not merely one of degree) then there seem to be good grounds for considering the species as distinct. Until this point is clarified it seems preferable to treat *B. ivongoensis* as a tentative synonym of *B. paludinosus*. My own opinion is that the difference is more likely to be of subspecific rank and that *B. ivongoensis* represents a southern, coastal form of the Natal *B. paludinosus*, themselves almost indefinably distinct from the other south and south-west African populations. Several other geographical regions have the same vaguely and unquantifiably distinct populations which may become more rigorously definable when larger regional collections are made and life colours known.

Description. Of all the species dealt with in this paper, *B. paludinosus* is the most variable. Yet, except for one character (dorsal " spine " length) no character can be considered sufficiently trenchant to define subspecies or even populations. Whether this is a reflection of the biological situation or whether it is merely a result of small and scattered collections, I cannot determine. Consequently, a comprehensive species description is given except for those characters which seem to show some intraspecific differentiation.

The description is based on 127 specimens, 31–114 mm. S.L. (including the paratypes of the species, the types of *B. welwitschii*, *B. macropristis* and *B. akakianus*). Where reference is made to *B. ivongoensis* it is to six specimens from Ibilanhlolo, Natal, identified by Mr. R. S. Crass ; they are mentioned only when they lie beyond the range of *B. paludinosus* and they have not been used in calculating the means.

In addition to this material, forty-nine specimens (49–108 mm. S.L.) from Lake Bangweulu were used to obtain data on intraspecific variation in the length of the last unbranched dorsal ray.

Material in the B.M. (N.H.) does not cover the smaller size ranges (11–20 mm.) but these have been carefully analysed and described by Barnard (1943).

Depth of body 21·1–31·2 ($M = 29{\cdot}0$), length of head 22·7–31·0 ($M = 27{\cdot}2$). Snout length 5·4–9·7 ($M = 7{\cdot}3$), diameter of eye 5·0–9·5 ($M = 7{\cdot}1$) except in fishes from Lake Bangweulu which appear to have larger eyes (8·2–9·5, $M = 8{\cdot}3$) ; the usual negative allometry of eye size with standard length is obscured by the high individual variability. Least interorbital width 8·6–12·8 ($M = 10·1$).

Length of anterior barbel is very variable, 1·8–5·2 (Mean, excluding fishes from Satansplatz, S.W.A., 2·9, and for Satansplatz fishes 2·4) ; in a few specimens from Satansplatz the barbel is vestigial. Length of posterior barbel also variable, 2·8–8·8(up to 9·5 in some specimens of *B. ivongoensis* ; in this sample the posterior barbel tends to be longer than is modal for *B. paludinosus*, in which the barbel is usually shorter than the eye. In all six specimens of *B. ivongoensis*, the barbel is longer than or equal to the eye. It is perhaps significant that specimens of *B. paludinosus* with relatively longer posterior barbels are not infrequent in samples from Natal and Zululand). Mean length of posterior barbel (excluding *B. ivongoensis*) 5·8.

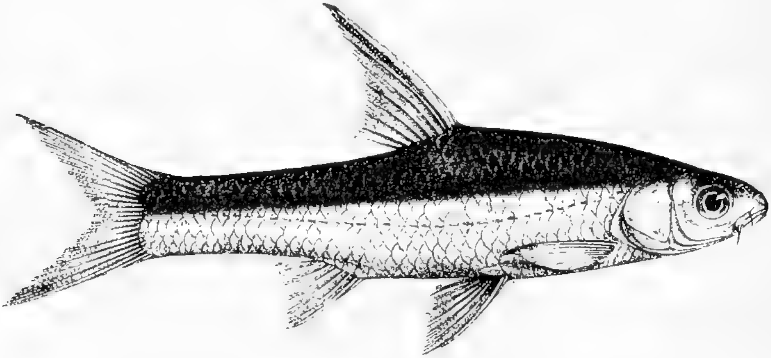

FIG. 4. *Barbus paludinosus* (syntype of *B. macropristis*, from Boulenger, *Fish. Nile*).

The length of the last unbranched dorsal ray shows considerable variation and certain populations are characterized by the length of this ray. The following Table summarizes the results of my analysis, arranged geographically. (See also Jackson, 1959, *Occ. pap. Nat. Mus. S. Rhod.* **23**b : 295–305.)

Care must be exercised when interpreting these results since most populations are represented by small samples. Also, " spine " length may have some allometric relationship with standard length. However, at least two populations (from Lake Rukwa, and Lake Bangweulu) do seem to be characterized by long spines. Furthermore, there seems to be an overall south to north trend of increasing spine length. Fishes from Ethiopia are exceptional to this generalization.

Pectoral fin length 16·9–23·7 ; distance from snout tip to origin of dorsal fin 47·0–56·0 ($M = 51·5$).

Caudal peduncle length 20·9–29·6 ($M = 24·6$), its depth 9·8–16·0 ($M = 12·8$).

Lateral line with 30 (f.1), 32 (f.4), 33 (f.4), 34 (f.19), 35 (f.34), 36 (f.45), 37 (f.2) or 38 (f.6) scales. As in so many characters the lateral-line scale count shows a wide range of variation. No population is characterized by scale size, although there is an ill-defined south to north trend of decreasing scale size ; the lower counts (30–34) occur amongst populations in the southern region of the species range.

Six to eight scales between the lateral line and the dorsal fin origin ; 3–5 between the lateral line and the pelvic origin ; 16–18 (less frequently 14) scales around the caudal fin and 13–16 (rarely 12) in the predorsal scale row.

TABLE I.—*Length of Last Unbranched Dorsal Ray in* B. paludinosus *expressed as % S.L.*

Locality	Range	Mean	Number of specimens	S.L. of specimens (mm.)
South Africa				
Kalkfontein TVL.	18·7–24·5	21·0	7	60–91
Vredefort O.F.S.	17·5–21·2	19·7	3	31–39
Buffalo R., Natal	17·5–20·0	19·0	5	40–45
Durban, Natal	17·3–21·7	19·6	7	37–42
Zululand (various localities)	20·8–26·8	23·5	9	43–67
Ibilanhlalo, Natal*	16·7–20·0	19·0	6	40–54
South-West Africa				
Satansplatz	16·4–25·2	21·3	10	38–77
Voigt's Ground	18·9–23·5	20·8	7	40–57
Angola				
Two localities	17·4–24·4	20·0	4	61–69
Mossambique				
Quellemane (Types)	22·6–23·5	23·0	3	50–53
Nr. Transvaal border	21·6–26·6	23·6	5	46–58
Rhodesia				
Bulovale, U. Zambezi	23·2–24·3	23·8	4	37–49
Luombura R.	21·5–26·0	24·5	10	44–68
Lulali R.	22·0–27·8	25·6	7	58–114
Lake Bangweulu	19·9–38·7	30·2	42	43–108
Katanga				
Two localities	20·4–21·6	—	2	51–97
Lake Nyasa	20·6–25·4	23·6	12	54–100
Tanganyika Territory				
Lake Rukwa	24·7–29·5	27·5	10	47–88
Luika R. (affluent of Lake Rukwa)	22·2–27·1	25·0	8	57–85
Lake Manyara	23·5–27·9	25·0	8	45–104
Other localities	21·0–27·0	24·6	8	40–85
Lake Victoria	21·6–28·7	24·5	4	81–113
Ethiopia	20·0–23·8	21·7	5	48–90

* Specimens identified as *B. ivongoensis*.

Dorsal fin with 3/7 (rarely 3/6) rays, the last unbranched ray enlarged, bony and serrated posteriorly (see also Barnard, 1943 for ontogenetic changes). One fish from the Akaki River (Ethiopia) has the first branched ray thickened and weakly serrated on the proximal part of the posterior face. When the dorsal is erected so that the last unbranched ray forms an angle of 60° with the horizontal, the margin of the fin is nearly vertical. The origin of the dorsal relative to that of the pelvic fins shows some variation; usually, the pelvic origin is clearly in advance of the dorsal (the greater part of the pelvic base is anterior to the first unbranched dorsal ray) but in some fishes the pelvic origin is only slightly in advance of the dorsal. *Anal fin* with 3/5 (rarely 3/6) rays. Length of pectoral fin 16·9–23·7% of standard length.

Coloration. In *alcohol-fixed* specimens there is always an overall silvery sheen especially on the cheeks and opercular region of the head, and on the ventral body surfaces. A midlateral stripe runs from behind the operculum to the caudal base. This stripe is always present but varies in intensity from a rather more intense silver than the body to a distinctly greyish-silver. The most posterior part of this stripe may be slightly expanded but in no specimen does it appear as a distinct spot or blotch (cf. *B. taitensis*). Beneath the silver sheen the ground coloration varies from dark grey to brown to yellowish-fawn. All fins are colourless.

In *formol-fixed* specimens there is little trace of silver and the ground colour is usually yellowish. The midlateral stripe appears as a black or greyish-black line. Fourteen fishes (27–44 mm. S.L.) from the Luangwa Valley, Zambezi system, show a well-defined black spot at the base of the anal fin. The intensity of this mark is greatest in smaller specimens, but it is still obvious even in the largest fishes. A slight concentration of melanophores has been observed at the anal base in some small fishes from other localities, but never in the form of distinct spots. In all probability the manifestation of an anal spot or blotch is correlated with environmental conditions and subsequently the method of preservation. Age too may be a factor because no spots have been found in fishes more than 50 mm. S.L. In contrast, such spots are generally present in the related *B. amphigramma*, even in individuals over 50 mm. long.

In a few populations of *B. paludinosus* some of the anterior lateral-line scales are pigmented, giving a superficial resemblance to *B. amphigramma*. In the latter species, however, the entire lateral-line scale series is pigmented whereas in *B. paludinosus* not more than the anterior third is pigmented. All fins are colourless.

Live coloration. Peters (1868) and Barnard (1943 and 1948) have described the live colours of this species in Mossambique, South and South-West Africa whilst I have colour notes on the Lake Victoria population. All descriptions of the body colour (greenish above, silvery to white below) are in agreement but there is some uncertainty about fin coloration. Peters describes all the fins as red whereas Barnard, for fishes from the Okavango River, described the dorsal and caudal fins as faintly pinkish, and the pectorals, pelvic and anal fins as slightly yellowish. For other specimens (from the Orange and Great Fish Rivers, S.W.A.) Barnard gives creamy-yellow as the fin colour. This latter coloration compares with that found in the Lake Victoria fishes. Barnard (1948) concludes that rosy or salmon is a better term for those fins described as red by Peters. Because of this apparent variation in fin colours it would be useful to know what correlation there is between colour and habitat or geographical location. There is, of course, also the possibility of a seasonal or reproductive variation in fin colours.

Diagnosis and affinities. Barbus paludinosus is most closely related, on superficial characters, to *B. taitensis* and *B. amphigramma*, the only other East African members of the group with small scales and strongly serrated dorsal fin spines. Morphometric differences between these three species are slight and they are more easily differentiated by their colour patterns (see pp. 159 and 167). *Barbus paludinosus* lacks a caudal spot and pigmentation of the entire lateral line (see above for a note on exceptional populations where part of the line may be pigmented) ; one or both characters are present in *B. amphigramma* and *B. taitensis*.

Distribution. *Barbus paludinosus* has the widest distribution of all the species considered in this paper. It extends from Ethiopia in the north through East and Central Africa, extending westwards into Angola and reaches the southernmost limits of its distribution in Natal. Fuller details are given in Table I. The habitats of the species include lakes, rivers and streams.

Barbus amphigramma Boulenger, 1903

(Text-fig. 5)

Barbus amphigramma Boulenger, 1903, *Ann. Mag. nat. Hist.* (7) **11** : 53, pl. 5, fig. 4 ; *Idem*, 1911, *Cat. Afr. Fish.* **2** : 145, fig. 121 ; Pellegrin, 1905, *Mem. Soc. zool. France* : 178.

Barbus thikensis, Boulenger, 1905, *Proc. zool. Soc. Lond.* **63** : pl. 7, fig. 2 ; *Idem*, 1911, *op. cit.* **120** : fig. 96.

Barbus longicauda (part) Blgr., 1905, *op. cit.* **63** ; *Idem*, 1911, *op. cit.* **121** (excluding the Zambezi specimens described by Peters [1852] as *B. gibbosus*).

Barbus macropristis meruensis Lönnberg, 1907, *Kilim.-Meru Exped., Fishes*, 3.

Barbus paludinosus (part), Blgr., 1911, *Cat. Afr. Fish.*, **2** : 115 (only the specimen of *B. macropristis meruensis* Lönnb.).

Barbus helleri Hubbs, 1918, *Fld. Mus. nat. Hist. Chicago*, Zool. Ser. **12** : 12, pl. 2.

The original work leading to this synonymy was carried out by Dr. Ethelwynn Trewavas. Her notes embodying the reasons for considering these species conspecific are extensive and reflect much careful work and thought ; Dr. Trewavas very graciously placed all this material at my disposal.

I have been able to check certain points and also to reinforce Trewavas's conclusions with the extra material now incorporated into the Museum's collections. We disagree on one point, namely the inclusion of *B. longicauda* in part. Dr. Trewavas considered, but with some uncertainty, that both the Zambezi and Athi populations identified as *B. longicauda* were actually referable to *B. amphigramma*. On the other hand, I think that only the Athi specimens are of *B. amphigramma* ; the Zambezi fishes (types of *B. gibbosus* Peters, *nec* C. & V.) being specimens of *B. paludinosus* (see p. 160). My conclusions are based on two factors ; first, Peters' description of the coloration and second, the locality. It seems unlikely that Peters' detailed description would have omitted the typical " *amphigramma* " markings; the colours described are those of fresh or newly preserved (in spirit) *Barbus paludinosus*. Regarding locality, there is no record yet of any *B. amphigramma* occurring in the region between Lake Manyara and the lower (or for that matter, upper) Zambezi River. But *B. paludinosus* does occur in the Zambezi and in East, Central and southern Africa.

Barbus amphigramma was described as having the last unbranched dorsal ray neither greatly enlarged nor serrate. Examination of the largest syntype (35 mm. S.L.) shows, however, a few small serrae. The serrae are absent in the smaller type specimens. The ontogeny of serrated dorsal rays and the relationship between size and the number of serrae has been well demonstrated in Barnard's work on South African *Barbus* (Barnard, 1948). Admittedly, very few other specimens of *B. amphigramma* have such a weak and feebly serrate spine as the largest syntype. Yet, there are no other distinguishing characters to separate this specimen from the others. Indeed, it differs only in the nature of its dorsal spine.

Once it is admitted that *B. amphigramma* belongs to the group of small *Barbus* with serrated, bony, last unbranched dorsal rays, it is impossible to separate *B. thikensis* from *B. amphigramma*. In Boulenger's description it is only the supposed nature of the dorsal spine which distinguishes the two species. Also, once this fact is accepted, attention is drawn to the resemblance between *B. helleri* and *B. amphigramma*.

Neither Dr. Trewavas nor I have examined the types of *B. helleri* but from Hubbs' very full description and detailed figure it is possible to check on the reasons he gives for distinguishing between this species and *B. thikensis* (= *B. amphigramma*).

Hubbs lists the following differences: "From *thikensis*, *helleri* differs in the narrower interorbital, lower dorsal spine, smaller scales, and apparently in the more distinct lateral band, and in the constant presence of the caudal spot."

The differences in coloration are invalid because the types of *B. thikensis* do have a caudal spot and the lateral band is distinct. Age and preservation have perhaps reduced the clarity of these characters in the types, but their presence is undoubted. Furthermore, in new specimens (formol fixed) from the Athi River the lateral band is as distinct as that in the figured type of *B. helleri*.

Dorsal spine length is a variable character and may even characterize particular populations. Certainly, in the material now available, the range covers the length of spine supposedly characterizing *B. helleri*.

I can find no disparity between the range of my scale counts for *B. thikensis* and those given by Hubbs for *B. helleri*.

Finally, there is the question of a narrower interorbital in *B. helleri*. As Trewavas first suggested, this may be due to different methods of measurement. Certainly the "least interorbital width" used by Boulenger, Trewavas and myself gives a wider interorbital distance for *B. thikensis* (2·2–2·7 in head cf. 2·9–3·6 for *B. helleri*). We measure, from margin to margin, the bony area between the eyes at its narrowest point. If, however, the "interorbital" is taken to exclude the narrow supraorbital shelves of bone then one gets ratios for *B. thikensis* which are comparable with Hubbs', viz. 3·0–3·7.

When all this evidence is taken into account it is impossible to maintain the specific distinctness of *B. helleri*.

Description. Based on forty-seven specimens, 31–74 mm. S.L. (including three syntypes of *B. amphigramma* and four syntypes of *B. thikensis*. I have examined Lönnberg's types of *B. macropristis meruensis* but these are not included in the morphometric data given below). All measurements are expressed as percentages of the standard length.

Depth of body 22·5–29·6 ($M = 26·4$), length of head 23·2–29·0 (slight negative allometry). Dorsal head profile sloping moderately steeply but in some fishes (especially those $>$60 mm. S.L.) there is a pronounced nuchal hump ; this may be a populational character since it is more marked in some specimens from certain areas (e.g. northern Eusso Nyiro River near Thompson's Falls). Snout length 6·1–9·6 (M = 7·1), eye diameter 5·0–8·3 (negatively allometric), least interorbital width 9·0–12·5 (M = 10·3).

Length of anterior barbel 1·4–5·9 (M = 3·3), length of posterior barbel 3·5–9·8 (M = 5·7).

Length of last unbranched dorsal ray highly variable and possibly showing geographical correlation. For the species as a whole, length of dorsal spine is 13·8–24·7 (M = 18·5) ; populations with characteristic spine lengths are : Namango River, Longido district, Tanganyika Territory 18·8–23·0%, M = 22·4% (N = 4), S.L.'s 61–73 mm.; Kadam Mountain, Uganda, 20·5–22·8%, M = 21·4% (N = 6), S.L 's 59–74 mm.; a river flowing into Lake Baringo, Kenya, 22·4–24·4%, M = 23·2%, (N = 3), S.L.'s 40–44·5. The mean for all 29 (31–70 mm. S.L.) other specimens from various localities is 16·3% and the range 12·2–19·1. The validity of this character as a population marker is still unestablished, particularly since the exceptional populations are each represented by so few specimens and because individuals of the former are amongst the largest known.

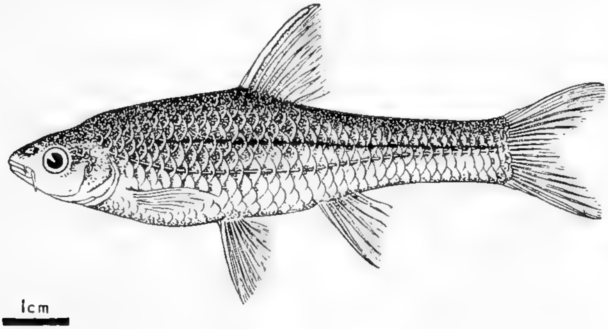

FIG. 5. *Barbus amphigramma*, drawn by Lavinia Buswell.

Distance from snout-tip to dorsal orgin 49·0–56·0 (M = 52·3), length of pectoral fin 17·2–22·2.

Caudal peduncle length 22·0–27·5 (M = 25·1), its depth 10·7–14·7 (M = 13·1).

Lateral line with 33 (f.1), 34 (f.9), 35 (f.15), 36 (f.17), 37 (f.2) or 38 (f.1) scales, 6 (f.1), $6\frac{1}{2}$ (f.11), 7 (f.23), $7\frac{1}{2}$ (f.4) or 8 (f.3) scales between the lateral line and the dorsal fin origin ; 3 (f.4), $3\frac{1}{2}$ (f.4), 4 (f.32), $4\frac{1}{2}$ (f.3) or 5 (f.1) between the lateral line and the pelvic origin ; 14 (f.11), 16 (f. 27) or 18 (f.3) scales around the caudal peduncle, 13–16 (mode 15) in the predorsal series.

Dorsal fin with 3/7 rays (3/8 in one specimen) the last unbranched ray ossified but relatively slender, serrated on its posterior face (at least in fishes $>$ 35 mm. S.L.). Origin of dorsal slightly behind that of pelvics. *Anal fin* with 3/5 rays.

Coloration (in formol-fixed specimens) above the midlateral line greyish-brown, yellowish below ; in some specimens the entire ground colour is uniformly yellow.

There is a thin, intensely black streak, slightly curved above a midlateral position on the flanks, but becoming midlateral posteriorly. This line is backed by a less intense, rather diffuse and broader black band. A second, even finer black line follows the course of the lateral-line scales. It is formed by small dots of pigment which outline the tubule on each lateral-line scale. In some specimens the tubule is flanked above and below by one or more spots and is not strictly outlined in black. Whatever type of pigmentation there may be, the entire lateral-line scale series carries black pigment (this is in contrast to certain populations of *B. paludinosus*, where some of the anterior lateral-line scales are pigmented, giving the fish a superficially " *amphigramma* "-like appearance). Anteriorly the two lines are clearly separate, but posteriorly they merge at about the mid-point of the caudal peduncle. A small but distinct black spot is found at the base of the caudal fin. At the anal fin base there is usually a darkened area extending over three or more scales. This blotch varies in intensity from a few scattered melanophores to a group of distinct spots. Such variation and even absence of the spot in specimens from one sample suggests that preservation may affect the constancy of the character.

The fins are predominantly hyaline, although in some fishes the anterior margin of the dorsal, anal and pelvic fins may be dusky.

Few specimens in the B.M. (N.H.) were fixed in alcohol. The major differences between spirit- and formol-fixed specimens is the generally darker ground colour (brown above, brownish-yellow below) on which the lateral stripes and the caudal and anal spots do not show up so clearly. There is also a faint silvery sheen both laterally and ventrally on the flanks and caudal peduncle.

Live coloration. I am indebted to Mr. P. J. Whitehead for this description. Olive-green on back, silvery below midlateral line, operculum silver ; a small black dot at the caudal base and a faint, dark midlateral line. Lateral-line scales pigmented around the tubules. A black mark at the base of about the first five anal rays. All fins colourless.

Habitat. The species appears to be almost exclusively fluviatile, although its sudden appearance in temporary streams around Lake Victoria suggests that some populations may be lacustrine for at least part of their life history ; this conclusion is supported by the single specimen from Kisumu Bay.

Distribution. Kenya : (Athi, Thika, Tana, Nzoia, Sagana and the northern Eusso Nyiro River systems ; the Amala River, Lake Baringo). *Uganda :* Affluent streams of Lake Victoria (possibly the lake itself) ; streams on Kadam Mountain. *Tanganyika :* Namanga River, Longido district ; Lake Manyara ; stream originating on Meru Mountain.

Nichols & Boulton's (*Amer. Mus. Novit.*: 264, 1927) record of this species from Angola is doubtful and should be checked.

Barbus kerstenii Peters, 1868

Barbus kerstenii Peters, 1868, *Mber. Akad. Wiss. Berl.* : 601 ; Boulenger, 1911, *Cat. Afr. Fish.* **2** : 130, fig. 107.

Barbus nigrilinea Pfeffer, 1889, *Jhb. wiss. Akad. Hamburg*, **6** : 19 ; *Idem*, 1893, *Ibid.* **10** : 36, pl. 1, fig. 3.

? *Barbus salmo* Pfeffer, 1896, *Thierw. O. Afr. Fische* : 56.
Barbus lumiensis Blgr., 1903, *Ann. Mag. nat. Hist.* (7) **11** : 52, pl. 5, fig. 2 ; *Idem*, 1911, *op. cit.* **2** : 125, fig. 102.
Barbus zanzibaricus var. *paucior* Hilgend., 1905, *Zool. Jahrb.* (*Syst.*) **22** : 414.
Barbus zanzibaricus part (two of *B. z. paucior* syntypes), Blgr., 1911, *op. cit.* **2** : 136.
Barbus minchinii Blgr., 1906, *Ann. Mag. nat. Hist.* (7) **17** : 436 ; *Idem*, 1907, *Fish Nile* : 245, pl. 45, fig. 4 ; *Idem*, 1911, *Cat. Afr. Fish.* **2** : 126, fig. 103.
Barbus serrifer (part), Blgr., 1911, *op. cit.* **2** : 124 (specimens from Kituta only).
Barbus mohasicus (part) Pappenheim & Boulenger, 1914, *Wiss. Ergebn. Deuts. Zentral-Afrika Exped.*, 1907–1908, *Zool.* **3** : 241, pl. 4, fig. 2 ; Boulenger, 1916, *Cat. Afr. Fish.* **4** : 253.
Barbus mohasicus var. *paucisquamulatus* Pellegrin, 1933, *Bull. Soc. zool. Fr.*: 58.
Barbus luhondo Papp. & Blgr., 1914, *tom. cit.* : 242, pl. 4, fig. 3 ; Blgr., 1916, *op. cit.*, *tom. cit.* : 255.
Barbus rufua (part) Papp. & Blgr., 1914, *tom. cit.* : 243, pl. 4, fig. 4 ; Blgr., 1916, *op. cit.*, *tom. cit.* : 256.
Barbus loveridgii part (one of the syntypes) Blgr., 1916, *Ann. Mag. nat. Hist.* (8) **17** : 244–245.
Barbus akeleyi Hubbs, 1918, *Fld. Mus. nat. Hist. Chicago*, Zool. Ser. **12** : 13, pl. 3.

Notes on the synonymy. Excepting *B. nigrilinea*, *B. salmo* and *B. akeleyi*, I have examined type specimens of all species listed above. This material, together with other specimens from a wide range of localities has demonstrated the difficulty of maintaining the various species. On my interpretation of *B. kerstenii*, intraspecific variation is moderately high and it may yet be necessary to recognize more than two subspecific groups (see below, p. 171). Regarding those species whose types I have not seen, there is little to discuss, except that the original descriptions are sufficiently comprehensive to leave no doubt as to their true identity. Nevertheless, *B. salmo* is included tentatively because the type is mislaid (Dr. Deckert, *in litt.*) and Pfeffer's description indicates a small eye. But the author did not state the size of the type, which, if it is a large fish could account for the discrepancy in relative eye sizes. In all other characters, *B. salmo* and *B. kerstenii* compare very closely.

Although it is virtually impossible to separate the " species " now considered conspecific with *B. kerstenii*, it must be stressed that this conclusion is based on preserved (and often old) material. Field work may still show some clearcut differences in coloration. Fishes previously identified as *Barbus minchinii* (i.e. populations from Lakes Victoria, Kivu, Bunyoni, and the rivers and lakes of north-east Ruanda Urundi) may yet have to be reconsidered as representing a subspecies.

A population showing some clear-cut departure from the majority of *B. kerstenii* is that represented by the type specimens of *B. luhondo*. I have given it subspecific status.

Besides these rather localized geographical variations there is a larger division of the species (based on scale size and barbel length) into fishes from Tanganyika and those from Kenya. The different groups are discussed below.

Lectotype. A fish 66 mm. standard length from the coast opposite Zanzibar (i.e. probably Bagamoyo), Berlin Museum Number 6818.

Description. Based on forty-three specimens, 38–75 mm. S.L. (including the lectotype and two paratypes of *B. kerstenii*, one type of *B. lumiensis*, two syntypes of

B. minchinii and four syntypes of *B. mohasicus*). Types and other specimens of *B. rufua* (38–41 mm. S.L.) and *B. luhondo* (44–71) are not included in the general description (see below, p. 171), except to note those characters which lie beyond the range of the other specimens (see below, p. 171).

All measurements are expressed as percentages of the standard length.

Depth of body 28·2–35·2 (*M* = 30·8), length of head 24·3–30·2 (*M* = 27·2). Snout length 6·8–9·5 (*M* = 8·1), eye diameter 6·7–9·5 (*M* = 7·6), least interorbital width 9·1–13·5 (*M* = 11·0).

Length of anterior barbel 4·9–9·4, mean 7·2 (range 2·6–9·6 in *B. rufua* and 3·7–6·8 in *B. luhondo*) ; length of posterior barbel 8·0–13·1, mean 10·1 (range 5·8–10·4 in *B. rufua* and 7·4 9·5 in *B. luhondo*). In relation to eye diameter the length of the anterior barbel for the species as a whole (including *B. rufua* and *B. luhondo* types) may be summarized as follows : equal to eye (=) 17%, longer than eye (>) 21%, shorter than eye (<) 62% of the studied material. In fishes from Kenya the proportions are : (=) 22%, (>) 52%, (<) 26% ; for Tanganyika fishes (including those from Lake Tanganyika (=) 48%, (>) 8% and (<) 44%. Specimens of *B. rufua*, *B. luhondo* and fishes identified as *B. minchinii* (including the types) fall within the " Tanganyika " group.

Length of last unbranched dorsal ray 16·2–23·9, mean 20·0 (this figure includes *B. rufua*, but excludes *B. luhondo* in which the range is 14·9–17·3) ; distance from snout to dorsal origin 49·3–61·5 (*M* = 54·5). Length of pectoral fin 19·4–24·4 (*B. luhondo* 16·1–19·3).

Length of caudal peduncle 18·5–23·6 (*M* = 21·5), its depth 12·7–15·8 (*M* = 14·6).

Lateral line scale count for the species as a whole (including *B. rufua* and *B. luhondo* types) 23 (f.2), 24 (f.11), 25 (f.22), 26 (f.11) and 27 (f.4) ; for Tanganyika specimens the counts are 23 (f.2), 24 (f.3), 25 (f.12), or 26 (f.2) and for those from Kenya, 25 (f.6), 26 (f.15) or 27 (f.4). There are insufficient specimens of *B. rufua, B. luhondo* and *B. mohasicus* to indicate the group with which they show greatest affinity. *Barbus minchinii* (at least the Lakes Victoria and Kivu populations) belong to the smaller scaled " Kenya " group.

All other scale counts are given for the species as a whole. There are 4½ or 5 (mode 5) scales between the lateral line and the dorsal origin and 2–3½ (mode 3) between the lateral line and the pelvic origin ; 10–12 (mode 12), rarely 14 scales around the caudal peduncle, and 9–11 (mode 10) in the predorsal row.

Dorsal fin with 3/7 rays (except in *B. luhondo* where the count is 3/6 [f.5] or 3/7 [f.3]). Last unbranched ray strong, bony and serrated posteriorly. Dorsal origin somewhat behind that of the pelvics or above the pelvic origin. *Anal fin* with 3/5 rays (including *B. luhondo*).

Coloration. In *alcohol-fixed* material the ground colour is brownish shading to yellowish-brown ventrally ; often a silver sheen. Operculum and cheeks bright silver. A faint, thin, black midlateral stripe runs through the centre of a broader, bright to dusky silver band which stretches from the posterior opercular margin to the caudal base. This band ends, posteriorly, in a more or less distinct black spot. All fins are colourless.

In *formol-fixed* material the ground colour varies from yellowish-grey to yellow, being darker above the lateral line ; no traces of silver are visible on the head or flanks. There is often a thin (one scale wide) dark band running mid-dorsally from the level of the operculum to the caudal origin. Laterally, there is a distinct but thin, black midlateral line originating below the dorsal and running through the centre of a broad, dusky to greyish band. The spot at the caudal base is of variable intensity. All fins are colourless.

Coloration of live fishes. This description is based on fishes from Lake Victoria (i.e. *B. minchinii*). Golden-silver above shading to silver below ; scales above the lateral line with dark centres. A bright orange spot on the operculum, the head otherwise bright silver. Caudal and anal fins clear orange, dorsal faintly orange. Pectoral and pelvic fins colourless.

Discussion. From the description given above there is a suggestion that at least one subdivision, and probably more could be recognized. The most distinctive subgroup is that represented by fishes from Lake Luhondo (i.e., the material given specific rank as *B. luhondo* by Pappenheim & Boulenger). This population occupies a small and isolated crater-lake in Ruanda Urundi. Its departure from the modal *B. kerstenii* condition is not, therefore, surprising. At present it is impossible to determine whether these specimens represent phenotypic (perhaps, since it is a crater-lake, ecophenotypic) or genotypic variants. The Luhondo fishes differ from other *B. kerstenii* in having shorter dorsal spines and pectoral fins, more bluntly rounded snouts, shorter barbels and an increase in the frequency of individuals with only six branched dorsal rays. Because I am ignorant of the causal factors underlying these deviations and because the material is so scanty, I propose to put the status of the Luhondo fishes into a suspense account and recognize them as constituting a distinct subspecies (see below).

The two other trends discernible are less clear-cut and I do not intend using them as a basis for a formal taxonomic division. These subdivisions can be made on a broad geographical basis into " Kenya " and " Tanganyika " fishes, the latter including specimens from Lake Tanganyika and streams in Tanganyika Territory, the type area for the species. The main character distinguishing Tanganyika from Kenya fishes is their shorter barbels : 92% of specimens have the posterior barbel shorter than or equal to the eye diameter, whereas in Kenya fishes only 48% have this relationship. Apparently there is also a tendency for Kenya fishes to have smaller scales, the mean number of lateral-line scales being 26 compared with 24·6 for Tanganyika individuals. However, the number of specimens available is insufficient to establish the significance of these slight differences. Likewise, lack of material makes it impossible to check on the possible divergence of populations from Lakes Victoria, Edward, Kivu, Mohasi and Bunyoni.

Thus, for the moment only two subspecies can be recognized, namely :

Barbus kerstenii kerstenii Peters

(Text-fig. 6)

A full description of the nominate subspecies is given on p. 169.

Distribution. Kenya : (Tana, Athi, Ragati, Sagana, Nyanza, Taveta and the

Northern Eusso Nyiro Rivers; the Amala River, an affluent of Lake Baringo; shores of Lake Victoria). *Uganda:* (the Lake Edward and Victoria basins including the Kyoga system; Lakes Bunyoni and Mutanda). *Tanganyika:* (Morogoro; Bagamoyo, Lake Tanganyika; the exact type locality is unknown but is given as the coast opposite Zanzibar and thus probably is in the Bagamoyo district). *Ruanda Urundi:* (Lake Mohasi, *Lake Kivu* and its drainage system).

Habitat. Judging from the wide range of localities in which *B. k. kerstenii* has been found, the species should be considered both fluviatile and lacustrine. In the Victoria basin it is found in the lake itself and in temporary as well as permanent streams, both large and small.

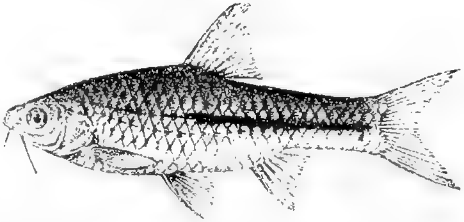

FIG. 6. *Barbus kerstenii kerstenii* (type of *B. lumiensis*, from Boulenger, *Cat. Afr. Fish.*).

Barbus kerstenii luhondo Papp. & Blgr.

Lectotype. A specimen 74 mm. S.L., from Lake Luhondo (Z.M. Berlin Number 19064).

Diagnosis. Differs from the nominate subspecies in having a shorter dorsal spine, shorter pectoral fins (16·1–19·3 cf. 19·4–24·4% S.L.), shorter barbels (anterior barbel 3·7–6·8 cf. 4·9–9·4% S.L.; posterior barbel 7·4–9·5 cf. 8·0–13·0% S.L.); snout more abruptly decurved (the photograph in Pappenheim & Boulenger (1914) is of a malformed individual with a strongly decurved snout); some individuals with only 6 branched dorsal rays.

In its coloration (alcohol-fixed specimens), *B. k. luhondo* does not differ greatly from *B. k. kerstenii* except that the broader lateral band is more intensely pigmented. In many places the band is broken up or represented by blotches. The spot at the caudal base is well defined.

Distribution. Known only from Lake Luhondo, Ruanda Urundi.

Affinities of Barbus kerstenii. In many characters *B. kerstenii* resembles four other species, one of which (*B. eutaenia*) occurs in eastern, central and southern Africa and the other three (*B. neumayeri*, *B. pellegrini* and *B. nyanzae*) in east Africa.

From *B. eutaenia*, *B. kerstenii* is immediately distinguished by its coloration (see p. 177), especially the absence of a dark scale at the base of the dorsal fin and because the dark midlateral band is not continued on to the snout and caudal fin membrane. Morphometric differences between the two species are slight.

Barbus kerstenii is readily distinguished from *B. neumayeri* by its coloration (cf. p. 170 and p. 180), particularly by the absence of a well-defined series of lateral spots, blotches or even a lateral band; a lateral band when present in *B. kerstenii* is less intense (even in formol-fixed fishes) and its margins are ill defined and not clear-cut as in *B. neumayeri*. Also, in no specimens of *B. kerstenii* is there a dark spot at or near the base of the anterior dorsal fin rays, an almost general characteristic of *B. neumayeri*. The spatial relationship and length of the barbels differ in the two species. In the majority of *B. neumayeri* the distal tip of the anterior barbel extends well beyond the base of the posterior barbel, often to a point midway along it. By contrast, in *B. kerstenii* the tip of the anterior barbel only rarely extends to beyond the base of the posterior barbel. The character is not, of course, trenchant but the area of overlap is slight. This different relationship of the barbels is not entirely due to a longer anterior barbel in *B. neumayeri*; it is due also to the different proportions of the parts of the head to which the barbels are attached. Two further characters distinguish *B. kerstenii* and *B. neumayeri*; in the former, the dorsal fin origin is clearly behind that of the pelvic fins whilst in *B. neumayeri* it is immediately above. Finally, there is a slight difference in the size of the scales, there being 24–31 (mode 28) lateral-line scales in *B. neumayeri* and 23–27 (mode 26) in *B. kerstenii*. This difference is, however, somewhat obscured by the geographical variation in scale numbers shown by both species. Differences between *B. kerstenii* and *B. pellegrini* are described on p. 182.

Perhaps the greatest resemblance is between *B. kerstenii* and *B. nyanzae* (Whitehead, 1960). *Barbus nyanzae* may be distinguished by the more posterior position of the dorsal origin relative to the pelvics (pelvic base entirely in advance of the dorsal fin), shorter barbels (2·6–3·7 and 3·9–5·0 cf. 3·7–9·4 and 7·4–13·0% of standard length for the barbels respectively [the figures for *B. kerstenii* include both subspecies]) and by its shallower caudal peduncle (11·4–13·0% cf. 12·5–17·8% of S.L.). Whitehead (*op. cit.*) also indicates that the coloration of living fishes may differ.

Superficially, *B. kerstenii* resembles *B. loveridgii*, a species so far known only from the Amala River, Kenya. It differs from *B. loveridgii* in several characters, such as its longer head (28–35% S.L. cf. 24%), longer barbels (5·0–9·4 cf. 1·6–2·0% S.L. for the anterior barbel and 8·0–13·0 cf. 2·9–4·0% for the posterior barbel). Other diagnostic characters are discussed on p. 183.

Barbus tangandensis Jubb, 1954

Barbus tangandensis Jubb, 1954, *Occ. pap. Nat. Mus. S. Rhodesia*, No. 19 : 690–698, pl. 1, figs. 5 and 6.

Barbus eutaenia (part), Blgr., 1911, *Cat. Afr. Fish.* **2** : 131 (specimens from a mountain stream near Petauke, Zambezi system, NE. Rhodesia).

In 1954 Jubb described a number of small *Barbus* which he was unable to identify with certainty. He compared them with both *B. eutaenia* and *B. serrifer* but also indicated that they might represent an undescribed species. In the latter event, he proposed that the species should be called *B. tangandensis*. Jubb's description is comprehensive and is accompanied by two figures which clearly show various diagnostic features. His proposed name is, therefore, valid and I have chosen a lectotype from amongst his material.

The description given below is based on twenty-two fishes, 25–55 mm. S.L.; three are from Petauke, three from the Chobe River (above the Victoria Falls) and sixteen from the type locality, the Tanganda River. In addition I have examined sixty-five other specimens from the Tanganda.

It is a pleasure to thank Mr. R. A. Jubb who has allowed me to examine his specimens and has also given me additional notes on the coloration of the species.

Lectotype. A specimen 40 mm. S.L. from the Tanganda River, B.M. (N.H.) reg. No. 1951.8.27.29.

Description. All measurements are expressed as percentages of the standard length.

Depth of body 27·7–32·0 (*M* = 29·2), length of head 25·0–31·9 (*M* = 27·4). Snout length 6·8–9·3 (*M* = 8·2); eye diameter 6·4–9·3 (*M* = 7·6) and showing slight negative allometry; least interorbital width 8·8–12·5 (*M* = 10·5).

Length of anterior barbel, except in three fishes from the Chobe River, 5·1–8·4 (*M* = 6·6); length of posterior barbel (including the Chobe fishes) 6·4–10·5 (*M* = 8·4). The anterior barbels of the Chobe fishes are short (3·7, 4·4 and 5·8%) but the sample is too small to determine the significance of this character.

Length of last unbranched dorsal ray 15·5–23·2 (*M* = 18·2); distance from snout tip to dorsal origin 51·0–59·3 (*M* = 53·0); length of pectoral fin 16·0–23·7 per cent.

Length of caudal peduncle 18·2–26·0 (*M* = 22·7), its depth 12·7–17·6 (*M* = 14·0).

Lateral line with 22 (f.1), 23 (f.8), 24 (f.11) or 25 (f.1) scales; 4½ (rarely 4) between the lateral line and the dorsal fin origin, 2–3½ (mode 3) between the pelvic origin and the lateral line; 10–14 (mode 12) scales around the caudal peduncle, 9–11 (mode 10) in the predorsal row.

Dorsal fin with 3/7 rays, the last unbranched ray stout, ossified and serrated on its posterior face. Dorsal origin slightly in advance of the first pelvic ray. *Anal fin* with 3/5 rays.

Coloration (*alcohol-fixed* specimens). Ground colour brownish dorsally becoming whitish below the lateral line. A broad, slightly arched midlateral stripe, silver to blackish in colour, runs from the upper angle of the operculum to the caudal origin. The posterior margin of the cleithrum, above the pectoral origin, is outlined in black and the first ten lateral line scales have dark centres. Scales along the dorsal midline (particularly those before the dorsal fin) with dark centres. All fins colourless.

In *formol-fixed* specimens the ground colour is lighter but the dark midlateral band is intensified and is visible from the *tip of the snout*, across the operculum to the caudal origin where it ends in a dark spot. All the lateral-line scales have dark centres, as do some of the scales in the row immediately above the lateral line. The dark posterior margin of the cleithrum is clearly defined, as are the scales along the dorsal midline. All fins are colourless.

Live specimens are dark green/brown on the dorsal surface and as far as the lateral line from whence the colour blends to silvery-white on the belly. The scales above the lateral line are edged with minute black spots. A dark lateral stripe which passes from the snout through the eye and across the operculum, ends in a distinct dot in the middle of the caudal peduncle. The dorsal and anal fins are edged with orange/pink. The operculum, which is golden, has a conspicuous bright red spot about the same diameter as the iris of the eye.

Diagnosis and affinities. Jubb (1954) compared *B. tangandensis* with *B. serrifer* (now, at least in part, a synonym of *B. neumayeri*) and *B. eutaenia*, but the relationship seems to be much closer to *B. kerstenii*. The species is distinguished from *B. neumayeri* and *B. eutaenia* by both morphometric and colour differences (in live and preserved specimens). For example, the bright red opercular spot has not been recorded in *B. neumayeri* and in this species the dark midlateral stripe—when present—does not extend on to the operculum and snout. In *B. eutaenia* the lateral band is more extensive than in *B. tangandensis* since it runs from the snout to the *margin* of the caudal fin ; the two species are also distinguished by several morphometric characters.

In sharp contrast to these differences are the great similarities existing between *B. tangandensis* and *B. kerstenii* (cf. above and pp. 170–173) especially the subspecies *B. k. kerstenii*. In the first place, their live coloration is unusually similar and secondly there are no trenchant anatomical differences. The only clear distinction I can detect is that in *B. kerstenii* (especially in preserved fishes) the broad lateral band does not extend anteriorly beyond the level of the dorsal fin and no trace is found on the snout and operculum. It is principally on this difference in colour pattern that I have refrained from considering *B. tangandensis* as a subspecies of *B. kerstenii*. Despite the variation shown by the latter species over its wide geographical range I have found no specimens in which the colour pattern could be considered intermediate between the *B. tangandensis* and the *B. kerstenii* condition.

The sum of these interspecific resemblances suggests that *B. tangandensis* could be looked upon as the Zambezi representative of the more northerly species, *B. kerstenii*.

Barbus tangandensis also resembles *B. miolepis* (Ubange River, Congo system) but there are few details published on the coloration of this species. Furthermore there are some slight morphological differences between the species ; e.g. the origin of the dorsal fin is slightly more anterior in *B. tangandensis ;* there are eight branched rays in *B. miolepis* and the course of the lateral line in the latter is more nearly straight. With regard to preserved coloration, the major difference seems to be that the midlateral stripe follows the course of the lateral line in *B. miolepis* whereas in *B. tangandensis* the greater part of the lateral line lies below the stripe. The difference is slight and thus *B. miolepis* could stand in the same relationship to *B. tangandensis* as the latter does to *B. kerstenii*. In other words, *B. miolepis* could be the Congo representative of *B. kerstenii*.

Habitat. According to Mr. Jubb, *B. tangandensis* occurs in fast flowing streams.

Distribution. Known only from Rhodesia where it is widely distributed (Petauke ; Tanganda River, a tributary of the Sabi-Lundi system ; Garizi River, a lower Zambezi tributary ; Chobe River, above the Victoria Falls ; Pungwe River.

Barbus eutaenia Boulenger, 1904

(Text-fig. 7)

Barbus eutaenia Boulenger, 1904, *Ann. Mag. nat. Hist.* (7) **14** : 218 ; *Idem.* 1911, (part), *Cat. Afr. Fish.* **2** : 131 (excluding specimens from Petauke, Zambezi system, NE. Rhodesia, first identified as *B. miolepis*) ; *Idem*, 1916 (part), *op. cit.* **4** : 256 (excluding two specimens from Quanza River, at Dondo, Angola).

Barbus kerstenii (*nec* Peters), Gilchrist & Thompson, 1913, *Ann. S. Afr. Mus.* **11** : 410, fig. 68 ; Groenewald, 1958, *Ann. Transv. Mus.* **23** : 313, pl. 65, fig. 3.

Notes on the synonymy. The very characters which Groenewald (*op. cit.*) selects as diagnostic for his " *B. kerstenii* " are those which distinguish *B. eutaenia* from *B. kerstenii*. Had Groenewald been able to compare the types of the two species, I am sure he would not have fallen into this error. Through the courtesy of Mr. Groenewald I have been able to examine some of his Transvaal material and thus to confirm the identity of these fishes. I have also examined three Transvaal fishes identified by Gilchrist & Thompson as *B. kerstenii*. These specimens, too, must be referred to *B. eutaenia*.

Specimens from Ruanda Urundi which David (1937) identified as *B. eutaenia* provide greater difficulty. My suspicions as to their identity were aroused by the fact that Ruanda lies considerably to the north of the main distributional area for *B. eutaenia*. Dr. Max Poll of the Musée Royal d'Afrique Centrale has kindly presented the B.M. (N.H.) with three specimens from David's collection. Superficially, these fishes do resemble *B. eutaenia*, as they also do in many morphometric characters and general coloration. However, in four morphometric characters and in the absence of a prominent, dark scale at the base of the dorsal fin, the specimens depart from the typical condition as manifest by fishes from Angola, South Africa and most Rhodesian populations. If more specimens from Ruanda confirm these differences then the population should be given some taxonomic rank, probably subspecific. At the moment there is insufficient material to warrant this step. Thus, those characters which show marked departure from the modal condition will be noted in the description below.

Another distinctive population is represented by seven specimens (37–64 mm. S.L.) from the Garizi River, a tributary of the Zambezi system. These specimens differ from typical fishes (and the Ruanda specimens) in having eight branched dorsal rays and somewhat longer barbels. Again, there are insufficient grounds for erecting a subspecies and the deviant characters will be noted in the description.

One other specimen, from the Luapula system near Lake Bangweulu, resembles the Garizi fishes. Worthington (1933*a*) noted the increased number of dorsal rays but did not comment on the longer posterior barbels.

Lectotype. A fish 71·0 mm. S.L. from Huilla, Mossamedes. B.M. (N.H.) reg. No. 1864.7.12.52.

Description based on twenty-three specimens, 37–122 mm. S.L. (including the lecto- and two paratypes, and the seven specimens from the Garizi River ; see above). The three Ruanda fishes were not included when determining means but are included in the ranges given for all characters.

Ranges for those characters in which the Garizi and Ruanda fishes lie beyond the range for other *B. eutaenia* are given in brackets, prefixed by G. or R. for the populations respectively. All measurements are expressed as percentages of the standard length.

Depth of body 26·6–33·4 (M = 29·9), length of head 24·2–28·2, M = 26·4 (R. 23·1–23·4). Snout length 7·1–9·3 (M = 8·1), (R. 5·4–6·3) ; eye diameter (negatively allometric) 6·3–8·5 ; least interorbital width 9·4–11·4 (M = 10·3), (R. 7·8–8·2).

Length of anterior barbel 4·5–8·4 (M = 5·8), (G. 7·3–8·7, M = 8·3) length of posterior barbel 5·8–10·4 (M = 7·4), (G. 8·9–10·9, M = 9·8 ; R. 5·4–5·5) ; length of anterior barbel relative to eye diameter : equal to f.2 ; longer, f.0 ; shorter than f.15 (G. equal to f.1; longer than f.4 ; shorter than f.1 ; the anterior barbel is shorter than the eye in the three Ruanda specimens examined).

Length of last unbranched dorsal ray 14·7–24·3 (M = 20·2) ; distance from snout tip to dorsal origin 46·0–56·0 (M = 51·7) ; length of pectoral fin 16·8–23·0.

Caudal peduncle length 20·3–25·4 (M = 22·7), its depth 12·5–15·5 (M = 13·8).

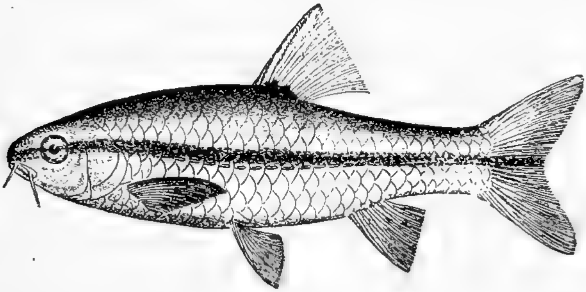

FIG. 7. *Barbus eutaenia* paratype, slightly less than N.S. (after Boulenger, *Cat. Afr. Fish.*)

Lateral line with 25 (f.5) ; 26 (f.14) or 27 (f.4) scales (two damaged specimens give counts of *ca.* 23 and *ca.* 24) ; $4\frac{1}{2}$ or 5 scales (rarely 4 or $5\frac{1}{2}$) between the dorsal fin origin and the lateral line, $2\frac{1}{2}$ or 3 (rarely $3\frac{1}{2}$) between the lateral line and the pelvic fin insertion. Twelve to fourteen scales around the caudal peduncle (10 or 11 in the Ruanda specimens) ; 9–11 (mode 10) in the predorsal row.

Dorsal fin origin behind or above the posterior pelvic rays, the fin with 3/7 rays (except Garizi fishes which have 3/8 or 3/9). Last unbranched dorsal ray moderately stout, serrated on its posterior face. *Anal fin* with 3/5 rays in all populations.

Coloration. In *alcohol-fixed* specimens the ground colour is brown above and yellowish-brown with sometimes a silver sheen on the flanks. In darkly coloured fishes the pigment is concentrated near the centre of the scales. A distinct and generally broad midlateral band extends from the snout tip, across the operculum, along the flank and on to the membrane of the caudal fin, ending near or at the fin margin. This band is invariably present but may be narrow on the flanks and difficult to distinguish on the snout and caudal fin ; however, under low-power magnification the melanophore patterns are readily distinguished. A very characteristic feature of all but the Ruanda Urundi specimens is the dark and dorsally directed scale (or scales) at the base of the first to fourth (usually the second to fourth) branched dorsal rays. These scales are dark in the Ruanda fishes but no one scale is darker and neither does it stand out from the other basal scales in its alignment.

In *formol-fixed* specimens the coloration is similar except that the dark scale centres and the dark scales of the dorsal base are more intense. Likewise, the lateral band is darker. All traces of a silvery sheen on the body are lost.

Distribution. Ruanda Urundi (Malagarazi River) ; *Lake Nyasa ; Lake Mweru : Rhodesia :* (Solwezi, Umsitu, Kafulafuta, Garizi and Luapula Rivers) : rivers and streams in *Katanga* ; rivers of the *Transvaal, South Africa.*

Barbus neumayeri Fischer, 1884

(Text-fig. 8)

Barbus neumayeri Fischer, 1884, *Jb. hamburg. wiss. Anst.* **1** : 31 ; Boulenger, 1911, *Cat. Afr. Fish.* **2** : 132.

Barbus serrifer Blgr., 1900 (types only), *Ann. Mag. nat. Hist.* (7) **6** : 479 ; *Idem,* 1911, *op. cit.* **2** : 124, fig. 101.

Barbus carpio Pfeffer, 1896, *Thierw. O. Afr. Fische* : 57 ; Boulenger, 1907, *Fish Nile :* 244, pl. 45, fig. 3 ; *Idem,* 1911, *Cat. Afr. Fish.* **2** : 134. fig. 111.

Barbus rufua (part ; 3 syntypes) Papp. & Blgr., 1914, *Wiss Ergebn. Deuts. Zentral-Afrika Exped.,* 1907–1908, *Zool.* **3**, 243.

Barbus mohasicus (part ; 6 syntypes) Papp. & Blgr., 1914, *op. cit., tom. cit.* ; 241.

Barbus percivali Blgr., 1903, *Ann. Mag. nat. Hist.* (7) **11** : 52, pl. 5, fig. 1 ; *Idem,* 1911, *Cat. Afr. Fish.* **2** : 135, fig. 112.

Barbus portali Blgr., 1906, *Ann. Mag. nat. Hist.* (7) **18** : 36 ; *Idem,* 1907, *Fish. Nile* : 243, pl. 45, fig. 2 ; *Idem,* 1911, *Cat. Afr. Fish.* **2** : 133, fig. 110.

Barbus nairobiensis Blgr., 1911, *op. cit.* **2** : 132, fig. 109.

Barbus luazomela Lönnberg, 1911, *Handl. svensk. vet. Akad.* **47** : 40 ; Boulenger, 1916, *Cat. Afr. Fish.* **4** : 254.

Notes on the synonymy. The close relationship of the species now referred to *B. neumayeri* is reflected in Boulenger's *Catalogue* (1911), especially in the keys. Additional specimens have now smothered the very slight morphological differences which had been used to separate the species. One point, not apparent from earlier descriptions, is the variation in colour patterns shown by the different species. The most general pattern is one of three lateral spots (as seen in most of the *B. percivali* types). A common variation is for the anterior spot to be elongated and the two posterior spots to be joined by a dark band, the spots either losing their identity or remaining visible within the band (seen in some *B. portali* types). A third variation is one in which the spots are replaced by an interrupted band, with its longest elements on the posterior half of the body (seen in the types of *B. carpio*). Finally, and rarely, the two anterior spots may be absent and only the caudal spot remains.

The various patterns show no correlation with locality and several patterns may be represented in a single sample, as occurs in the types of *B. percivali*, *B. portali* and *B. nairobiensis*. There is perhaps some correlation with age since the " three spot " form occurs most frequently in small fishes and the continuous or interrupted stripe in larger individuals (as in the types of *B. neumayeri*). Exceptions are, however, frequent.

Whatever the causal mechanism underlying these variations in pattern, the variety is continuous and certainly not interspecific, as might be inferred from the type specimens figured in Boulenger's *Catalogue* (1911).

Finally, some comment must be made on the two syntypes of *B. neumayeri.* In three characters these specimens are not modal for the species as defined on the basis of all the other specimens. But, despite this deviation the types are closer to the other specimens than to any related species of *Barbus*. Also, the deviant characters cannot be considered sufficiently trenchant to warrant the specific separation of *B. neumayeri* (*sensu stricto*) from the other specimens taken as a whole. Some specimens from this group approach the *B. neumayeri* types in the three characters under consideration. The near annectant specimens are from Tanganyika (and include *B. serrifer* types). Unfortunately I do not have enough material from Tanganyika to investigate this suggestion of geographical variation within the species. The characters in which *B. neumayeri* types depart from the mode are: a shorter head (24·4 and 24·8% S.L.), narrower interorbital (8·0–10·3% S.L.) and slightly smaller scales. Of these characters, only the width of the interorbital lies outside the range known from other specimens.

Lectotype. A fish 119·0 mm. S.L. from Nguruman, on a tributary of the southern Eusso Nyiro River, Kenya (Hamburg Museum, reg. No. H.334: see Ladiges *et al.*, 1958).

Description. Based on ninety fishes, 27–103 mm. S.L. (including the lecto- and one paratype of the species, the lecto- and three paratypes of *B. carpio*, four syntypes of *B. nairobiensis*, four syntypes of *B. portali* and two syntypes of *B. luazomela*). All measurements are expressed as percentages of the standard length.

Depth of body 24·7–35·2 ($M = 30{\cdot}1$), length of head 23·4–32·3 ($M = 27{\cdot}4$). Snout length 6·5–11·4 ($M = 8{\cdot}4$), eye diameter negatively allometric, 5·2–10·9; least interorbital width 8·0–13·6 ($M = 10{\cdot}6$).

Length of anterior barbel shows slight positive allometry in fishes less than 95 mm. S.L. but in larger individuals it shows weak negative allometry; range in fishes <30 mm. S.L. 4·4–5·5 and in larger individuals 6·9–12·3 ($M = 8{\cdot}8$) Length of posterior barbel shows some positive allometry, the range in fishes <30 mm. S.L. being 8·7–9·6 and in larger fishes 7·5–13·6 ($M = 10{\cdot}9$) Length of anterior barbel relative to eye diameter: equal to eye f.9 (or 11% of sample), shorter than eye f.9 (11%), longer than eye f.63 (78%). This distribution is probably skewed by the inclusion of smaller fishes which all fall in the second category.

Length of last unbranched dorsal ray very variable, the variation probably correlated with locality (larger samples are required to test this hypothesis), 11·6–26·0 ($M = 18{\cdot}4$); distance from snout tip to dorsal fin origin 48·8–60·5 ($M = 53{\cdot}5$). Length of pectoral fin 16·1–24·5.

Length of caudal peduncle 17·2–25·7 ($M = 20{\cdot}5$), its depth 11·2–15·9 ($M = 13{\cdot}7$).

Lateral line with 24–32 (mode 28) scales. Fishes from Uganda and Tanganyika appear to have slightly smaller scales than those from Kenya. The modal number in each area is the same (28) but the lower scale counts (24–26 lateral line scales) have only been recorded from Kenya fishes. Number of scales between the lateral line and the dorsal origin variable, 4 (f.3), 4½ (f.33), 5 (f.38), 5½ (f.10), 6(f.1) ; number of scales between the lateral line and the pelvic fin origin : 3 (f.36), 3½ (f.23), 4 (f.29) or 4½ (f.2) ; 10–16 (mode 12) scales around the caudal peduncle, 9–12 (mode 11) in the predorsal row.

The range of variation in scale counts is strikingly high, yet it is impossible to use these counts to define any of the species now synonymized with *B. neumayeri*. Intrapopulational ranges are extensive (even in the small samples available) and overlap at the interpopulational level. Only the weak correlation of scale size in Uganda and Tanganyika fishes as compared with fishes from Kenya, seems to hold.

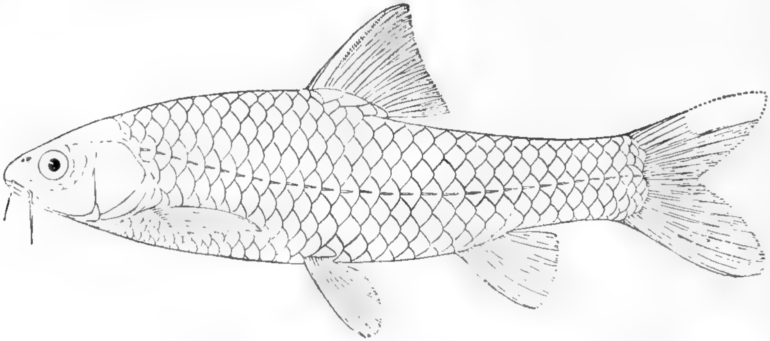

FIG. 8. *Barbus neumayeri* (syntype of *B. nairobiensis*, about natural size ; from Boulenger, *Cat. Afr. Fish.*).

Dorsal fin with, usually, 3/7 rays but with 4/7 in three of the four *B. carpio* types (specimens from Lake Albert) ; last unbranched ray stout and serrated posteriorly. Origin of dorsal fin above or very slightly behind that of the pelvic fins. *Anal fin* with 3/5 (rarely 3/6) rays.

Coloration of preserved specimens is variable (see p. 178). In alcohol-fixed fishes the ground colour is brownish, darker above and sometimes white or silvery below. Formol fixation produces a much lighter, almost yellow ground colour. All fins are colourless. The dark midlateral markings vary from the commonest condition of three spots (one between the origins of the pectoral and dorsal fins, one above the anal origin and one at the caudal base) through elongate, rather narrow blotches to a continuous lateral band terminating in the caudal spot. The first and second spots may or may not be visible when a continuous lateral band is present ; usually the band only appears on the posterior half of the body. A less common variant is that of a much interrupted band resembling a series of six or seven spots of unequal size.

In many specimens there is a prominent dark (brown) spot at, slightly posterior to or below the base of the last simple dorsal ray ; the spot is more often absent in large than in small fishes.

Coloration in live fishes. This description is based on specimens caught in and around the Uganda shores of Lake Victoria. Dorsal surfaces brownish olive-green, ventral surfaces silver. Fins faint brownish-green except the caudal which is pinkish-brown.

The lateral spots are most conspicuous in young fishes but even then are less obvious than in preserved material.

Diagnosis. The species closely resembles *B. pellegrini*, but is distinguished by the more posterior position of the pelvic fins relative to the dorsal, and by its relatively shorter barbels. Differences separating *B. neumayeri* and *B. kerstenii* are discussed on p. 173.

Distribution. Widely distributed in eastern Africa. *Kenya:* (Nzoia, Nairobi, Riara, Thika, Makindu and Tsavo Rivers, northern Eusso Nyiro [above the falls], southern Eusso Nyiro [near Lake Magadi], Suam River [Mount Elgon], Sabukia River, Seya River [Isiolo district], Sinet stream near Laitokitok). *Uganda:* (Malawa River, Mpanga River [near Fort Portal], stream in the Mabira forest, Hima and Waisoke Rivers and tributaries [flowing into Lake Albert], Kirima and Mongiro Rivers [tributaries of the Semliki River in the Bwamba district], small, permanent and temporary streams flowing into Lake Victoria). *Tanganyika:* (Lake Tanganyika; Lake Basuto).

Barbus pellegrini Poll, 1939

Barbus pellegrini Poll. 1939, *Inst. Parcs Nat. Congo Belge. Explor. Parc Nat. Albert*, fasc. 24 : 26, fig. 8, (*Nom. nov.* for *B. serrifer* var. *trimaculata* Pellegrin, 1935 in *Rev. Zool. Bot. Afr.* **27** : 381 ; type locality Kadjudju, Lake Kivu).

The description below is based on twenty-six specimens, 54–88 mm. S.L., from Luviro, Lake Kivu (R.G. Mus. Congo. 128495–519 [in part] and 128451–494 [in part]) kindly lent to me by Mr. H. Matthes and Dr. Max Poll.

All measurements are expressed as percentages of the standard length.

Depth of body 26·8–32·0 ($M = 29·8$), length of head 23·4–28·4 ($M = 25·7$). Profile of snout rather acute, snout length 6·5–8·3 ($M = 7·3$) ; eye diameter showing but slight negative allometry in the sample studied, 5·7–8·8 ($M = 6·5$) ; least interorbital width 8·2–10·6 ($M = 9·0$).

Length of anterior barbel 7·3–11·8 ($M = 9·4$), length of posterior barbel 10·6–14·8 ($M = 13·3$). In all specimens the anterior barbel is longer than the eye diameter.

Length of last unbranched dorsal ray 16·0–22·4 ($M = 19·1$). One specimen has a dorsal spine of 13·0% ; there is no indication of malformation or breakage. Distance from snout tip to dorsal fin origin 50·0–56·5 ($M = 53·3$).

Caudal peduncle length 19·5–24·6 ($M = 22·1$), its depth 12·3–15·0 ($M = 13·4$).

Lateral line with 26 (f.4), 27 (f.7), 28 (f.5) or 29 (f.10) scales ; 5 (mode) or 5½, rarely 4½, scales between the lateral line and the dorsal fin origin, 3 (f.10), 3½ (f.11) or 4 (f.4) between the lateral line and the pelvic fin origin ; 14 scales around the caudal peduncle and 10–14 (usually 11 or 12) in the predorsal row.

Dorsal fin origin clearly anterior to that of the pelvics, the fin with 3 or 4 unbranched and 7 (rarely 8) branched rays. The last unbranched ray is spinous, strong and serrated on its posterior face. *Anal fin* with 3/5 (less frequently 6) rays.

Coloration. In *formol-fixed* fishes the body is yellowish below the lateral line and greyish-brown above and on the head and cheeks. Scales in the row immediately below the lateral line are either outlined in brownish-grey or else the pigment is concentrated on the anterior border of each scale.

The midlateral colour pattern is highly variable and similar to that of *B. neumayeri* (see p. 180). Common patterns are : a continuous dark band from opercular margin to caudal origin ; an interrupted dark band ; a series of dark blotches connected by a less intense dark and interrupted streak, or finally, three dark spots, one above the middle of the pectoral fin, the second above the origin of the anal fin and the third slightly anterior to the caudal fin origin.

The dorsal and caudal fins are greyish, the other fins are hyaline.

In living fishes the colours are described as dark olive to greenish-brown above, silver or yellowish ventrally ; dark lateral spots of variable intensity. All fins either colourless or dorsal, caudal and anal yellowish the two former sometimes sooty. Operculum coppery or yellow, never red (M. H. Matthes, *in litt.*).

Diagnosis and affinities. The species is related to both *Barbus kerstenii* and *B. neumayeri* and is perhaps closest to the latter, particularly with regard to preserved colour patterns. Indeed, there is only one trenchant character (the more anterior origin of the pelvics relative to the dorsal fin) which readily distinguishes *B. pellegrini* from *B. neumayeri*. The barbels of *B. pellegrini* are proportionally somewhat longer (anterior barbels, Mean = 9·3% S.L. cf. 8·8% in *B. neumayeri* ; posterior barbels, Mean = 12·9% cf. 10·9% in *B. neumayeri*), a difference seen most clearly when specimens of the same size are compared. The two species occur together in many areas and I am told by Mr. Matthes that one or other is always predominant in any habitat.

From *Barbus kerstenii*, *B. pellegrini* is distinguished by its markedly different coloration, longer barbels and smaller scales (lateral-line scales 26–29, mode 29 in *B. pellegrini* and 23–27, mode 25 in *B. kerstenii*).

Distribution. Drainage basins of Lakes Kivu, Edward, and Tanganyika. The species occurs both in the rivers and in the lakes (see Poll, 1953).

Barbus loveridgii Boulenger, 1916

Barbus loveridgii (part) Boulenger, 1916, *Ann. Mag. nat. Hist.* (8) **17** : 244 (two of the syntypes).

The original description was based on " Several specimens from the Amala River . . . " ; the types are deposited in both the British Museum (Natural History) and the Nairobi Museum. I have examined the three specimens in the B.M. (N.H.) and find that one can be referred to *B. kerstenii*. The two remaining specimens are of a related but distinct species. Unfortunately, I have been unable to examine the type material in the Nairobi Museum.

Both types are rather poorly preserved but this does not seriously affect any diagnostic character.

Lectotype. A fish 50 mm. S.L. from the Amala River, an affluent of Lake Baringo, Kenya (B.M. [N.H.] reg. No. 1916.1.14.14).

Description. Based on the lectotype and one paratype, 65·5 mm. S.L. Proportions and counts of the lectotype are given first ; all measurements are expressed as percentages of the standard length.

Depth of body 25·0 and 27·2 ; length of head 24·0 in both ; snout length 7·0 and 7·2, lower jaw apparently shorter than the upper and closing within it ; least interorbital width 10·0 and 9·6 ; eye diameter 8·0 and 7·2.

Barbels short, length of anterior barbel 2·0 and *ca.* 1·6, length of posterior barbel 4·0 and *ca.* 2·9.

Length of last unbranched dorsal ray 22·0 and 24·0 ; distance from snout tip to dorsal origin 56·0 in both ; length of pectoral fin 26·0 and 24·0.

Caudal peduncle length 22·0 and 21·6, its depth 12·0 and 11·2.

Lateral line with 28 or 29 scales ; 5 or 5½ scales between the lateral line and the dorsal origin, 3 or 4 between the lateral line and the pelvic origin ; 10 or 12 scales around the caudal peduncle, 12 or 13 in the predorsal row.

Dorsal fin with 3/7 rays, the last unbranched ray stout, ossified and serrated on its posterior face. Origin of dorsal behind the pelvic origin (greater part of the pelvic base anterior to the first dorsal ray). *Anal fin* with 3/5 rays.

Coloration (*alcohol-fixed* specimens). Ground colour brownish ; lateral flank scales with a dark, narrow crescent at each scale centre, those in the midlateral line uniting to form a narrow, dark brown band which runs from behind the operculum to the level of the last anal ray. Anteriorly, this band is continuous across the operculum, through the eye and on to the snout. Posteriorly, the band is continuous with a very narrow, intensely black line which runs from the origin of the caudal fin to a point above the pelvic origin. The course of this line may be contiguous with the broader band or the two may run close together. In one specimen there is an ill-defined black spot at the caudal base. All fins are colourless.

Diagnosis and affinities. Superficially, *B. loveridgii* resembles *B. kerstenii* but is distinguished from the latter by the following characters : head shorter (24% S.L. cf. 28–35%) ; barbels markedly shorter, particularly in comparison with specimens of the same size (anterior 1·6–2·0% S.L. cf. 5·0–9·4% ; posterior 2·9–4·0% cf. 8·0–13·0%) ; body more slender (depth 25·0–27% S.L. cf. 28·2–35·2%) ; differences in coloration, particularly the presence of a dark bar through the snout, eye and on the operculum (no such cephalic markings were observed in specimens of *B. kerstenii*) ; the pelvic fin origin is more advanced relative to the dorsal origin ; the scales are smaller (lateral line scales 28–29 cf. 23–27). Admittedly, I have only studied two specimens of *B. loveridgii*, but I have been able to compare them with specimens of *B. kerstenii* from the same river and from numerous other east African localities. In all the diagnostic characters used above, the two specimens of *B. loveridgii* lie outside the range for *B. kerstenii*.

Distribution. Known only from the Amala River, an affluent of Lake Baringo, Kenya.

Barbus jacksonii Günther, 1889

(Text-fig. 9)

Barbus jacksonii Günther, 1889, *Proc. zool. Soc. Lond.* : 72 ; Pfeffer, 1896, *Thierw. O. Afr., Fische* : 67 ; Boulenger, 1911, *Cat. Afr. Fish.* **2** : 106, fig. 84.

Barbus nummifer Blgr., 1904, *Ann. Mag. nat. Hist.* (7) **13** : 449 ; *Idem*, 1907, *Fish Nile* : 239 ; *Idem*, 1911, *Cat. Afr. Fish.* **2** : 105, fig. 83.

Barbus trimaculatus (*non* Peters), Hilgendorf, 1888, *S.B. Ges. naturf. Fr. Berlin* : 78.

? *B. trimaculatus*, Fowler, 1930, *Proc. Acad. Nat. Sci. Philad.* **82** : 34 (specimens from Lake Victoria).

? *Barbus pappenheimi* Blgr., 1905, *Ann. Mag. nat. Hist.* (7) **16** : 44 ; *Idem*, 1911, *Cat. Afr. Fish.* **2** : 107.

Notes on the synonymy. The unique specimen of *B. jacksonii* differs from the type of *B. nummifer* only in having seven instead of eight branched dorsal rays. Since intraspecific variation in this character is known from several species (including *B. eutaenia* and *B. trimaculatus*) and because there are no other distinguishing characters, I consider the two specimens to be of one species. The localities of the two fishes are different and further collecting may show that the number of dorsal rays is a populational character.

Fowler's record of *B. trimaculatus* from an affluent stream in the Speke Gulf area of Lake Victoria is extremely dubious. First, the area lies far to the north of the *B. trimaculatus* range, but within the range of *B. jacksonii*. Secondly, his description of the specimens suggests that he may have misidentified young specimens of *B. neumayeri*. Fowler only comments on the coloration and does not mention the nature of the last unbranched dorsal ray. The latter character is, of course, very different in the two species. In *B. neumayeri* the ray is serrated posteriorly but is smooth in *B. jacksonii*. However, in such small specimens as Fowler had (24–49 mm.) the serrations would not be at all distinct. The coloration described fits that of *B. neumayeri* more closely than it does *B. trimaculatus*. If the dorsal spine is not of the *B. neumayeri* type, then doubtless Fowler's specimens should be referred to *B. jacksonii*.

I have not been able to examine the type of *B. pappenheimi* Blgr. from Lake Rukwa. However, from Boulenger's description there seems little doubt that it is inseparable from *B. jacksonii*. Until the type can be examined it seems advisable to keep the synonymy tentative.

Description. Based on eighteen specimens, 63–116 mm. S.L., (including the type of the species and of *B. nummifer*). All measurements are expressed as percentages of the standard length.

Depth of body 25·7–31·0 ($M = 28{\cdot}3$), length of head 23·0–26·4 ($M = 24{\cdot}4$) Snout length 6·5–8·7 ($M = 7{\cdot}4$), eye diameter (negatively allometric) 5·2–7·2, least interorbital width 8·5–11·1 ($M = 9{\cdot}9$).

Length of anterior barbel 3·3–6·4 (positively allometric). Length of posterior barbel 6·1–9·6 ($M = 7{\cdot}8$).

Length of last unbranched dorsal ray 18·2–25·4 ($M = 23{\cdot}5$), distance from snout tip to dorsal origin 46·0–50·0 ($M = 48{\cdot}3$) ; length of pectoral fin 17·8–20·8.

Length of caudal peduncle 21·6–27·0 ($M = 24{\cdot}5$), its depth 13·2–14·6 ($M = 13{\cdot}9$).

Lateral line with 35 (f.2), 36 (f.3), 37 (f.5), 38 (f.6) or 39 (f.2) scales ; 6½ or 7 (rarely 6) scales between the lateral line and the dorsal origin, 3½ or 4 between the lateral line and the insertion of the pelvic fin ; 12–14 (rarely 11) scales around the caudal peduncle, 12–14 (rarely 11) in the predorsal row.

Dorsal fin origin above that of the pelvics, rarely somewhat anterior ; the fin with 3/7 or 8 (mode 8) rays, the last unbranched ray stout and ossified but without posterior serrations. *Anal fin* with 3/5 (in one specimen 3/6) rays.

Coloration. In both formol- and alcohol-fixed specimens the dorsal body surface is brown, the ventral surfaces yellowish-silver ; in alcohol-fixed fishes there is a distinct overall silvery sheen. Three midlateral spots are always present, one above the middle of the pectoral fin, one at about the midpoint of the body and one at the base of the caudal fin. As many as three smaller spots may be visible between the larger ones. The major spots show some variation in size and intensity ; the middle spot is sometimes double. In no specimen is there a spot at the base of the anal fin. All fins are colourless.

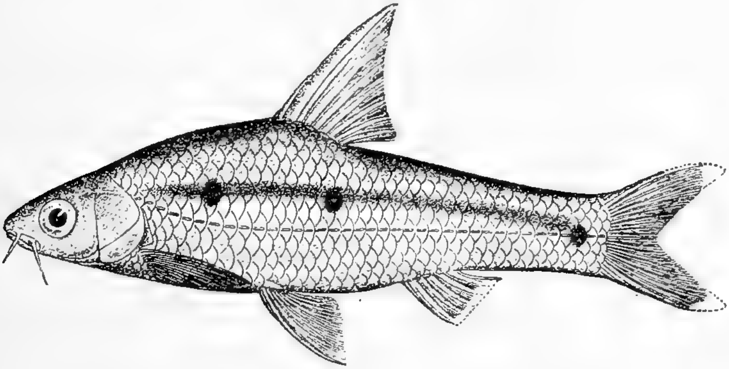

FIG. 9. *Barbus jacksonii*, holotype, about $\frac{3}{4}$ N.S. (from Boulenger, *Cat. Afr. Fish.*).

Coloration in life (described from Lake Victoria specimens). The body is sandy above, silver below ; spots are present as described above. All the fins are hyaline.

Distribution. Known only from *East Africa* : (the Lake Victoria basin ; Malawa River ; Pangani River [near Arusha] ; Bubu River. Also probably Lake Rukwa).

Discussion. Barbus jacksonii is closely related to *B. trimaculatus* of central and southern Africa. *Barbus trimaculatus* differs principally in having larger scales (modal range of lateral line scales 32–33 cf. 37–38) and somewhat longer barbels. However, the lateral-line scale count in one population of *B. trimaculatus* (from Lake Bangweulu) is within the upper limits of the *B. jacksonii* range. Because of this general similarity and overlap in most characters it seems possible that *B. jacksonii* is merely a northern representative of *B. trimaculatus.*

Barbus trimaculatus Peters, 1852

Barbus trimaculatus Peters, 1852, *Mber. Akad. Wiss. Berlin* : 683 ; Boulenger, 1911, *Cat. Afr. Fish.* **2** : 103, fig. 82 (gives a full synonymy to that date) ; Barnard, 1948, *Ann. S. Afr. Mus.* **36** : 423 (detailed synonymy, including *B. kurumanni* Casteln., 1861) ; Groenewald, 1958, *Ann. Transv. Mus.* **23** : 326, pl. 70, fig. 2.

I have not examined the type but from Peters' original description and figure, together with a knowledge of *Barbus* species from the type locality (Zambezi) I have no doubt that the specimens described below should be referred to this species.

Several fairly distinct populations are represented in the Museum's collection. The distinctive characters of these populations are, however, relatively minor ones so a composite species description can be given. The differentiae of the populations are given after the description.

Description based on fifty-five specimens, 40 -121 mm. S.L. All measurements are expressed as percentages of the standard length.

Depth of body 26·4–34·2 (M = 29·2), length of head 22·4–27·5 (M = 24·9). Snout length 5·9–8·8 (M = 7·3, but this character may show slight negative allometry) ; eye diameter 4·9–8·4 (negatively allometric), least interorbital width 8·3–11·2 (M = 9·7).

Length of anterior barbel 3·4–8·7 (M = 6·4), of posterior barbel 5·8–11·2 (M = 8·3).

Length of last unbranched dorsal ray 16·2 29·4 (M = 22·6, but this character shows interpopulation variation) ; distance from snout tip to origin of dorsal fin 45·5–52·5 (M = 49·3). Length of pectoral fin 16·8–21·5.

Length of caudal peduncle 18·8–26·9 (M = 23·8), its depth 11·9–15·8 (M = 13·5).

Lateral line with 30 (f.3), 31 (f.12), 32 (f.15), 33 (f.16), 34 (f.8) or 35 (f.4) scales. Five and a half or six (rarely 6½) scales between the lateral line and the dorsal origin, 3 or 4 between the lateral line and the pelvic origin ; 14–16 (rarely 13 or 17) scales around the caudal peduncle, 10–13 in the predorsal row.

Dorsal fin origin above that of the pelvics, the fin with 3/8 (rarely 3/7) rays, the last unbranched ray stout and ossified, without serrations. *Anal fin* with 3/5 rays.

Coloration is similar in both formol- and alcohol-fixed specimens. Ground colour usually brownish above and silvery-yellow below, with an overall silvery sheen, especially in spirit-fixed fishes. In some specimens there is a narrow, greyish midlateral stripe. Many specimens have three midlateral spots in the same positions as those of *B. jacksonii* (see p. 185) ; from the available material it seems that the intensity, shape and even the presence of these spots is more variable in *B. trimaculatus*. Groenewald (1958) observed that specimens from turbid water showed only the caudal spot. This spot is generally round, but in certain fishes (from the Zambezi system, Beira and Lake Ngami) it is elongate and rather pointed (see below). No specimens have a spot at the anal fin base, but Groenewald (*op. cit.*) believes that a very faint spot is developed in juvenile fishes (visible in specimens <70 mm. long).

Intraspecific (? populational) variation. On the basis of this material it is possible to recognize six fairly distinct group facies, namely :

Zambezi system. Specimens have a tendency for the lateral spots to be weak (except the peduncular blotch which is intense and elongate [see above]).

Beira, Lake Ngami and the Okavango River samples. Despite the great distance separating Beira and the other localities, fishes from these places are remarkably similar and perhaps closest to the Zambezi fishes in coloration (see also Barnard, 1948) ; the peduncular blotch is large and elongate. These populations differ from the Zambezi form in having longer last unbranched dorsal fin rays (Ngami 23·2–25·3%

S.L.; Beira 22·9–27·3, cf. 17·5–24·6 for Zambezi specimens). Fishes from *Mossamedes* have a somewhat similar facies (dorsal spine length 23·2–27·0) but in all nine specimens examined the caudal blotch is weak and only in two is it elongate. Traces of the two anterior midlateral spots can be seen in three specimens. However, in view of Groenewald's observations, the intensity of the spots may only reflect the turbidity of the water at any particular locality and time.

Transvaal, South Africa (based on two localities, the Klein Olifants River and another east of Pietersburg). These fishes have a typical three-spot coloration and rather long last unbranched dorsal rays (22·9–25·7% S.L.). In addition, the Pietersburg fishes have small scales on the caudal peduncle (15–17), a count which overlaps with that of *B. jacksonii* (see p. 184). Groenewald (*op. cit.*) does not mention any local differences within his material from the Transvaal, neither does he record any specimens with such a high caudal peduncle scale count (14 scales is the modal and highest count).

Lake Bangweulu, the Lukulu River and the Chambesi-Chilola confluence. These fishes have long dorsal spines (22·0–29·4% S.L.), those from the Chambesi having the longest spines, and small scales. Indeed, all the scale counts overlap with those of *B. jacksonii*. With regard to dorsal spine length it should be noted that specimens of *B. paludinosus* from this area (particularly Lake Bangweulu) are characterized by their long spines (see also Ricardo-Bertram, 1943; now that the range of variability for the species is better known, the other differences noted by this author no longer apply).

Lake Nyasa. Specimens from this lake have longer posterior barbels, a character most clearly seen when the ratio

$$\frac{\text{Length of barbel}}{\text{eye diameter}}$$

is compared. For example, this ratio for fishes from the Zambezi, Beira and Lake Bangweulu is 0·8–1·3 (mean 1·1) whereas in fishes from Nyasa it is 1·5–2·1 (mean 1·8).

Other areas. The characteristics here are rather negative in that fishes from localities other than those detailed above do not show clearly the characteristics of these populations. Doubtless the picture will become clearer when more material is examined.

Distribution. Zambezi system, Lake Ngami and the Okavango River; Lake Nyasa and the Ruo River; Lake Bangweulu and associated rivers and streams; Luapula and Lualaba Rivers; Orange River system; Limpopo, Incomati and Vaal River systems; Zululand; Angola (Kunene and Cubango Rivers, the latter being the upper portion of the Okavango River).

Affinities. *Barbus trimaculatus* is clearly related to *B. jacksonii* of East Africa. The affinities of the two species are discussed on p. 185.

Barbus sexradiatus Boulenger, 1911

(Text-fig. 10)

Barbus sexradiatus Blgr., 1911, *Cat. Afr. Fish.* **2** : 128, fig. 106.

Holotype. A specimen 56 mm. S.L. from Kisumu Bay, Lake Victoria (B.M. [N.H.] reg. No. 1909.11.15.11).

Description. Based on the unique holotype. All measurements are expressed as percentages of the standard length.

Depth of body 27·6, length of head 28·5. Snout strongly decurved, its length 8·9 ; suborbital lateral line canal prominent, diameter of eye 7·1 ; least interorbital width 10·7.

Length of anterior barbel 8·9, of posterior barbel 10·7.

Length of last unbranched dorsal ray 15·2 ; distance from snout tip to dorsal origin 53·5. Length of pectoral fin 21·4.

Length of caudal peduncle 19·6, its depth 14·3.

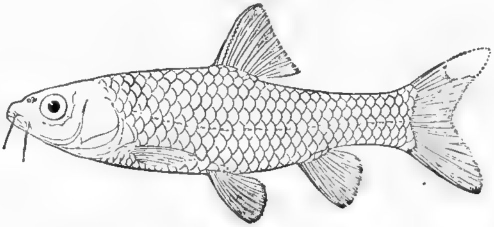

FIG. 10. *Barbus sexradiatus*, holotype, natural size (from Boulenger, *Cat. Afr. Fish.*).

Lateral line with 28 scales ; 4½ scales between the lateral line and the dorsal origin, 4 between the lateral line and the pelvic origin. Twelve scales around the caudal peduncle, 10 in the predorsal row. Scales along the entire base of the dorsal fin extend upwards on to the lowermost part of the fin itself.

Dorsal fin origin above that of the pelvics, the fin with 3/6 rays. The last unbranched ray is stout, ossified and serrated on its posterior face. *Anal fin* with 3/5 rays.

Coloration (specimen fixed in alcohol). Brownish-silver above, silvery below, with a very faint trace of an interrupted dark midlateral band along the posterior half of the body. There is also a faint and small, black midlateral spot at the base of the caudal fin. All fins are colourless.

Affinities. On most morphometric characters *B. sexradiatus* could be contained within *B. kerstenii* ; but it differs most markedly in having a blunt, strongly decurved snout. Also, *B. sexradiatus* has one less branched dorsal fin ray (a character, in some cases, of doubtful significance) and the raised, obliquely directed scales at the dorsal fin base are more obvious in this species.

The characters separating *B. sexradiatus* from *B. kerstenii* are those that link the species with *B. laticeps*. Indeed, the two species are almost indistinguishable superficially. In addition to having strongly decurved snouts and broad preorbital faces, both *B. laticeps* and *B. sexradiatus* possess suborbital lateral line canals which are more prominent than those of *B. kerstenii* and most other East African *Barbus*. On the material available (one specimen of *B. sexradiatus* and six of *B. laticeps*), *B. sexradiatus* may be distinguished by its slightly longer head (28·5% S.L. cf. 25·6%), snout (8·9 cf. 8·3), eye (7·1 cf. 6·7) and barbels (anterior 8·9 cf. 7·6, posterior 10·7 cf. 10·0). Further differences are the presence of a distinct midlateral dark stripe and a precaudal spot in *B. sexradiatus*, and seven branched dorsal rays in *B. laticeps*. All these differences are slight, especially when compared with the known intraspecific variation amongst other *Barbus*. I strongly suspect that *B. sexradiatus* and *B. laticeps* may prove to be conspecific when more specimens of both are obtained.

Barbus sexradiatus must be a rare species in Lake Victoria (or else confined to inaccessible habitats) because no specimens other than the unique holotype have been found and this despite intensive collecting between 1951 and 1957.

Distribution. Known only from Kisumu Bay, Lake Victoria.

Barbus laticeps Pfeffer, 1893

(Text-fig. 11)

Barbus laticeps Pfeffer, 1893, *Jb. hamburg. Wiss. Anst.* **10** : 38, pl. 1, fig. 4 ; *Idem*, 1896, *Thierw. O. Afr.*, Fische, 57 ; Boulenger, 1911, *Cat. Afr. Fish.* **2** : 128, fig. 105.

Description. Based on five fishes, 57–68 mm. S.L., from the Wami River near Kilosa, Tanganyika Territory. (The type locality is given as the Wami River.) I have not studied the holotype (in the Berlin Museum) but Pfeffer's drawing and description show the most characteristic features of the species and I have no doubt as to the identity of the material in the B.M. (N.H.). Pfeffer's drawing shows a prominent suborbital canal system with large pores, and also gives the impression that the bone is inflated. A comparable condition has not been observed in any African species of *Barbus* and is certainly not developed in the additional specimens. Thus, I consider that the figured suborbital is either an artefact of preservation or the result of the artist's inaccuracy. I suspect the latter because Pfeffer does not comment on this bone and because in some of my material the suborbital canal and openings are prominent (but not noticeably enlarged).

Depth of body 27·2–30·2 ($M = 28{\cdot}7$), length of head 23·7–25·6 ($M = 24{\cdot}8$). Dorsal head profile sharply decurved from a point above the origin of the anterior barbel thereby giving the head a noticeably blunt appearance. The width of the head slowly decreases anteriorly from a point behind the orbit, so that the outline of the head (viewed from above) is more broadly rounded than in related species, for example, *B. kerstenii*. The skin covering the head, especially its dorsal surface, is somewhat thickened so that the general impression is one of a blunt and chubby-headed fish. It is this feature that most readily distinguishes preserved specimens of *B. laticeps* from *B. neumayeri* and *B. kerstenii*, species with which it overlaps in most morphometric characters.

Snout strongly decurved, its length 6·6–8·3 ($M = 7{\cdot}6$); least interorbital width 9·6–11·2 ($M = 10{\cdot}3$), eye diameter 5·8–6·7 ($M = 6{\cdot}3$).

Length of anterior barbel 5·0–7·6 ($M = 6{\cdot}5$), its tip reaching beyond the base of the posterior barbel; length of the latter 7·4–10·0 ($M = 8{\cdot}6$).

Length of caudal peduncle 19·1–22·4 ($M = 20{\cdot}3$), its depth 13·2–14·4 ($M = 13{\cdot}5$).

Length of last unbranched dorsal ray 15·0–17·6 ($M = 16{\cdot}2$) (apparently as long as the head in the type; in the B.M. (N.H.) specimens it is $\frac{5}{8}$–$\frac{2}{3}$ head length); distance from snout tip to dorsal origin 50·8–54·8 ($M = 52{\cdot}4$). Length of pectoral fin 16·7–19·3.

Lateral line with 28 (f.2), 29 (f.2) or 30 (f.1) scales; $4\frac{1}{2}$–$5\frac{1}{2}$ scales, between the lateral line and the dorsal fin origin, $3\frac{1}{2}$–4 between the lateral line and the pelvic origin; 12 or 14 scales around the caudal peduncle and 11 or 12 in the predorsal row.

Dorsal fin origin above or slightly posterior to that of the pelvics; the anterior two or three basal scales extend upwards on to the lowermost part of the fin; the fin with 3/7 rays, the last unbranched ray stout, ossified and serrated posteriorly. When this spine is erected at an angle of about 60° from the horizontal, the margin of the fin lies at an angle of 10–20° from the vertical. *Anal fin* with 3/5 rays.

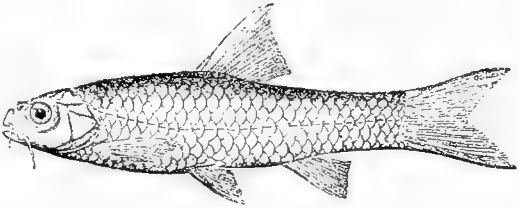

FIG. 11. *Barbus laticeps*, type (after Pfeffer, from Boulenger, *Cat. Afr. Fish.*).

Coloration (known only from alcohol-fixed specimens). Brownish above, dead white below, with an overall silver sheen. There are no dark markings on the body and all fins are colourless.

Diagnosis and affinities. Except for its strongly decurved snout and broad preorbital face, *B. laticeps* resembles both *B. neumayeri* and *B. kerstenii*. No other characters are sufficiently trenchant to separate the three species. Preserved material of *B. laticeps* does differ from both *B. neumayeri* and *B. kerstenii* in the complete absence of dark markings on the body. The very close relationship of *B. laticeps* with *B. sexradiatus* is discussed on p. 188.

Distribution. Known only from the Wami River system Tanganyika Territory.

Barbus magdalenae Boulenger, 1906

(Text-fig. 12)

Barbus magdalenae Blgr., 1906, *Ann. Mag. nat. Hist.* (7) **17**: 437; *Idem*, 1907, *Fish. Nile*: 256; *Idem*, 1911, *Cat. Afr. Fish.* **2**: 179, fig. 157.

Lectotype. A specimen 66 mm. S.L. from Bunjako, Lake Victoria (B.M. [N.H.] reg. No. 1906.5.30.125).

Description. Based principally on the lectotype and seven paratypes, 56–66 mm. S.L., all from the same locality. Data on certain characters, such as variability of head profile and coloration are derived from numerous specimens studied in the field. All measurements are expressed as percentages of the standard length.

Depth of body 26·8–32·2 ($M = 30{\cdot}0$), length of head 22·0–24·8 ($M = 23{\cdot}5$); dorsal head profile variable but usually decurved and noticeably rounded (see Text-fig. 12). Length of snout 6·1–7·1 ($M = 6{\cdot}6$), snout strongly decurved in most fishes; diameter of eye 6·1–8·1 ($M = 7{\cdot}5$), least interorbital width 9·1–10·6 ($M = 9{\cdot}8$).

Anterior barbel absent, length of posterior barbel variable, from minute to 3·5% of standard length.

Length of last unbranched dorsal ray 20·0–28·6 ($M = 23{\cdot}1$); distance from snout tip to origin of dorsal 45·5–52·5 ($M = 49{\cdot}5$). Length of pectoral fin 14·2–18·6.

Length of caudal peduncle 23·7–25·6 ($M = 24{\cdot}5$), its depth 12·0–14·3 ($M = 12{\cdot}9$).

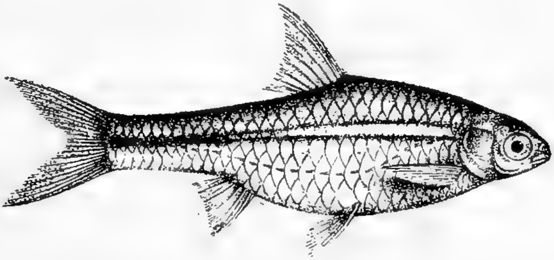

FIG. 12. *Barbus magdalenae*, lectotype, natural size (from Boulenger, *Fish. Nile*).

Lateral line with 25–31 scales (mode 29), its course with a pronounced ventral curvature on the flanks but returning to a midlateral position on the caudal peduncle. This extreme curvature of the lateral line is a distinctive feature of *B. magdalenae* and one not found in many African *Barbus* species; 4½–5½ scales between the lateral line and the dorsal fin origin, 1 or 2 between the lateral line and the pelvic origin; 11 or 12 scales around the caudal peduncle and 11–13 in the predorsal row.

Dorsal fin origin slightly posterior to that of the pelvics, the fin with 3/8 rays; last unbranched ray flexible and not enlarged. *Anal fin* with 3/5 rays.

Coloration (*alcohol-fixed* specimens). Entire body intensely silver, a more or less distinct, greyish midlateral stripe from behind the operculum to the caudal base. All fins colourless (Boulenger [1906] describes the fins of the same specimens as yellowish, but this pigment has now vanished). In *formol-fixed* specimens the silver is almost completely lost after a few months, the ground colour then becoming yellowish and the midlateral stripe intensely black; again, the fins are colourless.

In life the fishes are a tarnished silver colour with the midlateral band visible as an intense silver streak.

Habitat. The species occurs in the marginal water-lily swamps of Lakes Victoria and Nabugabo, but it is nowhere common. During the biannual floods specimens are found some distance up lakeside streams ; this migration may be connected with breeding.

Distribution. Known only from Lakes Victoria and Nabugabo.

Affinities. Apart from its group relationship (i.e. a member of the group with radiately striate scales and a flexible, unossified last unbranched dorsal ray) the affinities of *B. magdalenae* are difficult to determine. The strongly curved lateral line, absence of anterior barbels, reduced posterior barbels and the blunt snout are characters not found together in any other species of East African *Barbus*. Indeed, the course of the lateral line appears to be unique amongst African species. At present I can suggest no close relatives for the species ; it is certainly the most unusual *Barbus* occurring in Lake Victoria and is, of course, endemic to the Victoria basin.

Because of the reduced barbels, I examined the specimens critically for the presence of well-developed pit lines. Superficially, I can find no trace of such structures.

Barbus usambarae Lönnberg, 1907

Barbus usambarae Lönn., 1907, *Kilim.-Meru exped.*, 1905–1906. *Fishes* : 5.

This species was described from a unique holotype. Unfortunately this specimen has since dried out and is valueless for any critical determination. However, I have found amongst the collections of the Naturhistoriska Riksmuseet, Stockholm, a fish which agrees very closely with the original description and which was part of the collection containing the holotype. (Incidentally, this additional specimen of *B. usambarae* was found amongst the eighteen syntypes of the characin *Petersius tangensis*.)

The redescription given below is therefore based upon the second specimen, a fish 31 mm. standard length. All measurements are given as percentages of the standard length.

Depth of body 29·0, length of head 24·2. Snout length 6·5 ; eye diameter 7·4 ; least interorbital width 10·6.

Length of anterior barbel 3·2 (slightly less than half eye diameter), of posterior barbel 6·5 (slightly less than eye).

Length of last unbranched dorsal ray 25·2 ; distance from snout tip to dorsal origin 51·5. Length of pectoral fin 19·4.

Caudal peduncle length 25·0, its depth 14·5.

Lateral line with 30 scales, its course with a marked ventral dip ; 6 scales between the lateral line and the dorsal origin. Two scales between the pelvic insertion and the lateral line. Twelve scales around the caudal peduncle and about the same number in the predorsal row.

Dorsal fin origin slightly in advance of the first pelvic ray. Dorsal with 3/7 rays, the last unbranched ray thin, flexible and unossified. *Anal fin* with 3/5 rays.

Coloration (alcohol-fixed and preserved) silvery but profusely peppered with melanophores above the level of the lateral line ; a narrow greyish midlateral stripe runs from behind the operculum to the caudal origin, where it is expanded into a small but well-defined black spot. There are diffuse black spots at the base of the anal fin and numerous melanophores between the fin rays of the dorsal and anal fins.

Diagnosis. Species belonging to the group characterized by a slender, unossified last dorsal ray are not numerous in East Africa. The only other species which might be confused with *B. usambarae* is *B. lineomaculatus* Blgr. *Barbus usambarae* differs from the latter in its much shorter barbels (neither are as long as the eye, whereas in *B. lineomaculatus* both the anterior and posterior barbels are longer than the eye), in having the origin of the dorsal fin slightly behind the first pelvic ray and in the absence of dark spots along the lateral band. With only one specimen available it is impossible to speculate on the possible affinities of *B. usambarae.*

Distribution and habitat. The species is known only from one locality, a pool on inundated ground near Tanga, Tanganyika Territory.

THE SUBGENUS *BEIRABARBUS*

Both Herre (1936) and Schultz (1942) described genera of African cyprinids which differ from *Barbus* only in possessing an extensive system of sinuous, nearly parallel low ridges covering the greater part of the head. Later, Barnard (1948) showed that the ridges extend on to the anterior lateral-line scales and some scales in the shoulder region. Each ridge is composed of a single line of minute raised pores and resembles a short string of beads. Some lines on the cheek are branched. Similar cephalic ridges occur in the Asiatic genera *Cyclocheilichthys* and *Oreichthys.*

Apparently Schultz (*op. cit.*) was unaware of Herre's paper since he did not compare his genus *Mannichthys* with *Beirabarbus.* A comparison of the two generic diagnoses immediately shows that the " genera " cannot be distinguished by a single character of any taxonomic weight. This synonymy was either implicitly (Barnard) or explicitly (Johnels, 1954) accepted by later authors and is upheld here. However, the status of the taxon *Beirabarbus* has received somewhat different treatment by these authors and by Groenewald (1958). Barnard (*op. cit.*) expressed the view that" Some taxonomic distinction, either subgeneric or full generic, should be given to indicate this exceptional feature, which differentiates these two species (i.e. *Beirabarbus palustris* and *Barbus* (*Beirabarbus*) *okavangoensis*) from all other South African (? African) species ". Johnels, on the other hand, doubted the advisability of using secondary pit-lines as generic or subgeneric characters. He suggests, however, that " the pattern of the lateral-line system may be of importance in taxonomy ". The different attitudes of these authors is perhaps reconcilable with the fact that Barnard thought that his two species were probably distinct from all other African species whereas Johnels had examined many West African *Barbus* and found pit-lines in at least six species. Furthermore, he considered *B. leonensis* as representing a transitional stage between the well-marked pit-lines of *Beirabarbus* and their apparent absence in most *Barbus* species. Another factor influencing Johnels was his suspicion that secondary (accessory) pit-lines might be a characteristic of most cyprinid genera.

Recently, Whitehead (1960) has followed Johnels in evaluating the taxonomic value of pit-lines on certain East African species.

In order to check the distribution of pit-lines in African *Barbus* of the group with radiately striate scales, I have examined a large number of species from various areas and belonging to different subgroups of this division.

Briefly, the results of this survey are : (i) Pit-lines occur in many species from West Africa but in fewer species from other parts of Africa. (ii) Pit-lines are found in species with well-developed barbels as well as in those lacking barbels or with greatly reduced barbels. (iii) A distinction in superficial appearance of the lines can be drawn between the *Beirabarbus* type (ridges) and those in which the pits remain sunken. Finally, I agree with Barnard (*op. cit.*) that some distinction should be afforded to those species with the *Beirabarbus* type of cephalic pit-lines. Whitehead's (*op. cit.*) recent observations on the histological nature of the two types of pit-line are very suggestive. He finds a marked difference in the finer detail and says, of the *Beirabarbus* type, " . . . skin sections from the cheek showed that the supposed neuromasts were in fact small masses of fibrous tissue apparently connected by a fine network of canals Certainly their structure was in no way homologous with the cheek pit-line system found in other species ". Mr. Whitehead kindly lent me his slides and I hope at a later date to extend this comparative histological study to include all the species now referred to the subgenus *Beirabarbus*.

Macroscopically, the distinction I draw between the *Beirabarbus* pattern and the other types of pit-line distribution is as follows. In *Beirabarbus* the pits are small and tightly packed along any one line ; the lines are more numerous and, except on the dorsal head surface, clearly raised above the level of the intervening skin ; the cheek lines are close together and often branched, there being as many as fourteen distinct lines between the ventral preopercular margin and the anterior margin of the orbit; the transverse lines on the dorsal surface of the head are also more numerous (see Text-fig. 13).

In the other species, the pores are relatively larger and those constituting any one pit-line are clearly discrete ; the lines do not appear as ridges although the mouth of a pit may be raised above the skin ; there are fewer lines and not more than seven or eight between the preoperculum and the anterior orbital margin ; branching, if it occurs at all is obscured by the greater distance between the individual pores constituting a line.

Preservation undoubtedly affects the facility with which pits and pit-lines may be seen. Nevertheless, if care is taken with lighting arrangements it is possible to detect pores in even the most unpromising material. In badly preserved or old specimens of either group, the pores or ridges are often best seen on the ventro-lateral aspects of the head, at the junction of cheek and preoperculum.

Evidence on the ontogeny of *Beirabarbus*-type pit-lines is somewhat contradictory because in certain small specimens the ridges are like those of the adult whereas in other specimens the ridges are weakly delimited. In general, however, it seems that the juvenile *Beirabarbus* condition closely approaches that of adults in the group with sunken pit-lines.

No obvious intermediates between the *Beirabarbus* condition and the others as defined above were found in the collection examined macroscopically. Therefore, pending histological studies on the pit-line system I propose that Herre's genus

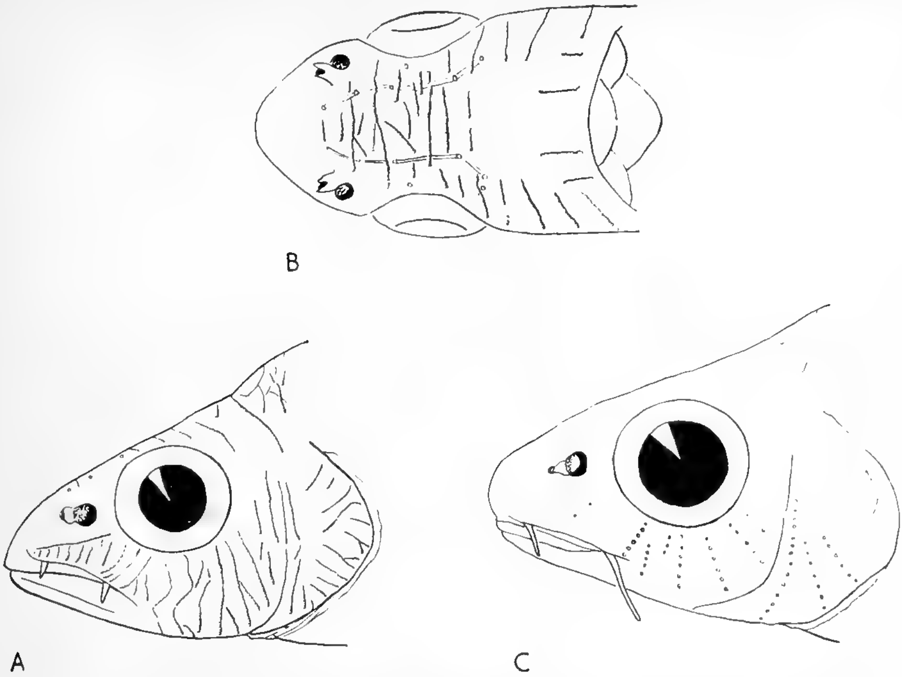

Fig. 13. Cephalic pit-line systems in *Barbus* and *Barbus* (*Beirabarbus*). A and B. Lateral and dorsal views of the head in *Barbus* (*Beirabarbus*) sp.; based on *B.* (*B.*) *aurantiacus*. C. Pit-line system in a *Barbus* species with macroscopically visible pits, based on *B. yongei* and *B. svenssoni*.

Beirabarbus be considered of subgeneric rank. The existence of other species-groups with and without obvious pit-lines must also be recognized but at present it is difficult to give them formal taxonomic status.

On the characters discussed above the following species may be referred to the subgenus *Beirabarbus* :

Barbus callipterus Blgr., 1907
Barbus ablabes (Bleeker), 1863
B. deserti Pelleg., 1909 (includes *B. gambiensis* Svensson ; see Daget, 1954)
B. macrops Blgr., 1911
B. spurrelli Blgr., 1913
B. lucileae (Schultz), 1942
B. aurantiacus Blgr., 1910
B. doggetti Blgr., 1904 (includes *Beirabarbus palustris* Herre, 1936 ; see below, p. 196)
B. aspilus Blgr., 1907
B. jae Blgr., 1903

With two exceptions (*B. ablabes* and *B. lucileae*) my observations are based on holotypes or paratypes, supplemented by other specimens in the Museum's collections. These studies also suggest that at least five species are probably synonymous, a conclusion reinforced in part by Daget (1954) and in its entirety by Dr. Trewavas' independent studies on West African *Barbus* species (Dr. Trewavas, personal communication). The species involved are *B. ablabes* (the nominate species), *B. deserti*, *B. macrops*, *B. spurrelli*, and *B. lucileae.* The supposed interspecific differences observable in preserved material or given in published descriptions, are certainly less than interpopulation differences found in other *Barbus* species (see also Daget, 1954 and Johnels, 1954). In general, differences in coloration are also slight and probably attributable to artefacts of preservation ; only critical field observations will be able to settle this question.

In view of this tentative synonymy, some comment is necessary on Daget's description of *B. spurrelli* in his account of the Niger fishes (Daget, 1954). The single specimen on which his description is based apparently has no cephalic pit-lines. If this is the true condition and not one due to poor preservation, then the specimen cannot be referred to *B. spurrelli.* Pit-lines are clearly visible in the type specimens of this species.

Two other species, *B. aurantiacus* and *B. doggetti*, are very closely related but differ in the course of the lateral line and longer posterior barbels of *B. doggetti.* Since the characters are consistent and trenchant the status of these species seems definite.

In brief then, the subgenus *Beirabarbus* would seem to comprise six and not ten species. Of these six, five are essentially West African in distribution and one (*B. doggetti*) eastern, its distribution extending from East Africa (Uganda) along the eastern seaboard to the eastern regions of South Africa (including Swaziland).

The phyletic significance of this subgenus is questionable, mainly because we know little about the phylogeny of African species referred to the genus *Barbus* (see Myers, 1960). Apart from the peculiar arrangement of pit-lines, there are no other characters which suggest that all species of *Beirabarbus* are derived from a common stem (I except Whitehead's observations on the histology of the pit-organs [see above, p. 194] until further investigations are made). On the other hand, similarity in coloration and general facies suggests a fairly close relationship between the *B. ablabes* group, *B. aurantiacus* and *B. doggetti.*

Two species referable to the subgenus *Beirabarbus* come within the terms of this revision :

Barbus (Beirabarbus) doggetti Boulenger, 1904

(Text-fig. 14)

Barbus doggetti Blgr., 1904, *Ann. Mag. nat. Hist.* (7) **13** : 450 ; *Idem*, 1907, *Fish. Nile* : 225, pl. 46, fig. 3 ; *Idem*, 1911, *Cat. Afr. Fish.* **2** : 174, fig. 151.

Beirabarbus palustris Herre, 1936, *Proc. biol. Soc. Washington*, **49** : 99.

Barbus (*Beirabarbus*) *palustris* Barnard, 1948, *Ann. S. Afr. Mus.* **36** : 439, fig. 6b ; Groenewald, 1958, *Ann. Transv. Mus.* **23** : 325, pl. 69, fig. 3.

Notes on the synonymy. The holotype and once unique specimen of *B. doggetti* is indistinguishable on morphometric characters and lateral-line course from *Beirabarbus palustris* (paratypes and other specimens). It appears to differ in some characters such as the rather slight predorsal eminence, more rounded snout and thicker lips (cf. fig. 174 in Boulenger [1911] and fig. 6b in Barnard [1948]). Also, in *B. doggetti* holotype there is no black lateral band (the band is plumbeous-silver) and the scales above the lateral line have a smaller dark lunate spot at the base.

Differences in coloration are of doubtful significance since the intensity of dark markings is dependent both on the fish's environment and on the preservatives used after death. *Barbus doggetti* holotype was undoubtedly fixed and preserved in alcohol, a medium which does not intensify dark markings. Specimens of *B. doggetti* from the Victoria basin which were fixed in formol and later preserved in alcohol show a coloration indistinguishable from that of the *Beirabarbus palustris* paratypes.

The other differences are difficult to assess, particularly since *B. doggetti* holotype is a larger (and presumably older) fish than any of the *Beirabarbus palustris* I examined. Superficially, the shape of the snout is unlike *B. palustris* and the body is more graceful since it lacks a pronounced predorsal eminence. However, it is possible to deform the snout of a *B. palustris* and produce an effect similar to that seen in *B. doggetti*, which was apparently preserved with the mouth maximally open. The almost imperceptible predorsal eminence of *B. doggetti* holotype is an obvious difference when the specimen is compared with the paratypes of *Beirabarbus palustris*. But, amongst fishes from the Aswa and Nzoia Rivers there are specimens which bridge this gap ; also, some of the South African fishes (see pl. 69, fig. 3 in Groenewald, *op. cit.*) do not differ greatly from the *B. doggetti* condition.

Thus, it is difficult to escape the conclusion that *Beirabarbus palustris* Herre, 1936, is a synonym of *Barbus doggetti* Blgr., 1904. When more specimens are available it may be possible to distinguish morphologically separable populations of this widespread species.

Description based on fourteen fishes, 35–85 mm. S.L. (including the holotype of *B. doggetti*). I have also examined fourteen paratypes of *Beirabarus palustris* but morphometric data from these fishes are not included. All measurements are expressed as percentages of the standard length.

Depth of body 26·1–34·4 (M = 28·3), length of head 26·7–29·5 (M = 27·4). The predorsal profile is variable, from gently sloping to sloping steeply in the nuchal region and then more moderately towards the dorsal fin origin ; the latter type of curve gives a humped profile and is typical of the sample from Beira (i.e. the paratypes of *Beirabarbus palustris*). Intermediates occur in populations from Dar es Salaam and the Aswa River (Uganda).

Snout, rounded, its length 6·8–9·5 (M = 8·3) ; mouth relatively small ; eye diameter 7·0–9·5 (M = 8·2) ; least interorbital width 8·0–11·9 (M = 9·7).

Length of barbels variable, the anterior pair generally minute but in the largest specimen (holotype *B. doggetti*) 1·2 ; posterior barbel minute to 5·6 (M = 2·3). The posterior barbels are shortest in fishes from Uganda ($\frac{1}{6}$–$\frac{1}{3}$ eye diameter) and longer in fishes from South Africa, Beira and Tanganyika ($\frac{1}{4}$–$\frac{1}{2}$ [mode $\frac{1}{2}$] eye) ; there is no apparent correlation between relative barbel length and the size of the fish.

Length of last unbranched dorsal ray 26·6–31·0 (*M* = 28·0); distance from snout tip to dorsal origin 47·8–52·3 (*M* = 49·5); length of pectoral fin 18·7–25·4.

Caudal peduncle length 20·3–26·2 (*M* = 23·2), its depth 11·4–14·0 (*M* = 13·5).

Lateral line with a distinct downward bend from its origin to about the tenth scale, thereafter it rises abruptly to a midlateral position. There are 25 (f.2), 26 (f.6) or 27 (f.6) scales in the lateral line (Groenewald, *op. cit.* gives 27–28 as the range for South African specimens); 3½ scales between the lateral line and the dorsal origin, 2 or 2½ (less frequently 3) between the lateral line and the pelvic origin (Herre, *op. cit.* gives 3½ scales in the transverse series below the lateral line; but for the count used in this paper there are 2 or 2½ scales in the paratypes I have examined), 12–14 scales around the caudal peduncle and 9 or 10 (less frequently 8) in the predorsal row.

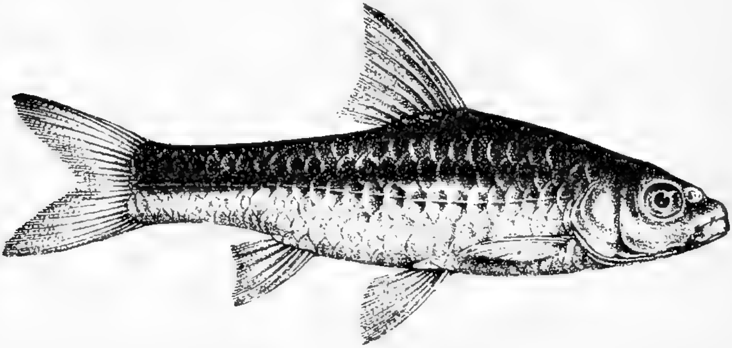

FIG. 14. *Barbus* (*Beirabarbus*) *doggetti*, holotype, slightly less than natural size (from Boulenger, *Fish. Nile*).

Dorsal fin origin above or slightly behind that of the pelvics, the fin with 3 or 4/8 rays, the last unbranched ray flexible and not enlarged. *Anal fin* with 3/5 rays.

Coloration. Most of the specimens I have examined were probably fixed in formol; the only specimen definitely not so treated is the holotype of *B. doggetti*, which does show certain differences in coloration and is described separately (see also p. 201).

Ground colour brownish to greyish-white; scales above the lateral line series with dark, lunate centres (of variable intensity) and a very faint dark outline. A dark midlateral streak originates on the snout, passes through the eye, across the operculum and continues along the flank to the caudal origin; this band is of variable intensity and its margins are somewhat blurred in the abdominal region, where it is broadest. The cephalic part is often difficult to detect. Macroscopically, all fins except the dorsal are colourless; the latter is dusky, especially near the distal margin and there is an oblique band which traverses the middle of the fin. Under a low-power microscope all the fins are seen to be peppered with small melanophores.

The holotype of *B. doggetti* (alcohol fixed) differs in being generally paler (although the dorsal and dorsolateral scales have dark, lunate centres) with a silver sheen ventrolaterally. The midlateral stripe is a leaden-silver and is broader than the black stripe in other specimens ; its course on the head cannot be traced. The fins appear colourless but melanophores are visible under low magnification.

The only data on the colour of live fishes are those given by Herre (*op. cit.*) for fishes from Beira. Herre's description is " . . . the general colour is reddish olive brown, with violet, bluish red, and purplish iridescence ; a black lateral stripe extends from tip of snout to caudal base."

Habitat. Little information is available, but from distribution records it would seem that *B.* (*Beirabarbus*) *doggetti* is essentially a fluviatile species sometimes occurring in swampy areas. Although the type locality is given as Lake Victoria no further specimens have been collected in the lake itself.

Affinities. The species is related to *B.* (*Beirabarbus*) *aurantiacus* from Angola and the Zambezi system (including the Okavango region) and differs from it mainly in having a curved lateral line.

Distribution. Lake Victoria and certain affluent rivers and streams ; Aswa River (Uganda) ; near Dar es Salaam ; near Beira ; Transvaal (Limpopo, Inkomati and and Umbeluzi River systems).

Barbus (Beirabus) aurantiacus Boulenger, 1910

(Text-fig. 15)

Barbus aurantiacus Blgr., 1910, *Ann. Mag. nat. Hist.* (8) **6** : 554 ; *Idem*, 1916, *Cat. Afr. Fish* **4** : 270, fig. 166.
Barbus rogersi Blgr., 1911, *Cat. Afr. Fish.* **2** : 180, fig. 158 ; Worthington, 1933, *Proc. zool. Soc. London* : 305.
Barbus okavangoensis Brnrd., 1941, *Ann. Mag. nat. Hist.* (11) **8** : 470 ; *Idem*, 1948, *Ann. S. Afr. Mus.* **36** : 437, fig. 6a.

Notes on the synonymy. Barnard (1941 and 1948) drew attention to the similarity (coloration, reduced barbels and straight lateral line) between *Barbus* (*Beirabarbus*) *okavangoensis*, *Barbus rogersi* and *Barbus aurantiacus*. He was, however, unable to confirm the presence of sensory ridges on the two latter species. This I have done and find that the types of both *B. aurantiacus* and *B. rogersi* possess ridges of the *Beirabarbus* type. Since the three species are so similar in other characters I have little hesitation in accepting Barnard's suggestion that *B. rogersi* and *B. okavangoensis* are synonyms of *B. aurantiacus*. I would add one reservation, namely : the Okovango sample may represent a characterizable population (see below).

There are two syntypes of *B. rogersi*, one from the Que River, Angola (B.M. [N.H.] reg. No. 1907.6.29.149) and one from the Umsitu River (near Broken Hill), Rhodesia (reg. No. 1910.1.26.5). Neither is perfectly preserved, but the Que River fish is less damaged, especially in the head region. In the original description, Boulenger figures the Que fish as type but does not specifically designate it as holotype. According to the legend of this figure the specimen is reproduced at 1½ × N.S. This enlargement is manifestly incorrect and could not be applied to either syntype.

In fact, the figure is fractionally larger than the fish it purports to represent. Careful comparison of the figure with both types shows an overall resemblance nearer that of the Que fish, although the eye in that specimen is proportionally larger than it is in the figure. In selecting the Que river fish as lectotype of *B. rogersi* I have been influenced both by the overall resemblance of this fish to the figure and the fact that it is in a better state of preservation than the specimen from Umsitu. The latter I cannot refer to the species with any certainty because the critical character of cephalic pit-lines has been destroyed. Certainly on other characters it could equally well be placed in at least two other species.

Specimens described by Barnard from the Okovango River differ slightly from the other specimens of *B.* (*B*) *aurantiacus.* The differences are slight and when making the comparison it must be remembered that there are but eleven other specimens as compared with seventy-five from the Okovango. Barnard stresses that in no Okovango fishes is the body depth greater than the head length ; four *B.* (*B*) *aurantiacus* have the depth greater than the head. Two other differences are : first, a higher lateral-line scale count for the Okovango fishes (the lowest number of scales is 26 whereas other specimens may have 24 or 25) and second, a tendency for fishes outside the Okovango area to have an extra unbranched dorsal fin ray. Even if further collections reinforce these slight differences, the Okovango fishes cannot be considered as being more than a distinct population.

Lectotype. A specimen 78 mm. S.L. B.M. (N.H.) reg. No. 1911.6.1.78 from the Lucalla River, Angola.

Description. Based on eleven fishes, 30–78 mm. S.L. (including the lectotype of *B. rogersi* and the types of the species). All measurements are given as percentages of standard length.

Depth of body 23·3–29·0, *M* = 27·0 (six specimens with the depth less than head length, one with head and depth equal and four with the depth greater than the head ; see Barnard, 1948) ; length of head 25·4–29·9 (*M* = 27·4), predorsal profile sloping moderately and without a marked nuchal hump (cf. *B.* (*B*) *doggetti*).

Snout length 7·2–10·0 (*M* = 8·5) ; mouth relatively small ; eye diameter 8·2–10·3 (*M* = 9·6) ; least interorbital width 9·0–11·7 (*M* = 10·3).

Barbels variable, the anterior pair absent or minute, the posterior pair minute in all fishes less than 48 mm. S.L. and 1·5–2·0 in larger individuals, thus suggesting a positive allometric relationship with length.

Last unbranched dorsal ray 25·6–30·8 (*M* = 29·2) ; distance from snout tip to dorsal origin 46·0–50·0 (*M* = 48·5) ; length of pectoral fin 15·0–20·8.

Lateral line virtually straight, without a pronounced ventral dip between the second and tenth scales ; 24 (f.1), 25 (f.3), 26 (f.4) or 27 (f.3) pore scales ; $3\frac{1}{2}$ or 4 scales between the lateral line and the dorsal origin, $2\frac{1}{2}$ (rarely 2) between the pelvic fin origin and the lateral line ; 12–14 scales around the caudal peduncle, 9 (less frequently 10 or 11) in the predorsal row.

Dorsal fin origin above that of the pelvics, the fin with 3/7 (f.1), 3/8 (f.4) or 4/8 (f.6) rays. *Anal fin* with 3/6 (in one specimen 3/5) rays.

Coloration. There is apparently little difference, except for intensity, between alcohol- and formol-fixed specimens ; the latter are lighter. Ground colour brownish-yellow to yellow-grey, scales above (and less frequently one or two rows below) the lateral line with dark centres or even the whole scale dark except for a narrow pale margin. In formol-fixed specimens there is a dark midlateral band from the snout, across the operculum and along the course of the lateral line to the caudal origin. The anterior (i.e. pre-opercular) part of the band is often less intense. In alcohol-fixed specimens (e.g. the types) the lateral band is bright silver with a narrow dark band underlying it ; the cephalic part of the band is not visible. In the material examined, all the fins are colourless except for a faint black margin to the dorsal fin ; in some fishes (formol fixed) there is a light scattering of melanophores, visible at low magnification, on all the fins. In newly preserved material some colour remains in the dorsal and other fins, described by Barnard (for *B. okavangoensis* in formalin) as salmon coloured and by Boulenger (for the dorsal only of *B. aurantiacus* fixed in spirit) as bright orange. These colour descriptions are rather at variance, but since both were made from material fixed in different fluids, little importance can be attached to the discrepancies.

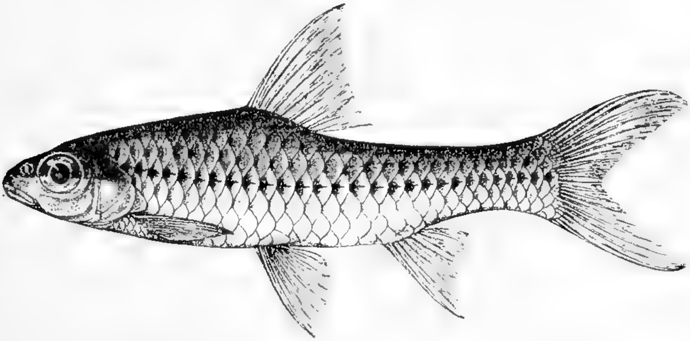

FIG. 15. *Barbus (Beirabarbus) aurantiacus* about $1\frac{1}{3}$ × N.S. (from an original drawing by F. Green).

Affinities. Barbus (Beirabarbus) aurantiacus is perhaps the western representative of *B.* (*B*) *doggetti* with which species it shows the closest relationships (see p. 199). Worthington (1933) compares *Barbus macrotaenia* with Lake Nyasa specimens of *B.* (*B*) *aurantiacus.* There is certainly a superficial resemblance mainly in coloration and the possession of a simple, unossified last dorsal ray. As *Barbus macrotaenia* does not have cephalic pit-lines, let alone ridges, it cannot be considered a close relative of *B.* (*B*) *aurantiacus.*

Distribution. Angola : (Que and Lucalla Rivers) ; Zambezi River (above the falls) ; Okavango River ; Lake Nyasa.

PIT-LINES IN *BARBUS*

Attention must now be turned to those species in which the pits are visible and linearly arranged but are neither so numerous as in *Beirabarbus* nor raised into ridges.

The typical condition of this group is well seen in Johnel's (1954) figure of *B. svenssoni* type specimen (see also Text-fig. 13).

The species comprising this group are as follows :

B. nigeriensis Blgr., 1902
B. kessleri (Steind.), 1866
B. trispilus (Bleek.), 1863
B. congicus Blgr., 1899
B. pseudognathodon Blgr., 1915
B. pleuropholis Blgr., 1899
B. urostigma Blgr., 1916
B. trispilomimus Blgr., 1907
B. pumilus Blgr., 1901
B. anema Blgr., 1903
B. svenssoni Johnels, 1954
B. collarti Poll, 1945
B. leonensis Blgr., 1915
B. cercops Whitehead, 1960

With the exception of *B. collarti* I have examined the types of all species listed above.

Barbus leonensis poses something of a problem. Johnels (1954) records the presence of pit-lines but I can find none in the two syntypes. However, since both types are very small (16 and 19 mm. S.L.) the absence of visible pit-lines may not invalidate Johnels' observations, particularly since weakly developed pits are visible in other and larger specimens from the type area (Sierra Leone).

In some specimens of *B. pseudognathodon* the pores appear slightly raised above the skin. The lines are not so distinctly raised as in *Beirabarbus*, nor are they so numerous. Nevertheless, both this species and the closely related *B. pleuropholis* may yet prove to be members of the *Beirabarbus* complex.

The additional evidence now available on *Barbus* species with macroscopic pit-lines calls for some amplification of Johnels' (*op. cit.*) remarks on the correlation between pit-lines and barbel development. Johnels drew attention to the fact that, of the species with pit-lines (*Beirabarbus* was included in his definition), only *B. leonensis* and *B. collarti* are without barbels. To this list of barbel-less species must now be added *B.* (*Beirabarbus*) *aspilus*, *B.* (*Beirabarbus*) *jae*, *B. trispilomimus*, *B. pumilus* and *B. anema.* Thus, it will be seen that there is apparently no correlation between the presence or absence of barbels, and the absence, presence or relative development of pit-line systems. There is also no correlation between pit-lines and the extent of the lateral line pore scales ; *Beirabarbus* contains species with complete and others with incomplete lateral lines. The majority, however, do have complete lateral lines.

One correlation, which may be of phyletic significance, is that of pit-line development and the nature of the last unbranched dorsal ray. Of the fourteen species with pit-lines (twenty-four if *Beirabarbus* is included) only one, *Barbus kessleri*, has the last unbranched ray ossified and serrated on its posterior face.

Also of possible phyletic significance is the fact that only one of the fourteen species, *B. cercops*, occurs in eastern Africa ; the remaining thirteen are essentially West African in their distribution. Furthermore, *B. cercops* seems more closely related to certain West African species than to its East African congeners (Whitehead, *op. cit.*). There is a similar correlation within *Beirabarbus* ; only one species (B. [B.] *doggetti*) does not occur in western Africa, although another, *B.* (*B.*) *aurantiacus*, extends eastwards to Lake Nyasa.

DISCUSSION

The taxonomy of *Barbus* has not yet reached the degree of refinement where it is possible to evaluate the phyletic significance of particular taxonomic characters. This is especially so with regard to coloration. Most workers (Barnard, 1943 and 1948 ; Groenewald, 1958 ; and Crass, 1960) agree that with discretion, colour patterns may be used as part of the character complex separating species. On the other hand, there are cases where certain patterns may be common to groups which otherwise show markedly different anatomical characters. For example, a continuous snout to caudal midlateral stripe occurs in groups characterized by a spinous and serrated last unbranched dorsal ray, in the group with a thin, pliable and slender last ray and also in the *Beirabarbus* subgeneric group (itself possibly polyphyletic). Likewise, it is difficult to choose any single anatomical character or group of characters which might provide a clue to the obviously intricate phylogeny of the genus (or perhaps generic complex?).

Any attempt to analyse the phyletic relationship of the species reviewed in this paper is hampered not only by these considerations but also by the fact that the species are merely a segment of the vast African *Barbus* complex. Nevertheless, certain relationships are apparent and may provide some framework for future synthesis.

Coloration is not taken into account when defining the four major supraspecific groups described below ; I have relied only on certain anatomical characters and the more nebulous concept of " general appearance ".

The *B. paludinosus* group (small scales [lateral line 30–38, modal range 34–36] ; dorsal spine serrated ; barbels well developed ; pelvic insertion anterior to dorsal origin) comprises *B. paludinosus*, *B. amphigramma* and *B. taitensis*. There is some overlap in the geographical ranges of all three species. However, *B. amphigramma* virtually replaces *B. paludinosus* in Kenya, and whereas *B. amphigramma* and *B. taitensis* are confined to East Africa, the range of *B. paludinosus* extends from Ethiopia to Natal (excepting some of the East African lakes). The range of *B. taitensis* is the least extensive ; indeed the species may not be strictly sympatric wih either *B. amphigramma* or *B. paludinosus*.

The second group contains *B. kerstenii*, *B. eutaenia*, *B. nyanzae*, *B. tangandensis*, *B. pellegrini* and *B. neumayeri*. Its members have moderately large scales (22–32 in the lateral line, modal range 25–29), a spinous and serrated last unbranched dorsal ray, well-developed barbels, pelvic fins inserted slightly anterior to or immediately below the dorsal origin and a prominent series of scales at the base of the dorsal fin.

Barbus eutaenia and *B. tangandensis* are outstanding because of their colour pattern (a black midlateral stripe extending from snout-tip to caudal fin or caudal base in the species respectively) but are anatomically members of the group. A seventh species, *B. loveridgii*, may belong to the *B. kerstenii* group but it is excluded here because of its short barbels and slightly higher range of lateral-line scale counts. The latter character is, however, paralleled within the group by *B. neumayeri*. Relatively short barbels would also seem to exclude *B. nyanzae* Whitehead, a species known only from affluent rivers in the Lake Victoria basin. But in this case the difference is less trenchant and the species is therefore included. When a more comprehensive definition of *B. loveridgii* is available it too may have to be added to the *B. kerstenii* group.

Barbus kerstenii appears to be polytypic, with at least one well-defined subspecies in Lake Luhondo (see p. 172) and possibly two others representing the northern and southern populations of its range in East Africa. The ranges of *B. neumayeri*, *B. pellegrini* and *B. kerstenii* overlap in several regions (Kenya, Uganda, and in Lake Tanganyika) but that of *B. eutaenia* is distinct except for fishes in Ruanda Urundi (see p. 176). *Barbus tangandensis* also has a distinct range (Rhodesia), but the species may be considered as the regional representative of the *B. kerstenii* stock (see p. 175). Within its restricted range, the distribution of *B. nyanzae* overlaps that of *B. neumayeri* and *B. kerstenii*.

The third group (scales small to moderate [lateral line with 28–30 scales] dorsal and pelvic fin origins in the same perpendicular line, last unbranched dorsal ray spinous and serrated, snout strongly decurved, broad preorbital face and barbels well-developed) comprises two rather poorly known species, *Barbus sexradiatus* (endemic to Lake Victoria) and *B. laticeps* (only recorded from the Wami River system of Tanganyika). The broad head and strongly decurved snout are the most obvious characteristics of the group. Until more specimens are available, particularly of *B. sexradiatus*, little more can be said.

The fourth and last group also comprises two species, *Barbus trimaculatus* and *B. jacksonii*; it is characterized by small scales (30–39 in the lateral line, modal ranges for the species 32–33 and 37–38 respectively), enlarged, spinous but non-serrate last unbranched dorsal ray, and well-developed barbels. In addition, both species have three distinct midlateral spots on the flanks, but this is not necessarily to be considered a group character. There is a clear gap in the distribution of these species, and each could be considered the geographical representative of the other (see p. 185).

There remain three species, *B. zanzibaricus*, *B. magdalenae* and *B. apleurogramma* which cannot be placed in any group within the broad geographical region of East, Central, and southern Africa.

Barbus zanzibaricus, a species of relatively restricted distribution, shows certain affinities with the *B. kerstenii* group, but is perhaps more closely allied to *B. argenteus* of Angola. Its group relationship must await further analysis, particularly of the West African species.

Barbus magdalenae, a Lake Victoria endemic, is unlikely to be grouped with any described species of eastern or western Africa; consequently its phyletic relationships also remain obscure.

The third species, *B. apleurogramma*, differs from the other two in having a much wider distribution, from the Sahara to the coastal regions of Tanganyika ; inexplicably it is absent from Kenya. Anatomically, *B. apleurogramma* is distinctive, with its large scales, poorly developed lateral line and minute barbels. At present I can find no grounds for linking it with any other African *Barbus*.

Two recently described species, *B. cercops* and *B. yongei*, from East Africa (the Victoria basin) should also be mentioned. Neither species shows any marked affinity with species occurring in the area covered by this revision. Whitehead (1960) has indicated that both have their nearest relatives amongst the *Barbus* of western Africa. Indeed, it should not prove difficult to fit either species into a West African species-group.

What then is the evolutionary status of these various supraspecific groups? Excepting the *B. trimaculatus* group, none can be considered as a superspecies *sensu* Mayr (1949) because the component species show too great a degree of sympatry. Yet, if the distribution is considered in detail there seems to be a certain amount of geographical restriction still apparent. For example, in the *B. paludinosus* complex, *B. amphigramma* almost replaces *B. paludinosus* in Kenya and *B. taitensis* occurs mainly outside the ranges of *B. amphigramma* and *B. paludinosus*. Again, considering the distribution of *B. kerstenii*, *B. pellegrini* and *B. neumayeri*, there is an indication that *B. neumayeri* is more northerly in its range whilst *B. kerstenii* and *B. pellegrini* are more southerly, the latter species having the most restricted distribution of the quartet. The area of overlap of these species is greater (on present records) than in the case of *B. paludinosus* and *B. amphigramma*. If *Barbus eutaenia* is a phyletic relative of *B. kerstenii* it does stand in superspecific relationship with both that species and *B. neumayeri; B. tangandensis* seems to have a similar relationship with *B. kerstenii* alone.

Thus, the *B. paludinosus* and the *B. kerstenii* groups may represent an evolutionary phase slightly beyond the superspecies level. This conclusion must remain conjectural until we are able to designate and assess characters of phylogenetic significance.

In contrast, the *B. trimaculatus* group seems to fulfil all Mayr's requirements for a superspecies in that the individual species are apparently of monophyletic origin, are morphologically distinct and are allopatric.

The other possible superspecies is the pair *B. sexradiatus* and *B. laticeps*. Here, regrettably, there is insufficient material to be certain of either the interspecific relationships or of the geographical range of the species. If later the restricted and spatially isolated ranges of the species are confirmed and their interspecific differences are maintained, then we shall have a superspecies equivalent to that of the *B. trimaculatus* pair.

It must be emphasized that these supraspecific groupings are extremely tentative and do not take full account of species from other parts of Africa (especially the west). The whole picture could well be altered when the pan-African *Barbus* complex is reviewed.

One other evolutionary point can be considered here, the so-called endemic species of the Lake Victoria basin (including Lakes Kyoga and Nabugabo). Prior to this revision four endemic species were recognized, *Barbus apleurogramma*, *B. minchini*, *B. magdalenae*, and *B. doggetti*. The first two species are also recorded from some of the crater-lakes in western Uganda. But, as these lakes were stocked with *Tilapia* from Lake Victoria the possibility of a simultaneous and accidental introduction of *Barbus* cannot be overlooked.

If my revision is acceptable, the ranges of both *B. apleurogramma* and *B. minchini* (now a synonym of *B. kerstenii*) have been greatly extended and neither species can now be considered a Victoria endemic. There is, of course, the possibility that endemic subspecies occur within the basin and this may apply in particular to the Victoria population of *B. kerstenii*. As *Barbus doggetti* is shown to be not only a widespread species in East and South Africa but also a member of the subgenus *Beirabarbus*, the sole endemic species of the quartet is *Barbus magdalenae*. Recently, however, Whitehead (1960) described three new and endemic species from the Victoria basin, so the total number of endemics remains unaltered at four.

From the zoogeographical viewpoint this revision has resulted in several changes. *Barbus kerstenii* was thought to occur in South Africa (Groenewald, 1958) but this record was based on the misidentification of *B. eutaenia* (see p. 176). As a consequence of synonymizing several species there is an increase in the known range of *B. kerstenii* in East Africa. Likewise, what was once a series of related species scattered over eastern Africa is now thought to be a single (but possibly polytypic), widespread species ; I refer to *Barbus neumayeri*. New material as well as synonymy has shown that *B. apleurogramma*, far from being a Lake Victoria endemic is widely distributed in East Africa and extends as far north as the Sahara.

The subgenus *Beirabarbus*, previously considered monotypic, is extended to include ten species, mostly from West Africa. It must be noted that the biological validity of at least five of these species is doubtful so that further study may reduce the number of *Beirabarbus* species. The history and status of this subgenus is not clearly understood ; some evidence suggests that it may be of polyphyletic origin.

The overall conclusion to be drawn from this revision is that the number of species is less than was previously thought and in consequence the geographical range of many has been increased. With regard to the phyletic picture we are only a little further advanced in being able to indicate the existence of some supraspecific groups and one subgeneric group. Further progress awaits the revision of all the African *Barbus* species.

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Finally, it is with great pleasure that I thank the Naturhistoriska Riksmuseet, Stockholm (and particularly Dr. A. G. Johnels) for making it possible for me to visit their Vertebrate section and there to study Lönnberg's collections and type material.

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KEY TO THE *Barbus* SPECIES OF THE LAKE VICTORIA BASIN

A. Exposed portion of scales with parallel striae . . . . ***B. altianalis radcliffii***

B. Exposed portion of scales with radiating striae.

(I) Head with or without macroscopic pit lines ; if present not raised into ridges.

(A) Last unbranched dorsal ray spine-like, *not* serrated on its posterior face ***B. jacksonii***

(B) Last unbranched dorsal ray spine-like, *serrated* on its posterior face.

(i) Lateral line with 30–36 scales.

Tubules on lateral line scales not outlined in black, or only the anterior scales outlined. Length of dorsal spine 22–29 ($M = 25$) % of S.L. . . . . ***B. paludinosus***

All lateral line scales with the pore outlined in black. Length of dorsal spine 14–25 ($M = 19{\cdot}0$) % S.L. . . . ***B. amphigramma***

(ii) Lateral line with 23–30 scales.

α Dorsal fin with 3 or 4/7 rays.

(*x*) No spots on flanks.

Anterior barbel equal to or shorter than eye (4·9–9·4, $M = 7{\cdot}2$% S.L.; posterior barbel 8·0–13·0, $M = 10{\cdot}0$). Origin of dorsal fin above or slightly behind pelvic origin . . . ***B. kerstenii***

Anterior barbel shorter than eye (2·6–3·7% S.L.; posterior barbel 3·9–5·0% S.L.). Origin of dorsal fin behind last pelvic ray or above the last pelvic ray . . . . ***B. nyanzae***
Anterior barbel minute or absent . . . ***B. apleurogramma***
(*y*) Three spots or an interrupted dark midlateral band on the flanks; anterior barbel longer than the eye (rarely equal to or shorter than the eye); origin of dorsal fin above that of pelvic fin . ***B. neumayeri***
β Dorsal fin with 3, 6 rays . . . . ***B. sexradiatus***
(c) Last unbranched dorsal ray thin and flexible.
Anterior barbel minute or absent; lateral line dips sharply downward ***B. magdalenae***
Anterior barbel $\frac{1}{2}$–$\frac{3}{4}$ eye; no pits visible on head . . . ***B. yongei***
Anterior barbel equal to or longer than eye; lateral line straight; pits visible on cheek . . . . ***B. cercops***
(II) Head and cheeks with pit lines raised into ridges . ***B. (Beirabarbus) doggetti***

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MARINE NEMATODES FROM BANYULS-SUR-MER: WITH A REVIEW OF THE GENUS *EURYSTOMINA*

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Pp. 209–283 ; 75 *Text-figures*

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MARINE NEMATODES FROM BANYULS-SUR-MER: WITH A REVIEW OF THE GENUS *EURYSTOMINA*

By WILLIAM G. INGLIS

CONTENTS

SYNOPSIS

Twelve species of free-living marine nematodes from Banyuls-sur-Mer, France, are described, of which seven are considered to be new, thus: *Enoplus quadridentatus* Berlin, 1853; *Phanoderma parafilipjevi* Allgén, 1939; *Oncholaimus dujardinii* de Man, 1876; *Prooncholaimus banyulensis* sp. nov. ; *Symplocostoma tenuicolle* (Eberth, 1863) ; *Eurystomina pettiti* sp. nov. ; *Chromadorina demani* sp. nov. ; *Euchromadora gaulica* sp. nov. ; *Euchromadora tyrrenica* Brunetti, 1952 ; *Hypodontolaimus colesi* sp. nov. ; *Paracanthonchus barka* sp. nov. and *Sphaerocephalum chabaudi* sp. nov. The genus *Eurystomina* Filipjev, 1921, is reviewed and four previously-recorded species are considered to be distinct species which are named as new, thus : *E. chilensis* = *E. retrocellatum* of Wieser, 1953*a* ; *E. chitwoodi* = *E. americana* of Chitwood, 1951 ; *E. gerlachi* = *E. assimile* of Gerlach, 1951 ; *E. wieseri* = *E. stenolaima* of Wieser, 1953*a*. A new genus, *Gerlachystomina*, is introduced for *Eurystomina filispiculum* Gerlach, 1954 (type species) and *E. sawayai* Gerlach, 1954*a*. The genus is characterized by simple pre-cloacal supplements and a simple gubernaculum without an apophysis in the male ; and by short cephalic setae and no bulbs in the posterior end of the oesophagus in both sexes. A summary of other changes in *Eurystomina* is given on p. 256. *Chromadorina laeta* of Micoletzky, 1924, is considered to be a distinct species and the name *C. micoletzkyi* is proposed for it. The cuticular capsules which are present at the anterior end of the oesophagus and the anterior end of the body in some Enoploids are discussed. The presence of a dorso-lateral pore-like sense (?) organ on the head of at least some species of *Euchromadora* and on one species of *Hypodontolaimus* is reported and the name *amphidule* is proposed for it. The possible significance of this organ is briefly discussed. It is argued that the structure of the cuticle in *Euchromadora* is probably to be explained on a functional basis, elaborations being restricted to the lateral parts of the body since the degree of expansion and contraction to which it is exposed must be less there than in a more dorsal or ventral position. Support is expressed for De Coninck's theory of the primitive arrangement of the sense organs on the nematode head but the argument is advanced that the presence of six lips, considered primitive by both De Coninck and Chitwood & Wehr, is not primitive. It is suggested that more probably an arrangement similar to that found in the family Chromadoridae, for example, is primitive. That is, a mouth opening which is roughly circular, without lips. The male of *Sphaerocephalum chabaudi* is described and as this is the first time a male of this genus has been found the genus is re-diagnosed. The nomenclatorial changes proposed in this report are listed on p. 278.

INTRODUCTION

THE study of the free-living marine Nematoda has tended to be characterized by the enthusiastic naming of " new " species rather than by the thoroughness of the descriptions. As a result the systematics of the group are chaotic since it is probably fair to estimate that at least a third of the published records are unreliable.

The thorough study of free-living nematodes is so difficult when the specimens are in a good condition, or preferably alive, that to attempt to study poorly-preserved material is a waste of time and, further, the general lack of knowledge of the morphology of almost all groups renders it extremely difficult, if not impossible, to identify species on the basis of females or larvae alone. Wieser (1955) and Chitwood (1960) both make this point and Wieser goes so far as to state " One certainly could not be proved wrong if one refused to accept the determination of marine nematodes from lesser-known regions . . . if they are not based on both males and females and accompanied by figures, or at least by absolute measurements and a succinct description." He later adds " I do not advocate the suppression of all determinations based on females and juveniles . . . but I am convinced that . . . much more precise and painstaking methods of detecting and describing differential characters in nematodes have to be employed than has been (and still is) the case." With all this I am in complete agreement but I am prepared to go much further—I will not, in general, accept identifications based solely on females or larvae and I will insist on treating almost all species based originally on females or larvae alone as *species dubiae*. The treatment of such species and records as valueless cannot upset the study of the distribution of the free-living marine nematodes since, outside European waters (with some laudable exceptions), the study of such nematodes is not even in its infancy but is embryonic and unless some such radical step as I propose is taken now the position in the future can only become worse.

Much of the difficulty facing anyone wishing to study free-living marine nematodes must be attributed to the superficial way in which some authors have described a multiplicity of nominal species. In particular I would mention Allgén's publication (1959) " Free-living marine nematodes ". *Further Zoological Results of the Swedish Antarctic Expedition* 1901–03. Vol. V, No. 2, pp. 1–293, which is clearly based on a study of badly-preserved specimens with the result that all the descriptions are very poor. They are not only inadequate, they are not consistent. The figures, for example, in many cases do not agree with the descriptions and, where more than one figure is given of the same species, the figures do not correspond. I, therefore, propose to treat every species named or reported in this publication as a *species dubia*.

Wieser (1953*a*) claims in the introduction to his paper that he will present evidence confirming the "... untenability of the view that marine nematodes are cosmopolitan as a whole—" but later (1955) says that the latter (1955) report "... certainly supports the idea of the general cosmopolitan occurrence of marine nematodes ...". However, in the case of at least one of the species reported by him—*Eurystomina ornata*—it is clear that his species is not conspecific with the European form (see p. 249) and it is also probable that another of his reported species, *Oncholaimus dujardinii*, is not the European species but *O. steineri* (see p. 228). Further, of the remaining eight " Species with a more or less cosmopolitan distribution " one identification is based on a single juvenile and another on one female. In fact, as Wieser points out, one-third of the species recorded in his paper have been identified on the basis of females and (or) juveniles. Wieser's descriptions are, on the whole, good but I cannot accept that he has here established anything about the cosmopolitan distribution of nematodes. It is possible only to repeat what is said above, and what has been said before (Chitwood, 1951 ; Inglis, 1961) that attempts at the present time to reach any conclusions on the geographical distribution of free-living marine nematodes are foredoomed to failure because of insufficient information.

REMARKS ON THE MORPHOLOGY OF MARINE NEMATODES

The Structure of the Head in the Enoploids[1]

Wieser (1954*a*) considers the structure of the head in the family Leptosomatidae and demonstrates that there are two cuticular capsules present at the anterior end of the body. One capsule is produced by a thickening of the inner layers of the cuticular covering of the body, the *cephalic capsule*, and the other by a thickening

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[1] While agreeing with Chitwood (1960) that the higher classification of the Nematoda is so unsatisfactory that many of the groups recognized are of little significance it is, nevertheless, essential to have some names covering large groups even although their exact limits cannot be satisfactorily established. In this sense the Enoploids correspond to the Enoploidea as treated by Wieser (1953).

of the outer covering of the oesophagus, the *stomodaeal capsule*. The foremost part of the stomodaeal capsule is called by Wieser the *stomodaeal ring* and it is at this ring that the main attachment of the stomodaeal and cephalic capsules takes place. Wieser further suggests that the stomodaeal ring is derived from the stomodaeal capsule and that, apparently, the ring is not fused to the cephalic capsule around its entire circumference but only opposite the three sectors of the oesophagus.

I accept this interpretation of the structure of the head, at least in part. Two capsules tend to be present not only in the Leptosomatidae but also in the Enoplidae, the Phanodermatidae and the Ironidae and this is the condition referred to by Chitwood (in Chitwood & Chitwood, 1950) as " Cuticle of head duplicate ; . . ." but it does not apply to the genera of the families Oncholaimidae, Enchelidiidae and Dorylaimidae. Functionally the two capsules appear to be associated with the presence of jaws and/or teeth and it may be noted that the degree of development of the capsules is associated with the degree of development of such tooth-like structures. In both the forms I have studied in detail, *Enoplus quadridentatus* (see p. 219) and *Phanoderma parafilipjevi* (see p. 224), the oesophagus and body wall appear to be joined over a much greater area than the stomodaeal ring, and this also appears to be true of several species of *Thoracostoma* which I have studied for purposes of comparison. In *Enoplus* the fusion occurs over three sectors of the outer surface of the oesophagus which correspond to the three sectors of the tri-radiate oesophagus. That is, the fusion is opposite the three jaws of the head, the three places at which increased strengthening is required for simple mechanical reasons. In *Phanoderma*—and *Thoracostoma*—on the other hand the fusion appears to be much more extensive and appears to take place around the entire circumference of the oesophagus for some distance posterior to the anterior limit of that organ. This appears to be associated with the presence of anteriorly directed tooth-like structures in these genera. However, even in *Enoplus* the cephalic capsule is completely fused to the oesophagus at the anterior end, although a stomodaeal capsule does not appear to be present. This zone of complete attachment appears to correspond to the stomodaeal ring of Wieser.

In *Enoplus* the attachment of the oesophagus to the body wall is complete around the stomodaeal ring except for the presence of six foramina through which pass the nerves which supply the inner circle of cephalic papillae (see Text-fig. 1). These foramina are bounded internally by the covering of the oesophagus and externally by the cephalic capsule. The presence of such foramina, associated with the attachment of the oesophagus to the body wall represents a clear convergence with the condition found in *Sphaerolaimus anterides* (see Inglis, 1961) in which the cuticular wall of the buccal cavity is attached to the body wall by a series of buttresses and the nerves which supply the anterior sense organs of the head pass through the foramina between the buttresses. In the case of *Sphaerolaimus* the fusion of the buccal capsule and the body wall appears to have occurred to overcome the weaknesses inherent in developing a very large buccal cavity, while in the genus *Enoplus* it appears to be associated with the necessity for supplying some reinforcement to a head equipped with three large jaws. The fusion cannot be complete since some provision must be made for the passage of the nerves to the anterior sense organs of the head. This is done by the foramina in some cases but also explains the form of the cephalic capsule in genera such as *Thoracostoma* in which the cephalic capsule is divided posteriorly into six lobes (see almost any good figure of the head of this genus, e.g. de Man, 1904; Wieser, 1956*a*; Mawson, 1956 and 1958; Inglis, 1958*a*). In all cases the posterior incisions (terminology of Wieser, 1954) correspond to the arrangement of the cephalic sense organs and provide a passage for the nerves which go to them. A similar condition appears to apply to some genera of the Enoplidae in which the cephalic capsule is more extensive than it is in *Enoplus*.

It should be noted that, although the degree of development of the two capsules may be of value in delimiting groups of nematodes, or in establishing trends and relationships, since these structures appear to be functionally associated with the complexity of the tooth- or jaw-like structures, the head must be treated as a functional unit. Thus the additional information obtained by an analysis of the capsules may simply parallel that available in the form and arrangement of the cephalic tooth- and jaw-like structures.

The Theoretical Importance of the Chromadoroids

The same difficulty is encountered here as in the discussion of the Enoploids, that of defining the group under discussion. The Chromadoroids in the sense intended here include the families Chromadoridae, Cyatholaimidae and some, at least, of the Desmodoridae as given by Wieser (1954*b*), since this appears to constitute a relatively homogeneous group although, as with the Enoploids, it is difficult to determine the limits in a wholly satisfactory manner.

The Head in Euchromadora *and* Hypodontolaimus

The head in all, or at least most of, the genera referred to the three families mentioned above is characterized by the presence of twelve rugae, that is—twelve cuticular rod-like structures which support a cuticular sheath around a circular, poorly delimited mouth opening (see Filipjev, 1918–21; Chitwood in Chitwood & Chitwood, 1950; De Coninck, 1942; Steiner & Hoeppli, 1926; Inglis, 1961 and 1961*a*). The head in the genera *Euchromadora* and *Hypodontolaimus* is characterized by this form of mouth opening and carries a pair of what appear to be sense organs which are additional to the usual slit-like lateral amphids. These pore-like structures are dorso-lateral in position (see Text-figs. 41 and 59) and appear to have been figured on only one other occasion, by Steiner & Hoeppli (1926, fig. M, 1) who do not refer to them in their description of *Euchromadora archaica* although they do figure the usual amphids. I have also seen such dorso-lateral structures in *Euchromadora vulgaris* where the slit-like lateral amphids are also present. The importance of these structures is not clear since their occurrence in other genera is unknown (possibly the structures I called the amphids (Inglis, 1961) in *Hypodontolaimus angolae* may, in fact, be similar structures) but it is interesting to contrast them with the cephalic slits which occur in so many of the Enoploids (e.g. *Enoplus*, *Trissonchulus* and many others. See Filipjev, 1927). To draw attention to this organ I propose for it the name AMPHIDULE.

Cuticular Structures in the Genus Euchromadora

The complicated basket-work arrangement of fibres in the cuticle of many species of the genus *Euchromadora* is well known but reports of the presence of what I later describe as *lateral-plates* (see p. 261) are rare. These structures, which are probably of value in delimiting species within this genus (I am studying this at present in conjunction with Mr. John W. Coles), are, like most of the other elaborations of the nematode cuticle, restricted to the lateral surfaces of the body. Modifications to the cuticle on the lateral surface of the body are common throughout the Nematoda but in the Chromadoroids are internal rather than external. That is, they take the form of structures buried within the cuticle and do not produce bumps or ridges on the outer surface. Wieser (1953*a*) says " The cuticular ornamentation of marine nematodes plays an important role in the act of motion of the worms ", by which I take him to mean, also taking into consideration what he says later, that the cuticular markings help to grip the substrate. This may apply in some cases but certainly cannot apply to the Chromadoroids. Steiner & Hoeppli (1926) give what appears to me to be the best discussion of the significance of the rod-like structures in cuticle of the *Euchromadora*-type, they act as structural elements which strengthen the cuticle and, also, perhaps confer a certain amount of additional protection. Steiner & Hoeppli conclude their discussion of *E. archaica* with two questions " Why is this arrangement (of rods in the cuticle)? Is it because all these regions with lamelles or rods need to be stiffened, need strength and yet more elasticity?" The answer, I would suggest, is simply that such structures can only occur on the lateral parts of the body without reducing the flexibility of the body. Thus, the body only bends in the dorso-ventral plane so that the zone of least extension or compression of the cuticle must be on the lateral sides of the body, the extent of the extension or compression increasing the more dorsal or ventral the zone considered. If any special form of strengthening is required this must, if it is to be effective, have a low elasticity (conversely increased rigidity) and such structures can only be introduced into parts of the body in which this lack of elasticity will be of relatively little importance. This zone being the lateral parts of the body. In connection with this it should be noted that the lateral rod-like structures in the cuticle become shorter and less massive towards the dorsal and ventral limits of the lateral fields. The lateral plates conform to this in that they are broadest where fully lateral and become narrower towards their dorsal and ventral extremities. The reversal of the direction of the lateral plates is also explained—at least in part—by the Steiner-Hoeppli analysis in which they demonstrate a similar reversal of the annulations of the body in *Dicriconema tenuis* and argue that " the vulvar region forms the base of mobility for the anterior as well as for the posterior body part ". This must certainly play some part but is clearly not the full explanation for this remarkable reversal since Cobb (1917) reports that a similar reversal occurs in a wide range of species and genera (without specifying any of them).

The Primitive Nematode Head

In discussing the form of the nematode head only two theories appear to be worthy of serious consideration, those of Chitwood & Wehr (1934) (further elaborated by Chitwood (in Chitwood & Chitwood, 1950) and of De Coninck (1942)). Both of these theories accept that the primitive nematode was equipped with a six-lipped mouth opening and disagree largely on the distribution of the cephalic sense organs, with the result that the Chitwood theory argues that the primitive number and arrangement of the cephalic sense organs was an inner circle of six and an outer circle of twelve while De Coninck argues for an inner circle of six, an intermediate circle of six and an outer circle of four. Of these two theories I prefer that of De Coninck which corresponds much more closely to the conditions found in most free-living nematodes and in many parasitic forms. The Chitwood theory not only necessitates the postulation of an additional, hypothetical, papilla but simply does not accord with the facts in many cases. Thus his argument on the segregation of the papillae of the so-called external circle (pp. 56 and 57 of Chitwood & Chitwood, 1950) in the Ascaridoidea, at least, is simply not true as can be easily seen by studying the figures reproduced by Hartwich (1951). Chitwood & Wehr (1934) appear to be attempting to superimpose a secondary symmetry on the head in that they have six lips with three papillae, arranged in a triangular fashion, on each.

However, I disagree with both theories on one major point. I cannot accept that the presence of six lips is a primitive character. It appears to me to be much more probable that the primitive mouth opening is that shown by the Chromadoroids. That is, a circular mouth opening surrounded by a series of rugae. Not only does this correspond to the condition found in the Gastrotrichs, the presumptive ancestors of the Nematoda (or at least part of the Nematoda), but also simplifies the consideration of the head forms occurring in many of the groups of both free-living and parasitic nematodes. For Chitwood & Wehr the Rhabditid nematodes are primitive, for De Coninck a Plectid type is primitive while Hyman (1951) argues that the Chromadoroids are primitive. I agree with Hyman. The detailed argument in support of this thesis will be presented elsewhere but it is worth pointing out that the cuticular modifications found in the Chromadoroids suggest an early attempt to overcome the difficulties inherent in an elongate body, an attempt which has imposed certain restrictions on the resulting body form which have been overcome in other groups, along other lines. Thus, as Chitwood & Chitwood (1950) point out, the structure of the cuticle in the Chromadoroids does not appear to possess the oblique fibres found in other groups and I would suggest that the cuticular modifications characteristic of this group are a reflection of this fact. One further point in connection with the Chromadoroid head is of interest, the presence of amphidules in at least two genera (? others. Possibly confused with amphids?). Do the amphidules correspond to the cephalic slits of the Enoploids? If they do, do both sets of sense organs (cephalic slits and amphidules) represent corresponding sense organs in the Gastrotrichs? The final, and much the most important, question is, if the presence of two sets of lateral cephalic organs of this type is widespread in the free-living nematodes are the posteriorly situated amphids of, for example, *Enoplus* homologous with the amphids of such forms as *Ascaris* or are the so-called amphids of the latter genus homologous with the amphidules or cephalic slits of the free-living forms?

TECHNIQUES

The adequate study of free-living nematodes depends on patience, good fixation in conjunction with the study of living specimens and careful preparation of specimens after fixation. All the specimens studied here were heat paralysed, fixed in sea-water " TAF " (see Goodey, 1957) and cleared in glycerine by the slow method. That is, the specimens were placed in dilute glycerine made up as follows: 5 c.c. glycerine in 95 c.c. 30% alcohol and the alcohol was allowed to evaporate slowly in a desiccator. The evaporation taking about six to seven days. The specimens were then studied in pure glycerine under a free cover-slip supported at one side by lens-cleaning tissue. This method has the great advantage that if the specimen moves it is trapped between the cover-slip and the slide by the movement of the glycerine only and is not subject to distortion due to pressure. This method is virtually essential if an adequate study is to be made since it allows the specimen to be rolled and, with practice, it is possible to roll specimens below 1 mm. in total length.

The study of the heads of nematodes in *en face* preparations is most important if the morphology and interrelationships of the various parts of the head are to be fully understood. In addition it is valuable in establishing the distribution of the sense organs of the head. As an example the presence of the amphidule on the head of *Euchromadora* species can only be established by the use of such preparations and, of course, the shape of the mouth opening cannot be established in any other way. The method I employ is a combination of those published by Basir (1949) and Anderson (1958). The specimen is put into a drop of glycerine jelly *on a cover-slip* and is pulled out into a streak of glycerine jelly. The jelly is allowed partly to harden and the head is cut off by means of a piece of razor-blade held in a watchmaker's pin-vice. The head is then orientated so that it *faces* the surface of the cover-slip, the slip is then inverted on a slide and the orientation of the head is checked. As Anderson (1958) points out, this method has the great advantage that the cut surface does not have to be at right angles to the longitudinal axis of the body and the length of the anterior end of the body which is cut off is not crucial. In the case of the small free-living species this is a very great advantage. Anderson recommends that the drop of glycerine jelly be sufficiently large to touch the surface of the slide when the cover-slip is supported on pieces of wire, paper or glass rod but this I have found to be not wholly satisfactory under some conditions, particularly in cases where the piece of worm cut off is long. I find that if the head is orientated under a dissecting microscope at a magnification of about ×100, with practice it is possible to get it virtually vertical and I prefer to mount the head preparation over the cavity of a cavity-slide which I flood with liquid glycerine. However, the use of mounts of this kind, although virtually essential with the very small forms has one very grave disadvantage. It is impossible to incline the head to various angles while studying it. For a full study of the head several specimens are required some of which are studied as above and others of which are studied using the complete method of Anderson with which the angle from which the head is studied can be varied, but if only one specimen is available a full *en face* view should be aimed at and under such conditions I prefer the use of a cavity-slide.

SYSTEMATIC SECTION

All the specimens reported on here were collected during a visit to the Laboratoire " Arago ", Banyuls-sur-Mer during September, 1959. They all came from one locality, among low-growing sea-weeds with very little sediment on the rocks near the laboratory lying on the Spanish side of the causeway between the laboratory and the rocky islands which lie just off-shore (Ile Grosse or Mont aux Morts). Only species represented by both males and females are described and the intention of this report is to deal with the structure of these species in detail, particular stress being laid on the structure of the head. The marine nematodes of this area have been reported on by Allgén (1943) and by Gerlach (1954). Allgén's paper covers a wide range of habitats and a large number of species, but, as Schuurmans Stekhoven (1950) says " I do not in all respects agree with Allgén's identification(s) " while Gerlach's report is restricted to a study of a few species from the interstitial water of the beach. A list of all the species reported from the Mediterranean is given by Schuurmans Stekhoven (1950) but the value of such a list must be considered doubtful since it is quite certain that many of the records must be based on mis-identifications.

The following species are described in this report :

Enoplus quadridentatus Berlin, 1853 (p. 219).
Phanoderma parafilipjevi Allgén, 1939 (p. 224).
Oncholaimus dujardinii de Man, 1876 (p. 226).
Prooncholaimus banyulensis sp. nov. (p. 229).
Symplocostoma tenuicolle (Eberth, 1863) (p. 232).
Eurystomina pettiti sp. nov. (p. 234).
Chromadorina demani sp. nov. (p. 257).
Euchromadora gaulica sp. nov. (p. 260).
Euchromadora tyrrenica Brunetti, 1952 (p. 264).
Hypodontolaimus colesi sp. nov. (p. 266).
Paracanthonchus barka sp. nov. (p. 271).
Sphaerocephalum chabaudi sp. nov. (p. 273).

As a result of trying to establish the validity of certain characters in the delimitations of species within the genus *Eurystomina* it has been found necessary to review that genus. This review begins on p. 237.

Enoplus quadridentatus Berlin, 1853

Material Studied

6 ♂, 5♀, 53 larvae. B.M. (N.H.), Reg. Nos. 1961.237–283 and 1961.391–395.

	Ratios				
	a	*b*	*c*	V	Body length
Males . .	24·7	5·1	14·6	—	4·0*
	23·2	4·6	14·6	—	4·3
	35·4	5·4	15·8	—	4·6
	32·0	5·3	15·2	—	4·8
Females . .	25·8	6·7	13·4	56·4	3·1
	24·8	6·7	13·6	52·2	3·4
	29·0	6·4	14·8	53·5	4·3
Larvae . .	31·7	7·8	12·6	—	1·9
	26·3	4·6	15·6	—	4·2
	25·0	5·8	18·0	—	4·5

* This specimen was moulting from the fourth-stage to the adult-stage.

Measurements (*in mm.; in order of body lengths above*)

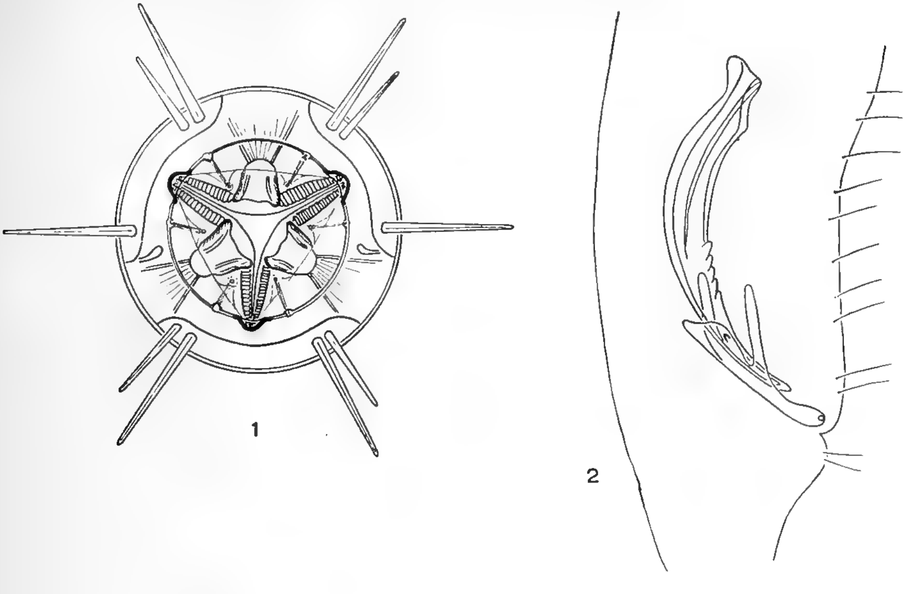
Males. Body breadth: 0·16; 0·18; 0·13; 0·15. Oesophagus length: 0·78; 0·92; 0·86; 0·91. Diameter of head: 0·039 (larva) and 0·048 (in adult); 0·047; 0·052. Cephalic capsule, posterior diameter/depth: 0·064 (larva) and 0·071 (adult)/0·037 (larva) and 0·043 (adult); 0·079/0·046; 0·076/0·044; 0·078/0·048. Lengths of cephalic setae: ... ; 0·016 and 0·023; 0·016 and 0·029; 0·017 and 0·028. Length of jaws: 0·035 (larva) and 0·042 (adult); 0·037; 0·043; 0·044. Eye spots from the anterior end: ... ; 0·078; 0·081; 0·084. Tail length: 0·28; 0·29; 0·29; 0·30. Cloacal diameter: 0·12; 0·12; 0·098; 0·13. Spicule length: 0·19; 0·15; 0·13; 0·16. Gubernaculum length: 0·091; 0·090; 0·104; 0·107. Length of pre-cloacal supplement: 0·066; 0·068; 0·069; 0·068. Distance of pre-cloacal supplement anterior to cloacal opening: 0·24; 0·27; 0·26; 0·28.

Females. Body breadth: 0·12; 0·16; 0·16. Oesophagus length: 0·46; 0·51; 0·67. Diameter of head: 0·041; 0·037; 0·045. Cephalic capsule, posterior diameter/depth: 0·054/0·031; 0·069/0·043; 0·071/0·046. Lengths of cephalic setae: 0·015 and 0·022; 0·016 and 0·028; 0·017 and 0·028. Length of jaws: 0·028; 0·036; 0·041. Eye spots not seen except in 3·4 mm. specimen where they were 0·079 mm. from the anterior end. Tail length: 0·23; 0·25; 0·29. Anal diameter: 0·078; 0·014; 0·013. Distance of vulva from the anterior end: 1·75; 1·78; 2·3. Only the largest female contained eggs, 0·058 × 0·143 mm. in size.

Larvae. Body breadth: 0·06; 0·16; 0·18. Oesophagus length: 0·36; 0·91; 0·78. Cephalic capsule, posterior diameter/depth: 0·031/0·014; 0·073/0·033; 0·075/0·032. Lengths of cephalic setae: 0·006 and 0·010; ... ; 0·011 and 0·018. Length of jaws: 0·012; 0·022; 0·028. Eye spots 0·09 mm. from the anterior end in the 4·2 mm. long specimen. Tail length: 0·15; 0·27. Anal diameter: 0·045; 0·011; 0·080.

Head and Oesophagus

The head bears six sessile papillae in an internal circle and ten stout setae, in an outer circle, of which six are longer than the others (Text-figs. 1, 3 and 4). The cephalic slits lie slightly ventral and anterior to the lateral setae (Text-figs. 1 and 4). The mouth opening is bounded by three lip-flaps on which lie the inner sessile papillae. The anterior end of the oesophagus carries the usual three large jaws and the edges of the sectors of the oesophagus at the extreme anterior end bear cuticular rod-like structures (Text-fig. 1). The mouth opening is strengthened at the junctions of the lips by three thickened cuticular structures (Text-fig. 1). The cuticle of the anterior end of the body is modified internally to form a cephalic capsule to which the oesophagus is attached at three places, dorsally and ventrolaterally (Text-figs. 1 and 3). The oesophagus is, however, attached to the cephalic capsule completely around its periphery near its anterior end to produce a fairly distinct stomodaeal ring. Wieser (1954*a*) argues that the stomodaeal ring in the Leptosomatidae is derived from the stomodaeal capsule (not present in a developed form in *Enoplus*). That is, it is derived from the anterior end of the oesophagus and this certainly appears to be true in *Enoplus* where the ring can be seen fairly easily



Figs. 1–4. *Enoplus quadridentatus* Berlin, 1853. Fig. 1. *En face* view of head. Note the way in which the oesophagus is attached to the body wall at three points and the way in which the nerves which supply the inner circle of papillae pass through foramina in the stomodaeal ring. Fig. 2. Lateral view of the male tail. Fig. 3. Dorsal view of head. Note the way in which the zone of attachment of oesophagus to the body wall, delimited by broken lines, expands anteriorly. Fig. 4. Lateral view of head with the dorsal surface to the right. Note the attachment of the oesophagus along its dorsal surface.

in *en face* preparations of the head (Text-fig. 1). It should be noted, that in the Leptosomatids Wieser thinks that the stomodaeal ring is not attached to the cephalic capsule along its whole circumference but is separated from it along the radial portions. In *Enoplus*, although the oesophagus is attached to the cephalic capsule at three points, the oesophagus is definitely attached to the cephalic capsule around the whole of its circumference at the level of the stomodaeal ring. As a result there are six foramina present through which pass the nerves which supply the inner sessile papillae, foramina which are bounded internally by the oesophagus and externally by the cuticle of the cephalic capsule (Text-fig. 1). It is these foramina which are figured by de Man (1886) as the inner papillae (de Man, pl. I, fig. 4) and the inner papillae themselves are not shown (see the further discussion of this above, p. 213).

Male

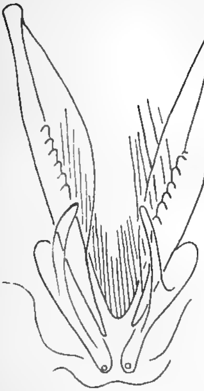
The spicules are equal in length and identical in structure with a series of plates developed on their ventral surfaces (Text-figs. 2 and 5). The number of plates present varies between five and eight. Distal to the plates and lateral in position each spicule always carries a small but distinct lateral process. The gubernaculum consists of three pieces, two lateral and one median ventral in position. The lateral pieces are fairly massive, blunt distally and each bears a distinct apophysis on its ventral surface about half-way along its length (Text-figs. 2 and 5). The median ventral piece is less obvious but is developed proximally into a large series of long hair-like structures which give the gubernaculum a beard-like appearance, particularly when viewed from the ventral aspect. The pre-cloacal supplement is fairly prominent, approximately the same distance as the length of the tail anterior to the cloacal opening (Text-fig. 6) and there is a series of pairs of relatively long setae on the ventral surface of the body anterior to the cloacal opening. There are in addition two pairs of slightly stouter, but otherwise similar setae carried on the posterior lip of the cloacal opening and there are many smaller setae scattered over the general surface of the tail. The tail is relatively short and stout, narrowing evenly, and rather rapidly about one-third of its length posterior to the cloacal opening. There are two opposed, non-reflexed testes of which the more anterior is slightly longer than the more posterior.

Female

The reproductive system is double with opposed, reflexed ovaries which lead into relatively large uteri. There do not appear to be any special spermathecal modifications of the reproductive tract. An egg has been seen in only one specimen and only one egg was present.

Discussion

This species has been previously recorded from Banyuls-sur-Mer by Allgén (1942) under the name *Enoplus hirtus* (Marion, 1870) with *E. quadridentatus* listed as a synonym. Similarly De Coninck & Schuurmans Stekhoven (1933) list *E. quadridentatus* as a synonym of *E. hirtus*. I am in agreement with these authors that the



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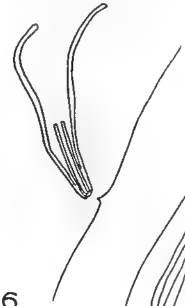

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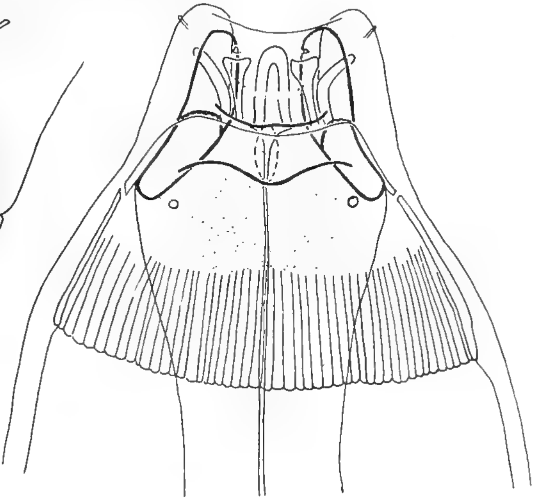

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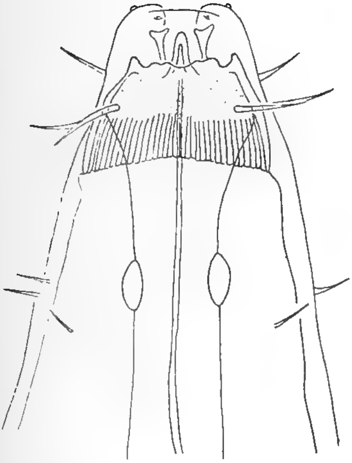

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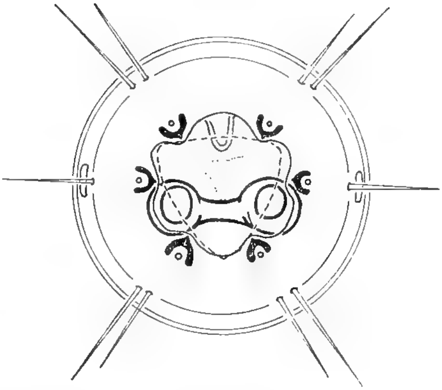

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FIGS. 5–6. *Enoplus quadridentatus* (continued). Fig. 5. Ventral view of spicules and gubernaculum. Fig. 6. Detail of pre-cloacal supplement from the lateral aspect.

FIGS. 7–9. *Phanoderma parafilipjevi* Allgén, 1939. Fig. 7. Ventral view of head. Fig. 8. Dorsal view of head showing the position of the eye spots. Fig. 9. *En face* view of head. The triangular shape outlined by dashes represents the outline of the buccal cavity while the six-lobed solid line represents the limits of the mouth opening. Note the way in which the papillae of the inner circle are enfolded by the bifurcate anterior ends of the six rod-like developments of the lining of the buccal cavity.

two names are synonymous but the name to be employed must be *E. quadridentatus*. Allgén (1942) lists *E. tridentatus* Dujardin, 1845 as a synonym of *E. hirtus* while De Coninck & Schuurmans Stekhoven (1933) suggest that possibly the two are indistinguishable. However, the description given by Dujardin is insufficient to allow the status of his specimens to be established and I propose to treat the name *Enoplus tridentatus* as that of a *species dubia*. *Enoplus euxinus* Filipjev, 1918, is also indistinguishable from *E. quadridentatus*.

Phanoderma parafilipjevi Allgén, 1939

Material Studied

2 ♂, 1 ♀, 22 larvae. B.M. (N.H.), Reg. Nos. 1961.335–347 and 1961.376–384. In addition many specimens were studied alive at Banyuls-sur-Mer.

	Ratios				
	a	*b*	*c*	V	Body length
Male . .	27·5	4·1	36·4	—	5·1
Larvae . .	34·1	3·1	17·6	—	1·5
	25·0	3·2	25·0	—	3·5

Measurements (in mm.; in order of body lengths)

MALE. Body breadth: 0·186. Oesophagus length: 1·24. Diameter of head: 0·030. Diameter of head at base of cephalic capsule: 0·053. Depth of cephalic capsule: 0·042. Nerve ring from the anterior end: 0·40. Excretory pore from the anterior end: 0·115. Eye spots from the anterior end: 0·046. Tail length: 0·14. Cloacal diameter: 0·069. Length of spicules: 0·19. Length of gubernaculum: 0·067. Length of pre-cloacal supplement: 0·046. Distance of pre-cloacal supplement anterior to cloacal opening: 0·22.

LARVAE. Body breadth: 0·044; 0·14. Oesophagus length: 0·49; 1·1. Diameter of head: 0·009; 0·014. Diameter of head at base of cephalic capsule: 0·022; 0·049. Depth of cephalic capsule: 0·019; 0·026. Nerve ring from the anterior end: . . . ; 0·35. Excretory pore from the anterior end: 0·096; 0·13. Eye spots from the anterior end: 0·031; 0·040. Tail length: 0·085; 0·14. Anal diameter: 0·032; 0·060.

This species was, as with many of the others, studied in detail while alive but the importance of the structures seen, particularly those of the head, was not appreciated at that time. Since then it has become clear that a redescription, particularly of the structure of the head, is required but, unfortunately, no measurements were taken at Banyuls and I have been able to find relatively few specimens among the material brought back to London. As a result I am unable to give measurements for females since the single female noted above is in a poor condition and I have measurements for only one male.

This species was originally described by Allgén (1939) but, as Wieser (1953*a*) points out, the description is poor, particularly with reference to the structure of the head. It is, however, adequate for the recognition of the species. It may be pointed out in anticipation of the description which follows that the structure of the head is remarkable in that the mouth opening is supported by six cuticular rod-like structures which do not appear to have been previously mentioned in connection with this genus.

Head and Oesophagus

The head, in spite of the great length of the body in adult specimens, is small and extremely complicated. It bears an inner circle of six sessile papillae and an outer circle of ten setae of which four are long and six are short. The amphids are small, pocket-like and lateral in position. No cephalic slits have been seen. The mouth opening is large and roughly hexagonal with six poorly-defined lip-lobes each of which is supported by a cuticular rod-like structure which is bifurcate anteriorly so that, when viewed *en face*, the papillae of the inner circle appear to be embraced by a cuticular horse-shoe (Text-fig. 9). These cuticular rods are modifications of the inner cuticular covering of the buccal cavity (Text-fig. 7). The mouth opening leads into a buccal cavity, triangular in cross-section (Text-fig. 9), into which project three cuticular tooth-like structures derived from the cuticular covering, i.e. pharyngeal capsule, of the anterior end of the oesophagus. The dorsal tooth-like structure is relatively small while the two ventro-lateral paired structures are very massive. The latter structures arise from a thickened basal portion which is the ventral part of the stomodaeal capsule. Thus the anterior end of the oesophagus bears a strongly developed stomodaeal capsule which is much more strongly developed ventrally than it is dorsally. Laterally the stomodaeal capsule is developed posteriorly on each side of each amphid as a distinct, narrow process. This is shown in Text-fig. 13 in which only the stomodaeal capsule is shown, from the lateral aspect. Dorsally the capsule is poorly developed and its full extent has not been definitely established so that in Text-fig. 13 the dotted dorsal part of the capsule is uncertain. The external cuticle covering the anterior end of the body is modified as a cephalic capsule which finishes anteriorly about the level of the anterior end of the stomodaeal capsule at which the three tooth-like structures become distinct. Posteriorly the cephalic capsule is marked by striations, this being the part called by Wieser (1953) the cervical capsule but it is definitely the posterior part of the cephalic capsule (Text-figs. 7, 8 and 12). The two capsules are fused over the whole of the pharyngeal capsule and the oesophagus may possibly be attached to the cephalic capsule more posteriorly as well. In some specimens the area between the cervical capsule and the pharyngeal capsule shows a distinct dotting which suggests a fusion and, further, this dotting appears in some specimens to cover a restricted zone as shown in Text-figs. 7 and 8 but I cannot be sure whether this is the true condition or not as it may have been due to the condition of the specimens studied. Nevertheless, the fusion between the two capsules occurs over a larger area than in the case of *Enoplus* although even here the fusion appears to begin posteriorly in three regions which expand until the capsules are fused completely around the periphery of the body. It should be noted that the shape of the pharyngeal capsule is such that the setae always originate posterior to its posterior edge (Text-figs. 7, 8 and 12). The eye spots are well developed and the oesophagus has the typical cellular appearance posteriorly (Text-fig. 11). The excretory pore is anterior to the nerve ring, e.g. in a larva 2·85 mm. long the oesophagus is 0·79 mm. long, the eye spots are 0·033 mm. from the anterior end, the excretory pore opens 0·11 mm. from the anterior end and the nerve ring is 0·31 mm. from the anterior end.

Male

The spicules are equal in length and identical in structure with plates developed on their posterior ends (Text-fig. 10). There are from five to nine such plates which are restricted to a relatively short zone. The spicules are long and narrow, the pre-cloacal supplement is relatively prominent and simple (Text-fig. 10) and the gubernaculum is relatively short with fairly large, plate-like lateral portions (Text-fig. 10). There are two rows of prominent setae, latero-ventral in position, on the surface of the body anterior to the cloacal opening and there are several prominent setae scattered over the surface of the tail (Text-fig. 10). The caudal glands lie posterior to and on a level with the cloacal opening.

Discussion

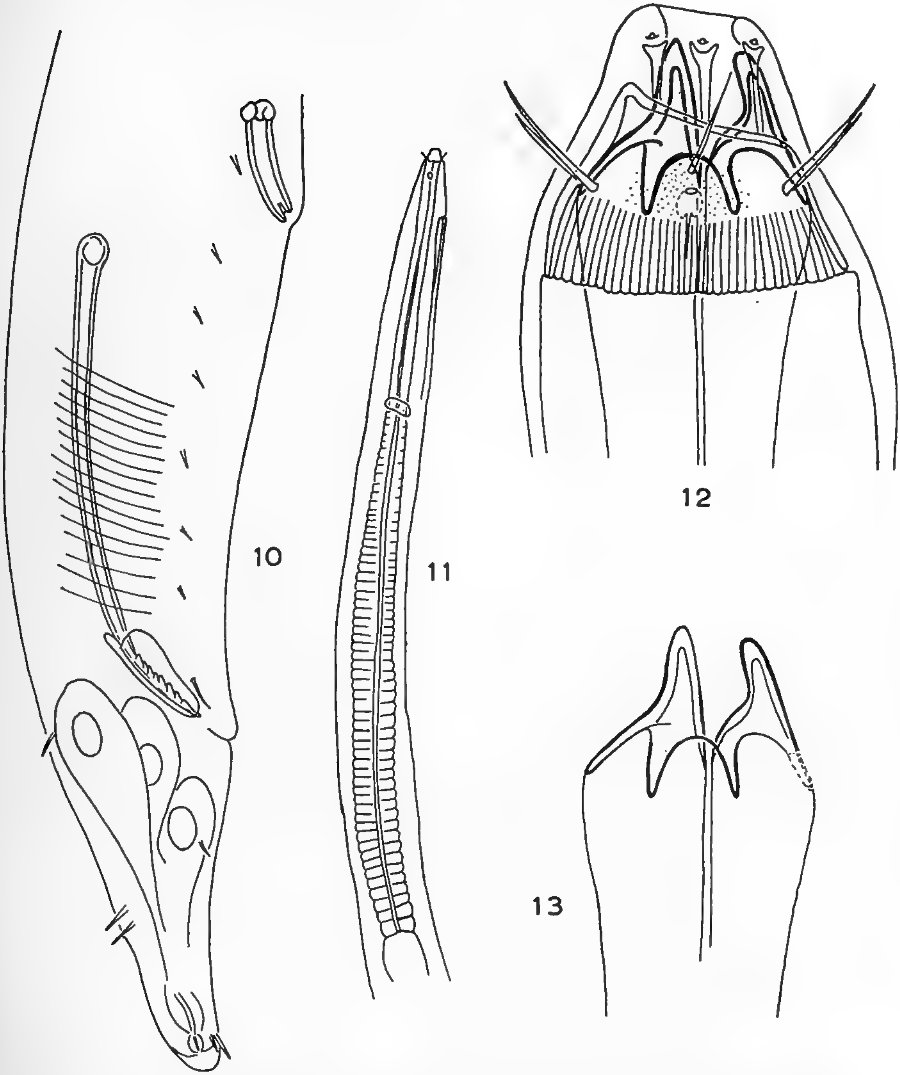
Wieser (1953*a*) surmises correctly that this species possesses a cervical capsule as is reported above. However, I have been unable to find a report of the cuticular bifurcate rods, which support the mouth opening, in any description of species of this or any related genus. Timm (1953) reports the presence of twelve cuticular rod-like structures in the anterior end of the oesophagus of *Leptosomatum acephalatum* Chitwood, 1936, but only in the female. There is a sexual dimorphism in this species as the male is not equipped with similar structures. This is not the case of *Phanoderma parafilipjevi*, the rods are present in both sexes as in *Leptosomatum ranjhai* Timm, 1960. *P. parafilipjevi* also differs in that the rods are not developed from the oesophagus but lie in the inner wall of the buccal cavity. Thus they also differ from the condition found in some Leptosomatids where there is a well-developed anterior part of the cephalic capsule anterior to the stomodaeal ring. The occurrence of these structures in at least one species of *Phanoderma* can contribute little to the taxonomy of the free-living nematodes so long as it remains an isolated record but it demonstrates the poverty of the available descriptions.

Oncholaimus dujardinii de Man, 1876

Material Studied

4 ♂, 6 ♀, 7 larvae. B.M. (N.H.), Reg. Nos. 1961.210–226.

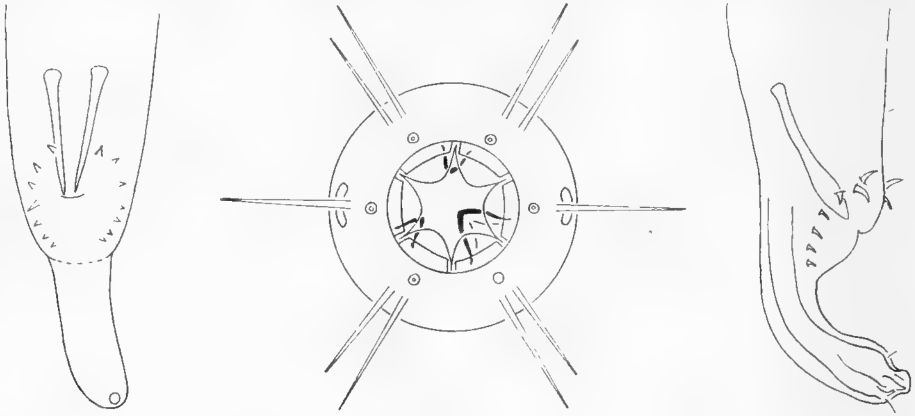
This, as is pointed out by Schuurmans Stekhoven (1950), is one of the most commonly reported species from the Mediterranean. It has been described by several authors and my specimens from Banyuls appear to be wholly typical. It has been previously reported from Banyuls, without description, by Allgén (1942) and full details of its reported occurrence within the Mediterranean are given by Schuurmans Stekhoven (1950). I, therefore, restrict this description to some figures, particularly of the shape of the spicules (Text-figs. 14 and 16) which do not appear to have been figured wholly accurately before, and an *en face* view of the head which has not been figured before (Text-fig. 15).



FIGS. 10–13. *Phanoderma parafilipjevi* (continued). Fig. 10. Male tail from the lateral aspect. Fig. 11. Oesophagus from the lateral aspect. Fig. 12. Lateral view of head. Fig. 13. Detail of the anterior end of oesophagus showing the shape of the pharyngeal capsule.

Discussion

Wieser (1955) lists this species among those which he considers to have a ". . . more or less cosmopolitan distribution " but, as Schuurmans Stekhoven (1950) points out, Steiner's (1915) description of *O. dujardinii* from Sumatra mentions the presence of a gubernaculum. Because of this Schuurmans Stekhoven, who was unable to find a gubernaculum in his Mediterranean specimens, proposed the name *O. steineri* for the species with a gubernaculum. I have also been unable to find any trace of a gubernaculum and agree with Schuurmans Stekhoven that *O. steineri* is a good species distinct from *O. dujardinii*. This view is supported by Ditlevsen's (1926) description of *O. groenlandicus* sp. nov., in which he found no trace of a gubernaculum, which is almost certainly indistinguishable from *O. dujardinii*.



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Figs. 14–16. *Oncholaimus dujardinii* de Man, 1876. Fig. 14. Ventral view of male tail. Fig. 15. *En face* view of head. Fig. 16. Male tail from the lateral aspect.

Wieser's (1953*a*) and Mawson's (1958) descriptions of *O. dujardinii* from Chile and the Subantarctic, in both of which a gubernaculum is figured and described, lend further support to this view. I treat both these records as almost certainly referring to *O. steineri*. The accessory sense organ near the tip of the male tail which is described by Steiner may be simply some small setae, such as are scattered generally over the surface of the tail, but his figure (taf. 24, fig. 29) suggests something more complex. Such a structure also appears to be illustrated in the figure given by Wieser (1953*a*, fig. 68*b*) and that given by Mawson (1958, fig. 28*b*). Wieser also treats some nominal species as synonyms of *O. dujardinii* but their status must be considered most uncertain. Thus, the description of *O. exilis* Cobb, 1889 is, as Wieser points out, unsatisfactory and without figures. I cannot accept it as a synonym of *O. dujardinii* but prefer to treat it as a *species dubia*. Similarly with Ditlevsen's (1930) species, *O. bollonsi* from New Zealand, I cannot accept that " there is no doubt that *O. bollonsi* is identical with *O. dujardini* " (Wieser, 1953*a* : 116). It may be indistinguishable from *O. steineri*—in which case the specific name *bollonsi* would have priority—but, until the male is known, it is better to treat it as a *species inquirenda.* Allgén (1959) records *O. dujardinii*, without description, from the Fuegian Archipelago, the Falkland Islands and from South Georgia but I consider it more probable that he actually had *O. steineri* but as this cannot be confirmed I treat these records as valueless (see p. 00).

To return to Wieser's (1955) record, as it is without a description the status of his specimens cannot be established and his contention that *O. dujardinii* falls into the group of cosmopolitan species of nematodes is unfounded.

Prooncholaimus banyulensis sp. nov.

Material Studied

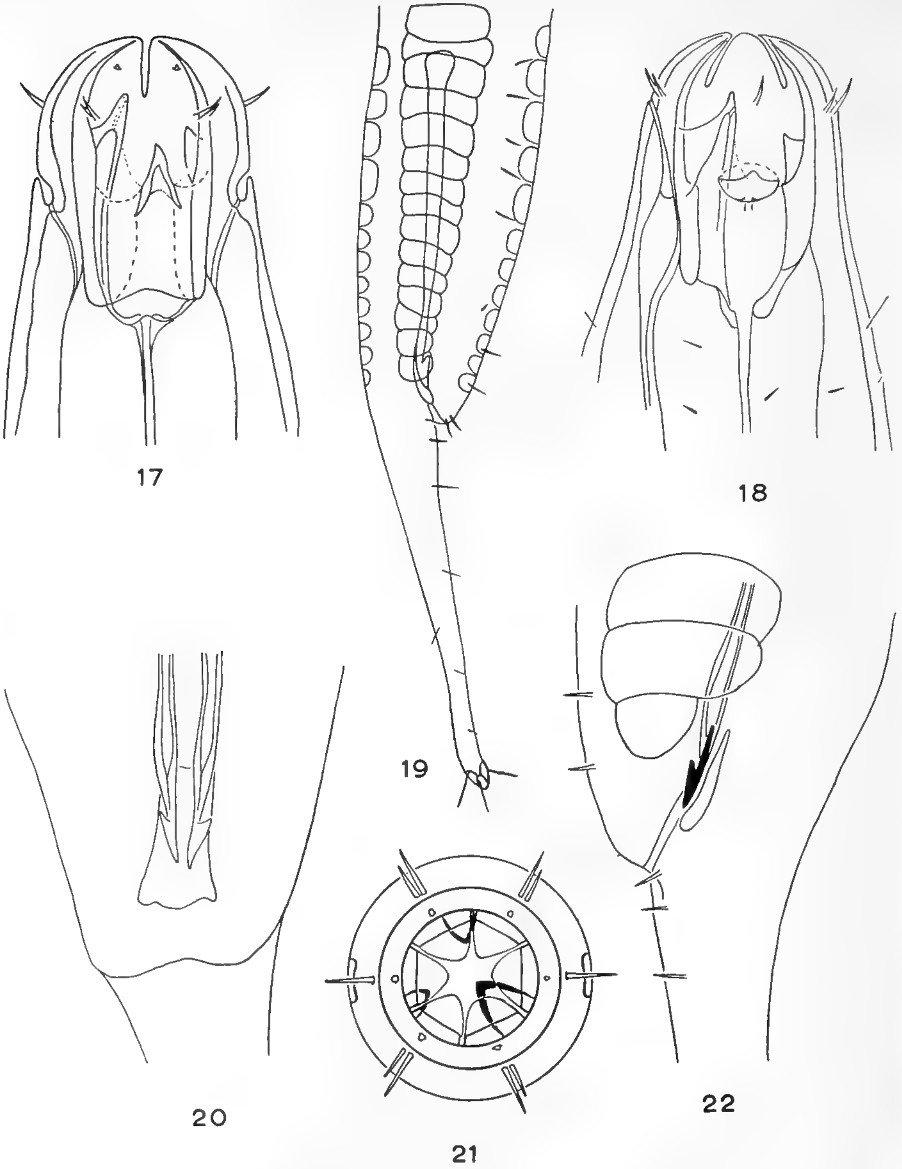
2 ♂, 1 larva. B.M. (N.H.), Reg. Nos. 1961.360–362. Holotype ♂, 1961.360.

	Ratios			
	a	*b*	*c*	Body length
Males . .	32·8	6·1	20·3	3·25
	33·3	6·6	21·4	3·60
Larva . .	31·5	5·5	15·5	2·33

Measurements (in mm. ; in order of body lengths)

MALES. Body breadth : 0·099 ; 0·108. Oesophagus length : 0·53 ; 0·55. Diameter of head at level of setae : 0·033 ; 0·032. Diameter of body at level of amphids : 0·041 ; 0·039. Length of cephalic setae : 0·005 and 0·007 ; 0·005 and 0·007. Distance of amphids from anterior end : 0·023 ; 0·026. Total length of buccal cavity : 0·049 ; 0·049. Length of first part of buccal cavity : 0·030 ; 0·029. Breadth of first and second parts of buccal cavity : 0·019 and 0·017 ; 0·021 and 0·014. Length of dorsal tooth : 0·034 ; 0·034. Length of left ventro-lateral tooth : 0·040 ; 0·036. Length of right ventro-lateral tooth : 0·033 ; 0·029. Nerve ring from anterior end : 0·27 ; 0·29. Excretory pore from anterior end : 0·015 ; 0·013. Tail length : 0·16 ; 0·17. Cloacal diameter (across anterior lip and across posterior lip) : 0·031 and 0·026 ; 0·035 and 0·026. Spicule length : 0·116 ; 0·139. Gubernaculum length : 0·019 ; 0·018. The cuticular inflations start 0·087 mm. from the anterior end on the 3·25 specimen and are 0·051 mm. wide at the mid-point of the body length.

LARVA. Body breadth : 0·074. Oesophagus length : 0·42. Diameter of head at level of setae : 0·027. Diameter of body at level of amphids : 0·034. Cephalic setae not measured. Total length of buccal cavity : 0·039. Length of first part of buccal cavity : 0·022. Breadth of first and second parts of buccal cavity : 0·017 and 0·011. Length of dorsal tooth : 0·024. Length of left ventro-lateral tooth : 0·031. Length of right ventro-lateral tooth : 0·026. Nerve ring from anterior end : 0·24. Excretory pore from anterior end : 0·010. Tail length : 0·15. Cloacal diameter (across anterior lip and across posterior lip) : 0·029 and 0·023.



FIGS. 17–22. *Prooncholaimus banyulensis* sp. nov. Fig. 17. Dorsal view of head. Fig. 18. Lateral view of head with the dorsal surface to the right. Fig. 19. Male tail from the lateral aspect. Fig. 20. Ventral detail of gubernaculum and tips of spicules. Fig. 21. *En face* view of head. Fig. 22. Lateral detail of gubernaculum and tips of spicules.

The cuticular inflation which occurs on the lateral and the dorsal and ventral surfaces is most prominent in all the specimens (Text-fig. 19). The body is marked by faint, close-set striations and contracts very sharply at the level of the cloacal opening so that the opening is covered anteriorly by a very thick ledge-like lip (Text-fig. 19).

Head and Oesophagus

The anterior end of the body is smoothly rounded and carries six small, semi-sessile papillae in the inner circle and an outer circle composed of six long setae and four shorter setae (Text-figs. 17, 18 and 21). The longer setae are about 1·4 times longer than the shorter in the adults. (It was not possible to measure them in the larva.) The mouth opening is large and is surrounded by six prominent lip-lobes. The buccal cavity is circular in cross-section and is developed into six lobes anteriorly, one corresponding to each lip-lobe. Within the buccal cavity are the usual three teeth of which the left ventro-lateral is the longest. The amphids lie about the level of the origins of the smaller teeth and the excretory pore opens just posterior to the cephalic setae. The oesophagus expands slightly along its entire length, there is no posterior bulb or distinct swelling and the nerve ring encircles it about half-way along its length. There are several short setae distributed over the oesophageal part of the body.

Tail

The tail is very characteristic. It contracts very sharply immediately posterior to the anal or cloacal opening, narrows evenly towards the posterior end and terminates in a very slight swelling. The anterior lip of the cloacal opening rises suddenly above the opening so that there is a sudden step in the outline of the ventral surface of the body at this point, when viewed from the lateral aspect (Text-figs. 19, 20 and 22).

Male

There is a series of stout setae around the cloacal opening, three pairs flanking the opening, two pairs arranged linearly just posterior to it and three pairs anterior to it (Text-figs. 19 and 22). In addition there are some long setae scattered over the posterior end of the body to just anterior to the anterior ends of the spicules. Similar, but shorter, setae occur on the tail proper.

The spicules are equal in length and identical in structure with distinct barbs on their posterior ends (Text-figs. 20 and 22). They are fairly stout anteriorly and narrow evenly towards their posterior ends where they swell slightly before constricting rather sharply just before the posterior barbs. The barbs are much more heavily cuticularized than the remainder of the spicules and are a deep brown in colour when cleared with glycerine, the remaining parts of the spicules being pale and translucent. The barbs are developed anteriorly into distinct narrow strips which run for a short distance along the sides of the more anterior parts of the spicules (Text-fig. 22). There is a short, simple gubernaculum which expands posteriorly where it is slightly tri-lobed (Text-fig. 20).

Discussion

This species is most similar to *P. eberthi* (Filipjev, 1918) and to *P. mediterraneus* Schuurmans Stekhoven, 1943 but appears to differ from them both in the structure of the spicules and, perhaps a less important character, in the shape of the tail. It is extremely difficult to be sure since the descriptions available of both species are somewhat sketchy. Nevertheless the form of the posterior ends of the spicules in *P. banyulensis* is so distinctive that it can be seen easily at low magnifications and it is difficult to believe that Filipjev could have drawn them as he has the posterior ends of the spicules of *P. eberthi* (Filipjev, 1921, pl. 4, fig. 27). Similarly, Schuurmans Stekhoven's (1950) figure of the spicules, which does not agree with his earlier figure (1943, fig. 15*d*), shows spicules with much less prominently modified ends. Schuurmans Stekhoven (1950) lays considerable stress on certain ratios in delimiting his species from that of Filipjev. I am extremely sceptical as to the value of using ratios in this way, particularly as Schuurmans Stekhoven only uses one ratio in all cases. Nevertheless in many of these ratios *P. banyulensis* differs from both *P. mediterraneus* and *P. eberthi*. However, Schuurmans Stekhoven uses the anal diameter as a reference measurement in several of his ratios and I do not know which diameter he measured ; across the large anterior lip of the cloacal opening or around the tail immediately posterior to the cloacal opening. I will, therefore, give two ratios for *P. banyulensis*, the first based on the measurement including the anterior lip and the other not including it. It is clear that, using this reference point the spicules of *P. banyulensis* are relatively, as well as absolutely, shorter than those of *P. mediterraneus*. The ratio of spicule length/anal diameter for the latter species is 6·6 while in *P. banyulensis* it is 3·7 or 4·5 (3·25 mm. long specimen) and in *P. eberthi* it is 5·0. Schuurmans Stekhoven also lays stress on the relative dimensions of the buccal cavity. In males of *P. mediterraneus* he gives the ratio of the length of the buccal cavity to its greatest width as 2·5–3·0, in *P. eberthi* as 2·37 while in *P. banyulensis* the same ratio is 1·6 in both adult specimens.

Prooncholaimus banyulensis is, therefore, characterized by relatively short spicules with distinct, heavily cuticularized, sharply pointed barbs on their posterior ends and by a relatively narrow buccal cavity.

Symplocostoma tenuicolle (Eberth, 1863)

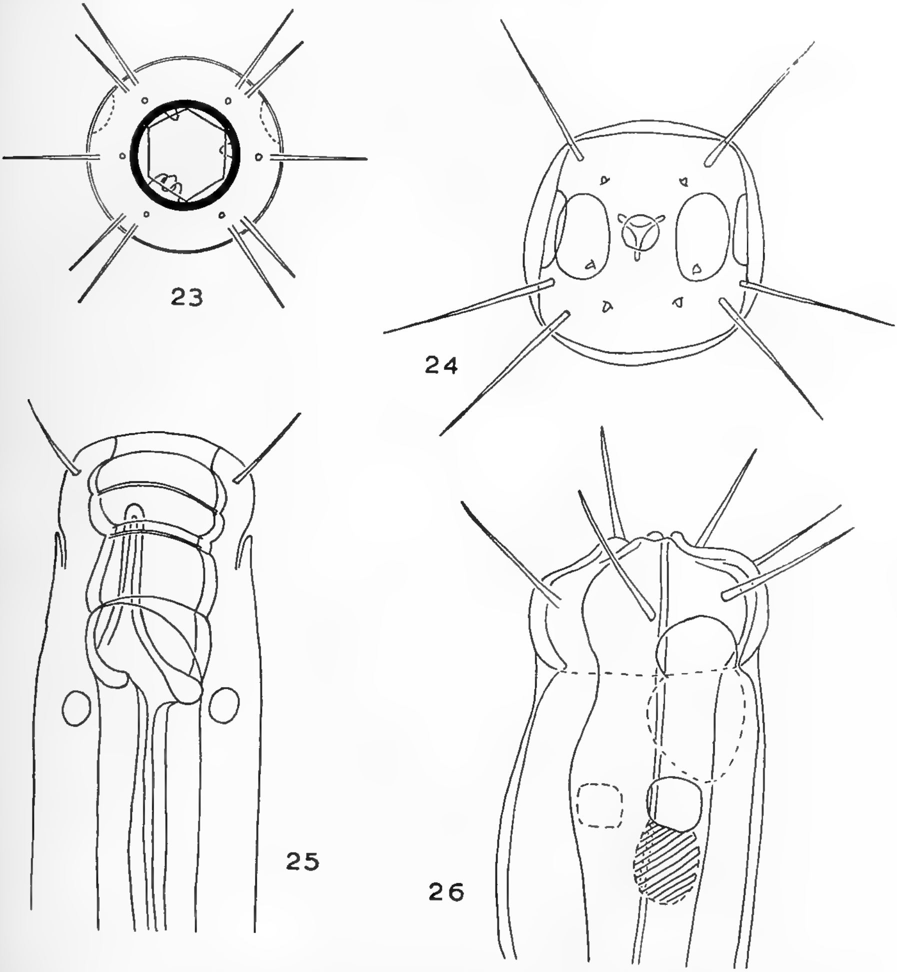
Material Studied

2 ♂, 5 ♀, 8 larvae. B.M. (N.H.), Reg. Nos. 1961.363–368.

This species has been considered in great detail by Wieser (1953) and I restrict myself to a few observations on the structure of the head. It is, however, worth noting that the female reproductive apparatus is double with opposed reflexed ovaries and that the uteri may contain up to ten eggs at one time.

The Head

In this genus, in fact in the entire subfamily Enchelidiinae, there is according to Wieser (1953*a*, 1954*a*) a marked sexual dimorphism. Such a dimorphism is exhibited by this species in which the buccal cavity is prominently developed in the female (Text-fig. 25) but is totally lacking in the male (Text-fig. 26). In the female the mouth opening is hexagonal and the long narrow buccal cavity contains three teeth of which the right ventro-lateral is much larger than the others. The large tooth, when viewed in *en face* preparations, appears to be doubled at the anterior end but this appears to be due to an optical section effect (Text-fig. 23). It should be noted that in this species, as in *Polygastrophora omercooperi* Inglis, 1961, the smaller



FIGS. 23–26. *Symplocostoma tenuicolle* (Eberth, 1863). Fig. 23. *En face* view of female head. Fig. 24. *En face* view of male head. Fig. 25. Dorsal view of female head. Fig. 26. Lateral view of male head with the dorsal surface to the right.

dorsal and left ventro-lateral teeth are directed towards each other when viewed *en face*. The amphids are dorso-lateral in position. In the male head the buccal capsule and teeth are totally lacking, although they are present in the fourth-stage larva. Instead the oesophagus continues to the anterior end of the body which is modified as a distinct cap (Text-fig. 26) which appears to be due to the oesophagus being attached to the covering of the body wall in a way analogous to that found in *Enoplus* and *Phanoderma*, although this is uncertain due to lack of specimens. No trace was seen of the cephalic cap-like structure figured by Filipjev (1918–21, pl. 4, figs. 28*a* and *b*). When studied *en face* the male head appears to be even more remarkable (Text-fig. 24). There is a marked asymmetry of the distribution of the six long setae so that the lateral members are more ventro-lateral than is usual and the amphids, which are distinctly dorso-lateral in position on the female head, are almost wholly lateral in position. This asymmetry also affects the inner circle of sessile papillae but not to the same marked extent as the setae. It should also be noted that the female head bears ten setae while the male head appears to have only six. The mouth opening is circular and small.

Discussion

The form of the male head is most remarkable and it is unfortunate that I have only been able to study one *en face* preparation. The asymmetry reported may be due to faulty technique but I am not wholly convinced that this is the explanation. The result is sufficiently startling to warrant this brief mention in the hope that some other worker may be able to check it and confirm or refute my observations.

Eurystomina pettiti sp. nov.

(?) *Eurystomina assimilis* of Schuurmans Stekhoven, 1943, pp. 348–349. Fig. 19*c* (in part).

Material Studied

4 ♂, 1 ♀, 8 larvae. B.M. (N.H.), Reg. Nos. 1961.6–10. Holotype male, 1961.6.

	a	*b*	*c*	V	Body length
Males	67·4	4·8	30·7	—	3·1
	69·3	5·0	32·9	—	3·2
	66·1	5·1	36·8	—	3·2
One suppl.	68·8	4·6	30·6	—	3·3
Female	53·7	4·7	27·1	55·0	3·2
Larvae	51·2	3·6	19·6	—	1·3
4th stage	56·3	4·1	32·5	58·7	3·2

Measurements (in mm. in order of body lengths above).

MALES. Oesophagus length: 0·64; 0·64; 0·64; 0·71. Buccal cavity depth: ...; 0·014; 0·014; 0·015. Buccal cavity width, first part ...; 0·010; 0·009; 0·010; second part: ...; 0·009; 0·009; 0·010. Length of longest tooth: 0·011; 0·010; 0·010; 0·012. Lengths of cephalic setae (long only):

0·010; 0·011; 0·010 (short 0·007); 0·009. Nerve ring from anterior end: 0·27; 0·24; 0·24; 0·24. Excretory pore from anterior end: ... ; ... ; immediately posterior to lips; immediately posterior to lips. Diameter of head: 0·018; 0·015; 0·015; 0·017. Tail length: 0·101; 0·097; 0·086; 0·108. Anal diameter: 0·049; 0·044; 0·044; 0·045. Spicule length: 0·056; 0·060; 0·057; 0·057. Gubernaculum length: 0·031; 0·032; 0·028; 0·032. Distance of pre-cloacal supplements anterior to cloaca; first: 0·071; 0·091; 0·074; 0·072 (only one); second: 0·124; 0·150; 0·115; second lacking.

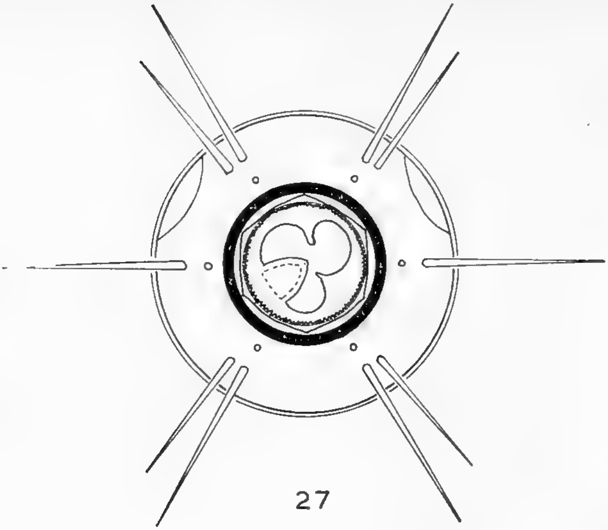
Females. Oesophagus length: 0·68. Buccal cavity depth: 0·017. Buccal cavity width, first part: 0·010; second part: 0·008. Length of longest tooth: 0·012. Lengths of cephalic setae: 0·011 and 0·008. Nerve ring from anterior end: 0·25. Excretory pore from anterior end: 0·006. Diameter of head: 0·15. Tail length: 0·117. Anal diameter: 0·032. Vulva from anterior end: 1·76.

Larvae. Oesophagus length: 0·37; 0·76. Buccal cavity depth: 0·010; 0·013. Buccal cavity width, first part: 0·007; 0·008; second part: 0·005; 0·007. Length of longest tooth: 0·007; ... . Lengths of cephalic setae: 0·005 and 0·003; 0·011 and 0·008. Nerve ring from anterior end: 0·168; ... . Excretory pore: immediately posterior to lips; ... . Diameter of head: 0·009; ... . Tail length: 0·068; 0·097. Anal diameter: 0·018; 0·035. Vulva from anterior end: no vulva; 1·85.

Head and Oesophagus

The head is rounded and is not off-set from the remainder of the body. It carries an outer circle of ten fairly long setae of which six are longer than the remaining four (Text-fig. 27). There is an internal circle of six sessile papillae surrounding the hexagonal mouth opening, which does not appear to be bordered by lips (see also Cobb, 1920). The amphids are fairly prominent, dorso-lateral in position but the nerves which supply them are lateral, as has been pointed out by Chitwood (1960). The mouth leads into a large buccal cavity, with relatively thick, cuticular walls, which is in two parts, a shallow anterior part and a relatively deep posterior chamber. The line of demarcation between these two chambers is marked by three rows of denticles of which those composing the most anterior row appear to be longer than those composing the more posterior rows. The first two rows are complete around the periphery of the cavity but the most posterior row is incomplete. The denticles are lacking along the left dorso-lateral sector, that is the part of the buccal cavity opposite the large ventro-lateral tooth. This large tooth arises from the floor of the buccal cavity in the right ventro-lateral sector, is very broad based and narrows evenly to a sharp point. There are two similar, but very much smaller teeth in the dorsal and left ventro-lateral sectors (Text-figs. 27 and 29).

The oesophagus is relatively long and narrow with no special modification. The excretory pore opens immediately posterior to the cephalic setae and there are several small setae scattered over the general surface of the anterior end of the body but there are none, or very few, posterior to the posterior end of the oesophagus. Eye-spots are present about 0·03 mm. from the anterior end of the body.



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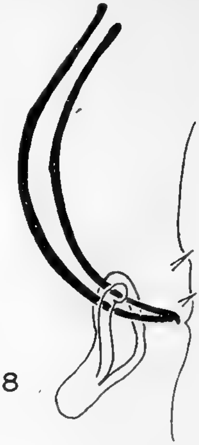

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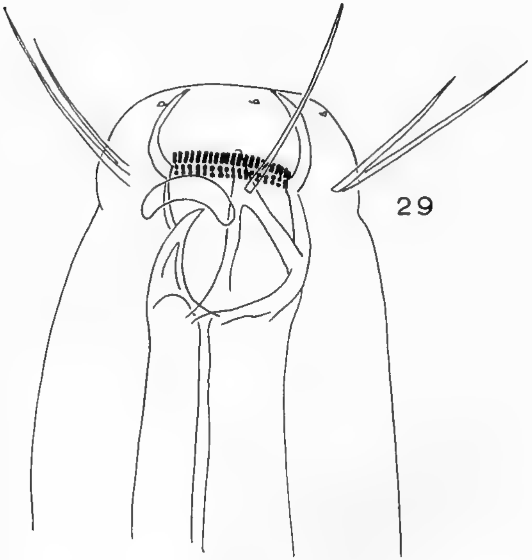

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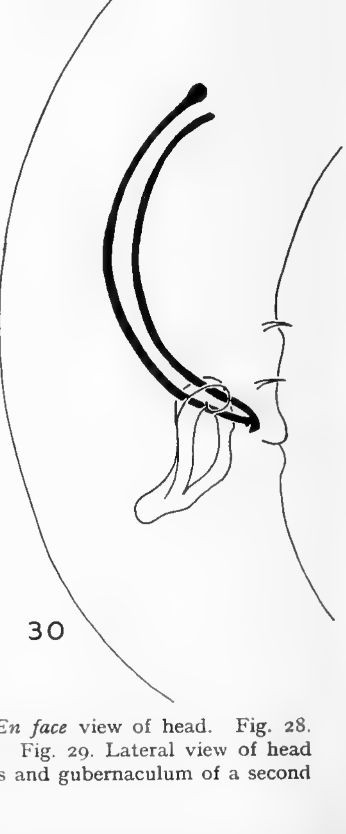

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FIGS. 27–30. *Eurystomina pettiti* sp. nov. Fig. 27. *En face* view of head. Fig. 28. Spicules and gubernaculum from the lateral aspect. Fig. 29. Lateral view of head with the dorsal surface to the left. Fig. 30. Spicules and gubernaculum of a second specimen from the lateral aspect.

Tail

The tail is roughly the same shape in both sexes. It is relatively short and stout, terminating posteriorly in a bluntly rounded tip. The caudal glands lie far anterior to the anus or cloacal opening.

Male

The spicules are equal in length and identical in structure (Text-figs. 28 and 30). They are evenly curved, without alae and with a slight barb-like swelling on their distal ends such as is shown by Filipjev (1921) in his figure (fig. 29*c*) of " *E. assimilis* ". Cobb (1922) reports that such a modification of the distal ends of the spicules is common. The gubernaculum is relatively massive with a fenestrate ventral mass which projects between the spicules and from which arises two lateral pieces which project on the outer sides of the spicules. These lateral pieces are rather narrow curved structures which are bluntly rounded at their tips (Text-figs. 28 and 30). The gubernaculum is so shaped that the outline of the ventral side is bent almost into a right angle and the proximal end is blunt and rounded (Text-figs. 28 and 30). The two pre-cloacal supplements are present in all the specimens except one and they lie closer to each other than the distance separating the more posterior from the cloacal opening. In the abnormal specimen, with only one supplement, it is clearly the more anterior supplement which has failed to develop. There are several pairs of stout setae on the ventral surface of the body anterior to the cloacal opening of which the first three or four pairs are clumped relatively closer together than the others and are also slightly more lateral in position.

Female

There are two opposed, reflexed ovaries. The eggs are relatively large, 0·129 × 0·046 mm. and 0·131 × 0·048 mm. in size. The only gravid female contains two eggs.

Discussion

Schuurmans Stekhoven (1943) describes what he considered to be *Eurystomina assimilis* but the figures of the male tail suggest that he confused two distinct species (compare Text-figs. 31, *q* and *r*). The first figure suggests *E. gerlachi* while the second suggests the present species and is referred above to the synonymy as a probable synonym.

E. pettiti is characterized as a short-tailed species with eye spots and a gubernaculum which is relatively short, blunt and massive.

Review of the Genus Eurystomina

Marion (1870) creates a new genus, *Eurystoma*, for two new species which he discovered in the Mediterranean, *E. spectabilis* (type species) and *E. tenue*. The generic name is, however, pre-occupied by that for a genus of molluscs and a new

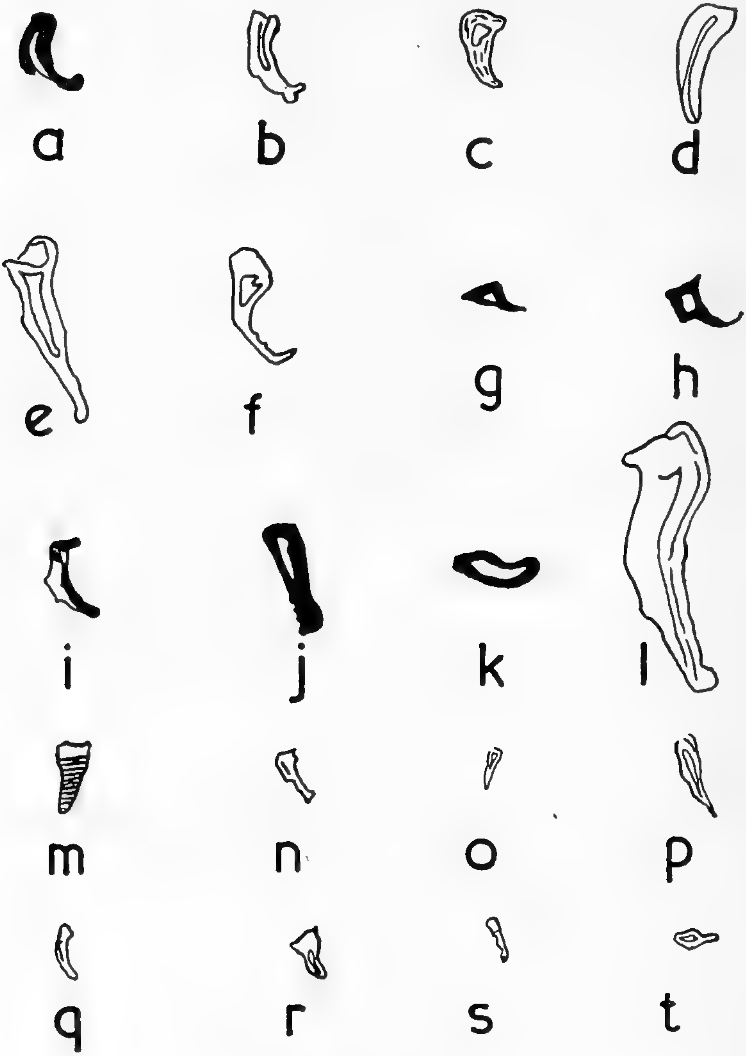

FIG. 31. Lateral views of the gubernacula of various species of *Eurystomina*, redrawn after various authors. The ventral surface of the body is to the left in all the figures. *a*—*E. filiformis* (= *E. assimilis* of Filipjev, 1918, fig. 29*f*) ; *b*—*E. ornata* (= *E. assimilis*

name, *Eurystomina*, is proposed by Filipjev (1921—not 1918 as stated by Filipjev, 1934 ; Wieser, 1953 and 1953*a*). Cobb (1922) also proposes a new name, *Marionella*, to replace *Eurystomina*. Then Schuurmans Stekhoven (1935) unwarrantably proposes an emendation of the name to *Eurystomatina* and he, and Allgén, continue to use this form.

This review is a direct result of the attempt to identify *E. pettiti* during which it became apparent that many of the characters used in delimiting species within the genus were either misleading or of only doubtful value and that many of the nominal species referred to the genus were based on insufficient specimens or inadequate morphological data. For example Schuurmans Stekhoven (1950) describes a new species, *E. stenolaima*, based on only part of a specimen (the tail, apparently, was missing) and many other species are based on females only. A further indication of this is given by the difficulties involved in identifying and separating the European species (i.e. those from the best known area), *E. ornata*, *E. tenue*, *E. assimilis* and *E. filiformis*, all of which have been considered indistinguishable, in whole or in part, by some authors although I will demonstrate later that at least two of them are distinct species, one is a synonym of another species not in the group, and the fourth is best considered a *species dubia*. Further, *E. ornata* has been reported from many localities outside European waters and several other species have been treated as indistinguishable from it although I will show that such species, i.e. *E. opthalmophora*, *E. ornata* var. *indica* and *E. ornatum* of Wieser, 1955, are in fact distinct from *E. ornata*.

Characters of Value in Delimiting Species

Wieser (1953*a*) states " I should like to emphasize that the best distinguishing characters (in *Eurystomina*) are to be found in the head region and not—contrary to what is the case in most other marine nematodes—in the male genital apparatus. Without a detailed knowledge of the cephalic setae, the transverse rows of denticles in the buccal cavity, the position of the ocelli etc. the status of a given species cannot be defined with certainty." In spite of this Wieser (1953, 1953*a*) refers to the large tooth as being dorsal in position while it is clearly ventro-lateral in position in all

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of Filipjev, 1918, fig. 29*c*) ; *c*—*E. opthalmophora* (= *E. ornatum* var. *indicum* Micoletzky, 1930) ; *d*—*E. opthalmophora* (after Steiner, 1922) ; *e*—*E. eurylaima* (after Ditlevsen, 1930) ; *f*—*E. stenolaima* (after Ditlevsen, 1930) ; *g*—*E. wieseri* sp. nom. nov. (= *E. stenolaima* of Wieser, 1953*a*) ; *h*—*E. fenestrella* (after Wieser, 1953*a*) ; *i*—*E. chilensis* sp. nom. nov. (= *E. retrocellatum* of Wieser, 1953*a*) ; *j*—*E. minutisculae* (after Chitwood, 1951) ; *k*—*E. chitwoodi* sp. nom. nov. (= *E. americana* of Chitwood, 1951) ; *l*—*E. filiformis* (after de Man, 1888) ; *m*—*E. repanda* (after Wieser, 1953*a*) ; *n*—*E. ornata* (after Eberth, 1863) ; *o*—*E. spectabilis* (= *E. tenue* of Marion, 1870) ; *p*—*E. spectabilis* (after Marion, 1870) ; *q*—*E.* (?) *gerlachi* sp. nom. nov. (after *E. assimile* of Schuurmans Stekhoven, 1943, fig. 19B) ; *r*—*E.* (?) *pettiti* sp. nov. (after *E. assimile* of Schuurmans Stekhoven, 1943, fig. 19C) ; *s*—*E. tenuicaudata* (after Allgén, 1931) ; *t*—*E. americana* (after Chitwood, 1936).

the species in which the head has been adequately described. Mawson (1958) points this out with reference to *E. fenestrella* ; the large tooth is ventro-lateral in *E. pettiti* (see below) ; Luc and De Coninck (1959) show it so in *E. ornatum* and Cobb (1922) reports that in all the species he studied the large tooth was invariably right ventro-lateral in position. It is also right ventro-lateral in *E. pettiti* and appears to be so positioned in all the figures I have seen, except that given by Luc and De Coninck (1959) who show it to be left ventro-lateral. The importance of this is not clear since the two authors may have been in error or it may indicate that the large tooth may be either left or right ventro-lateral but it is quite clear that whichever side it may occupy the large tooth is always ventro-lateral.

The greatest difficulty about using the structure of the head in the delimitation of species within this genus is that the head tends to be small and is extremely difficult to study so that one cannot be sure that all the structures, for example rows of small denticles, have been seen. In studying *E. pettiti* the three rows of denticles could not be seen in all the specimens but I am quite sure that this does not indicate that I was studying several species but only that the condition of the specimens was such that it was impossible to establish the presence of all the structures. The presence or absence of ocellae is much more difficult to assess since they may easily be dissolved out in the storage fluid and their occurrence cannot, I feel, be treated as a character of any great significance. Thus the first dichotomy in Wieser's key (1953*a* : 135) is probably without significance, as he appreciates himself.

In spite of the criticism of the value of the male genital apparatus by Wieser (1953*a*), quoted above, and his further comment, after redescribing what he considers to be *E. retrocellata*, that " The male genital apparatus provides no good distinguishing character ; . . ." I would suggest that, in fact, the male genital apparatus affords very good characters, particularly the form of the gubernaculum. This suggestion is advanced from a study of the literature but is supported by the relative ease with which it is possible to separate species previously considered to be indistinguishable and the apparent degree of constancy in the shape of the gubernaculum when figures by different authors are compared. Compare, for example, Eberth's figure of the gubernaculum of *E. ornata* (fig. 31, *n*) with that by Filipjev (1918, fig. 31, *b*) of what he considered to be *E. assimilis* ; also compare the other gubernaculum figured by Filipjev as *E. assimilis* (fig. 31, *a*) with that of *E. filiformis* (fig. 31, *l*). In fact a superficial glance at the various figures of the gubernaculum which are redrawn as Text-figs. 31 and 32 is sufficient to establish my thesis.

Attempts to use measurements and ratios in delimiting nematode species are fraught with difficulties since they are, as in any group of soft-bodied animals, liable to considerable distortion during fixation. The possible effects of this have been discussed in detail elsewhere (Inglis, 1958) but I would point out that I look on almost all attempts to separate species on the basis of measurements or ratios, whether largely or alone, as suspect.

Biblio-systematic studies, such as this review, are always fraught with danger but the results are interesting and supply a more rational basis for the delimitation of species within the genus *Eurystomina* than that available at present. It may be objected that in dismissing records based on females or juveniles I have been excessive but it is quite clear that if this is not done now, while the study of the free-living nematodes is in an early stage, the position will simply become more difficult instead of easier since the way in which many species, particularly the European which have been most extensively studied, have been confused shows quite clearly the, I suspect, insurmountable difficulties involved in delimiting species on the only characters which are available in the females, the structure of the head, the position of the eye spots, various measurements and ratios, etc.

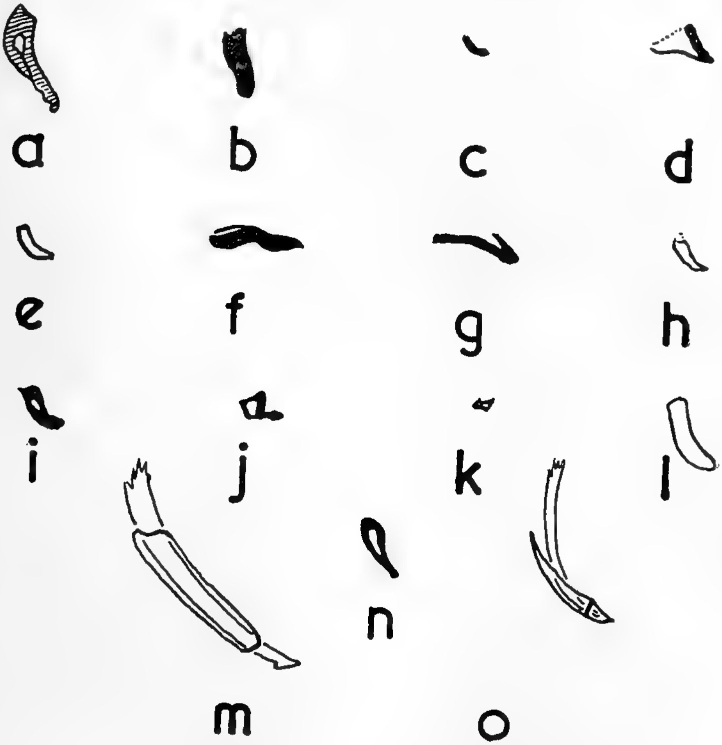

Fig. 32. Lateral views of the gubernacula of various species of *Eurystomina* (continued). Arranged as in fig. 31 with the ventral surface to the left except for " *m* " and " *o* " where the ventral surface is to the right. *a*—*E. opthalmophora* (= *E. ornatum* of Wieser, 1955); *b*—*E. terricolum* var. *opthalmophorum* (after Allgén, 1947); *c*—*E. spissidentata* (after Allgén, 1947); *d*—*E. trichophora* (after Allgén, 1959); *e*—*E. filicaudata* (after Allgén, 1959); *f*—*E. mirabilis* (after Allgén, 1959); *g*—*E. linstowi* (after Allgén, 1959); *h*—*E. stenolaima* (after Allgén, 1959, fig. 84*c*); *i*—*E. stenolaima* (after Allgén, 1959, fig. 84*b*); *j*—*E. fenestrella* (after Mawson, 1958); *k*—*E. norvegica* (after Allgén, 1947); *l*—*E. gerlachi* sp. nov. (after *E. assimile* of Gerlach, 1951); *m*—*Gerlachystomina sawayai* (after Gerlach, 1954*a*); *n*—*E. americana* (after *E. minutisculae* of Timm, 1954); *o*—*G. filispicula* (after Gerlach, 1954).

EURYSTOMINA Filipjev, 1921

Eurystoma Marion, 1870 ; *Eurystomina* Filipjev, 1921 ; *Marionella* Cobb, 1922 ; *Eurystomatina* Schuurmans Stekhoven, 1935 (invalid emendation).

Type species : *Eurystoma spectabile* Marion, 1870.

DISTRIBUTION. Cosmopolitan, as constituted here.

The genus *Eurystomina* is the type genus of the subfamily Eurystominae Filipjev, 1934 and differs from the other genera of the subfamily in the following characters:

> Oesophagus without posterior bulbs ; cephalic setae relatively short ; caudal glands present ; two well-developed, winged, pre-cloacal supplements on the male tail ; gubernaculum developed dorsally away from the spicules.

Two groups of species may be recognized within the genus, either on the presence or absence of eye spots or, another grouping, on whether the tail is short, stout and rounded posteriorly or is long and narrow posteriorly. It is not clear whether or not the two groups coincide since the pigment of the eye spots appears to be very easily removed during fixation or subsequent storage and in many cases where eye spots are not reported they may in fact have been overlooked because of this. As Wieser (1953*a*) points out " In this genus about 50% of the species are incompletely described which makes faultless classification and grouping nearly impossible ". As a result no attempt is made here to propose any groupings for the species referred to the genus except for the two species described by Gerlach (1954, 1954*a*) which are referred to a new genus (see p. 254).

Analysis of the Species of Eurystomina

1. **Eurystomina abyssalis** Micoletzky, 1930[1]

Eurystomina abyssale Micoletzky, 1930, pp. 291–293. Fig. 11.

LOCALITY. Kei Island, the Sunda Islands.

This species, which is known from females only, appears to be distinct and is characterized, particularly, by a rounded, relatively simple head. No ocelli are mentioned. This species may not, in fact, be referable to the genus *Eurystomina* as the head appears to be much simpler than that characteristic of the genus and I shall treat it as only provisionally a member of the genus.

2. **Eurystomina americana** Chitwood, 1936

Eurystomina americana Chitwood, 1936, pp. 212–213. Figs. 24–26 ; Chitwood & Timm, 1954, p. 315.

Eurystomina minutisculae of Timm, 1954, p. 15. Figs. 21–22, non Chitwood, 1951.

non *Eurystomina americana* of Chitwood, 1951, pp. 628–629. Figs. 3, A–C (= *Eurystomina chitwoodi* sp. nov.).

LOCALITIES. Shackleford's Banks, N.C., U.S.A. (type locality) ; Solomons Island, Md., U.S.A.

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[1] The specific names used are as emended by Andrassy (1959).

This species is characterized by the shape of the gubernaculum which is relatively broad and rounded distally and then constricts evenly to a narrow proximal part (Text-fig. 31, *t*). Chitwood (1936) reports only one row of denticles in the buccal cavity and the absence of ocelli while Timm (1954), in describing his *E. minutisculae*, mentions three rows of denticles and ocelli. Nevertheless, I consider Timm's specimens to be, almost certainly, conspecific with *E. americana* of Chitwood (1936) since the form of the gubernaculum is almost identical in both descriptions, compare Chitwood's figure (fig. 31, *t*) with that of Timm (fig. 32, *n*). Certainly Timm's species is not conspecific with *E. minutisculae* as described by Chitwood (1951) nor is *E. americana* as described by Chitwood (1951) conspecific with the original specimens (see below, p. 244).

3. **Eurystomina assimilis** (de Man, 1876), *species dubia*

Oncholaimus assimilis de Man, 1876, p. 95, Pl. 7, figs. 5, *a–b*.
non *Eurystoma assimile* of Filipjev, 1918, pp. 157–161. Pl. 5, fig. 29 (= in part *E. ornatum* and *E. filiforme*).
non *Eurystomina assimilis* of Allgén, 1929*a*, p. 20 (*species dubia*) ; of Allgén, 1931, p. 230 (listed as *E. filiforme* on p. 213 ; *species dubia*) ; of Allgén, 1933, p. 36 (*species dubia*).
non *Eurystomina assimilis* of Filipjev, 1922, p. 568 (= in part *E. ornatum* and *E. filiforme*).
non *Eurystomina assimile* of Schuurmans Stekhoven, 1943, pp. 348–349. Figs. 19, A–C (= ? *E. gerlachi*, in part and *E. pettiti*, in part).
non *Eurystomina assimile* of Gerlach, 1951, pp. 199–200. Fig. 4, *a–c* (= *E. gerlachi* nom. nov.).

LOCALITY. Coast of Holland (type locality).

The original description of this species is based on a female only and, in spite of the good description given by de Man (1876) the redescriptions given by Filipjev (1918) and Gerlach (1951) clearly refer to different species. Filipjev in fact has confused two species, *E. ornata* and *E. filiformis*, as apparently has Schuurmans Stekhoven (1943). *E. assimilis* has also been treated as a synonym of *E. ornatum* by various authors (e.g. Micoletzky, 1924 ; Wieser, 1953 ; Allgén, 1959 ; among others) thus demonstrating the difficulties involved in attempting to identify the species de Man actually studied. As a result I propose that *E. assimilis* be treated as a *species dubia*. Allgén's records (1931 and 1933) are based on females and his 1929*a* record is, as are the others, without a description.

4. **Eurystomina bilineata** Wieser, 1953*a*, *species inquirenda*

Eurystomina bilineata Wieser, 1953*a*, pp. 138–139. Figs. 85, *a–b*.

LOCALITY. Islas Gueitecas, Archipiellago de los Chonos and Peninsula Taitao ; Canal Errazuriz " Islote Elena " (Faro Islote Diego).

This species is known from females only and Wieser apparently considers it to be distinct in having only six cephalic setae and one row of denticles with a sclerotized ring between the anterior and posterior chambers of the buccal cavity.

5. *Eurystomina californica* (Allgén, 1947), *species dubia*

Eurystomatina californicum Allgén, 1947, p. 129. Fig. 35 ; Allgén, 1959, p. 89.
Eurystomina californicum Wieser, 1953, p. 136 (doubtful species).

LOCALITIES. San Diego, California, U.S.A. (type locality) ; Falkland Islands.

The original description of the species is based on one juvenile specimen and the second record (Allgén, 1959) is based on a further juvenile which "... in the shape of its tooth and its tail seems to be identical with this species [*E. californica*] ". The description of this species is totally inadequate and I agree with Wieser (1953*a*) that it is " doubtful ". I propose to treat it as a *species dubia*.

6. *Eurystomina chilensis* nom. nov.

Eurystomina retrocellatum of Wieser, 1953*a*, p. 138. Figs. 84, *a–c*.
non *Eurystomina retrocellatum* Micoletzky, 1930, pp. 289–291. Fig. 10.

LOCALITY. Many localities on the coast of Chile, see Wieser (1953*a*) for details.

This species is quite clearly different from all the others referred to the genus, except *E. retrocellata*, not only in having a rasp-like arrangement of many rows of small denticles in the buccal cavity but also in the shape of the gubernaculum (Text-fig. 31, *i*). It may in fact be conspecific with *E. retrocellata* of Micoletzky (1930) but without a detailed figure of the male genital apparatus of that species it is impossible to be sure. The presence of many rows of denticles may prove sufficient to warrant the introduction of a new genus at some later date.

7. *Eurystomina chitwoodi* nom. nov.

Eurystomina americana of Chitwood, 1951, pp. 628–629. Figs. 3, A–C ; non Chitwood, 1936.

LOCALITY. Rockport Habor, Texas, U.S.A.

The redescription given by Chitwood (1951) of the species he originally described in 1936 clearly does not apply to the same species. It differs most markedly in the form of the gubernaculum which in the true *americana* (Text-fig. 31, *t*) is very narrow proximally while in the redescription it is broad along its whole length (Text-fig. 31, *k*). As the second description cannot be applied to any of the other named species within the genus I name it here as new.

8. *Eurystomina eurylaima* (Ditlevsen, 1930)

Marionella eurylaima Ditlevsen, 1930, pp. 225–227, 37–39.
Eurystomina eurylaima, Wieser, 1953*a*, p. 135.

LOCALITY. Three Kings Island (♂) and Bay of Islands (♀), New Zealand.

The description of this species is based on one male and one female collected from different localities and I here select the locality from which the male was obtained as the type locality. No eye spots are mentioned and no cephalic setae were found. It is distinguishable by the form of the gubernaculum (Text-fig. 31, *e*), which is long, narrow and tapers to a rather fine, rounded point proximally.

9. *Eurystomina fenestrella* Wieser, 1953*a*

Eurystomina fenestrella Wieser, 1953*a*, p. 140. Figs. 87, *a–d*; Mawson, 1958, pp. 355–356. Figs. 41, *a–c*.

Localities. Various localities on the coast of Chile (see Wieser, 1953, for details) and Heard Island and Macquarie Island, Subantarctica.

This species is distinct and is characterized by the form of the gubernaculum which is squarish in outline and massive distally bearing a rather narrow, small proximal part (Text-fig. 31, *h*). The specific name is obtained from the very large and prominent fenestra which occurs in the distal part of the gubernaculum. As Mawson (1958) points out, the proximal part of the gubernaculum in her specimens is shorter than that figured by Wieser, it is also rather stouter (see Mawson's, 1958, fig. 41*b*—redrawn here as Text-fig. 32, *j*), but it is possible that Mawson has been unable to see the extreme end of the proximal part of the gubernaculum which Wieser's figure shows to be very delicate (Text-fig. 31, *h*). Even if the difference shown by Mawson truly exists I would treat it as variation and accept that she studied the same species as that described by Wieser.

10. *Eurystomina filicaudata* (Allgén, 1959), *species dubia*

Eurystomatina filicaudatum Allgén, 1959, p. 92. Figs. 86, *a–b*.

Locality. South Georgia, Antarctica.

See p. 213 for a discussion of all species described by Allgén (1959).

11. *Eurystomina filicolle* (Allgén, 1959), *species dubia*

Eurystomatina filicolle Allgén, 1959, pp. 92–93. Figs. 87, *a–b*.

Localities. Falkland Islands; South Georgia and Graham Land, Antarctica. See p. 213.

12. *Eurystomina filiformis* (de Man, 1888)

Eurystoma filiforme de Man, 1888, pp. 26–28. Pl. 3, figs. 13–13*d*; ? Ditlevsen, 1919, pp. 202–203.
Eurystoma assimile of Filipjev, 1918–21, pp. 157–161. Pl. 5, fig. 29, *f* (in part).
Eurystomina assimile of Filipjev, 1922, p. 568 (in part).
non *Eurystoma filiforme* of Steiner, 1916, p. 602. Pl. 16, fig. 24*a*; pl. 28, 24, *b* (*species dubia*).

Localities. North Sea, Black Sea.

Filipjev (1918) treats this species as a synonym of *E. assimilis* while Micoletzky (1924) and Wieser (1953*a*), although the latter author expresses some reservations, treat it as a synonym of *E. ornata*. Wieser argues that the original description of *E. ornata* is insufficient to allow any conclusions as to its independence from various nominal species to be drawn (see Wieser, 1953*a* : 136) but, as will be pointed out later (p. 250), the figure of the gubernaculum given by Eberth (1863) for *E. ornata* (redrawn as Text-fig. 31, *n*) is sufficient to allow the species to be identified and it is clear that *E. filiformis* is distinct from it (see Text-figs. 31, *l* and *a*). Further it is clear that Filipjev's (1921) figures of *E. assimilis* represent two species, *E. ornata* (fig. 29*c*—redrawn here as Text-fig. 31, *b*) and *E. filiformis* (fig. 29*f*—redrawn here as Text-fig. 31, *a*). Filipjev's figure 29*f* corresponds almost exactly with the original description given by de Man (1888, pl. 3, figs. 13*b* and 13*c*—13*c* redrawn here as Text-fig. 31, *l*) and I therefore treat *E. assimilis* of Filipjev, 1918 as partly *E. ornata* and partly *E. filiformis*.

E. filiformis is a good species which can be distinguished by the form of the gubernaculum with its evenly-rounded ball-like proximal end (Text-figs. 31, *a* and *l*) and, perhaps a less reliable character, by the relative distribution of the pre-cloacal supplements on the posterior end of the male which are closer together than the more posterior is close to the cloacal opening, in contradistinction to the condition in *E. ornata* in which the supplements are not so markedly bunched together.

13. ***Eurystomina filispicula*** Gerlach, 1954

= *Gerlachystomina filispiculum* (Gerlach, 1954) (see p. 255)

14. ***Eurystomina frøyense*** (Allgén, 1946), *species dubia*

Eurystomatina fryense Allgén, 1946, p. **161**.
Eurystomina froyense Wieser, 1953*a*, p. 136 (doubtful species).

Locality. Froya Island, Norway.

The status of this species, which is based on one juvenile specimen, is, as is pointed out by Wieser (1953), very doubtful. No figures have been published and I propose to treat it as a *species dubia*.

15. ***Eurystomina gerlachi*** nom. nov.

Eurystomina assimile of Gerlach, 1951, pp. 199–200. Figs. 1, *a–c*, non de Man, 1876.
? *Eurystomatina assimile* of Schuurmans Stekhoven, 1943, pp. 348–349. Fig. 19, B (in part).

Locality. Varna, Bulgarian coast of the Black Sea.

As is pointed out above under *E. assimilis* de Man's description of that species is based on females and I treat it as a *species dubia*. The difficulties involved in identifying that species are exemplied by the fact that Filipjev (1918) confuses two species in giving his redescription and Gerlach (1951) describes yet a third species. Gerlach's species does, however, at least have the distinction of apparently being different from any other referred to the genus, with the possible exception of *E. assimilis* of Schuurmans Stekhoven (1943) in part, and is here named *E. gerlachi* sp. nov. The *Eurystomatina assimilis* of Schuurmans Stekhoven (1943) appears to have been based on a mixture of two species, *E. gerlachi* (fig. 19, B—redrawn here as Text-fig. 31, *q*) and *E. pettiti* (fig. 19, C—redrawn here as Text-fig. 31, *r*), although the figures given by Schuurmans Stekhoven are insufficient for certainty. It does, however, appear certain that his redescription is based on two species.

E. gerlachi may be distinguished by the relative simplicity of the gubernaculum which is about the same width along its whole length (Text-fig. 1, *l*). Schuurmans Stekhoven's figure (Text-fig. 31, *q*) suggests that the gubernaculum may be fenestrated although Gerlach figures it as entire.

16. ***Eurystomina linstowi*** (Allgén, 1959), *species dubia*

Eurystomatina linstowi Allgén, 1959, p. 94. Figs. 89, *a–c*.

Locality. Falkland Islands.

See p. 213.

17. ***Eurystomina lithothamnii*** (Saveljev, 1912), *species inquirenda*

Eurystoma lithothamnii Saveljev, 1912, pp. 117–118.
Eurystomina lithothamnii, Wieser, 1953*a*, p. 136.

LOCALITY. Palafjord, Relictensee Mogilnoje.

This species is described by Saveljev (1912) without figures but it appears to be distinct in the distance separating the pre-cloacal supplements on the male tail. Its status is, nevertheless, open to question and I must treat it as a *species inquirenda*.

Filipjev (1918 : 157) lists *E. filiforme* of Steiner (1916) as a possible synonym of this species but Steiner's record is based on one moulting juvenile specimen and I treat it above as a *species dubia*.

18. ***Eurystomina littoralis*** Allgén, 1929, *species dubia*

Eurystomina littorale Allgén, 1929, pp. 13–14. Figs. 1, *a–b*.
Eurystomatina littorale Bresslau & Schuurmans Stekhoven in Schuurmans Stekhoven, 1935. p. V, b. 57. Figs. 149, A–B ; Bresslau & Schuurmans Stekhoven, 1940, p. 32. Pl. 7, figs, 32, A–B.

LOCALITY. South coast of Sweden.

The original description of this species is based on one juvenile specimen and it is extremely doubtful whether it will ever be possible to refer it definitely to an adult worm. Bresslau & Schuurmans Stekhoven (1940) describe a single young female which they consider to be conspecific with that described by Allgén but this record must be considered to be of little value and I treat it also as that of a *species dubia*.

19. ***Eurystomina minutisculae*** Chitwood, 1951

Eurystomina minutisculae Chitwood, 1951, p. 629. Figs. 3, D–G. non *Eurystomina minutisculae* of Timm, 1954, p. 15. Figs. 21-22 (= *E. americana*).

LOCALITY. Mud Island, Aransas Bay, Texas, U.S.A.

Chitwood chooses to contrast this species with *E. filiforme* from which it clearly differs not only in the measurements and ratios referred to by Chitwood but also in the highly characteristic form of the broad, massive, bluntly rounded gubernaculum (Text-fig. 31, *j*). This species can hardly in fact, be confused with any other species of the genus, the shape of the gubernaculum is so very characteristic. Timm (1954) redescribes what he considers to be this species but the outline of the gubernaculum as he figures it (Text-fig. 32, *n*) is so totally different from that figured by Chitwood that there is no doubt that Timm misidentified his specimens and they are considered above probably to represent specimens of *E. americana*.

Wieser (1953*a*) suggests that this species may be the same as *E. retrocellatum* but Chitwood specifically mentions three rows of minute denticles in the buccal cavity while *E. retrocellatum* is characterized by a very large number of denticles and the two species cannot be confused.

20. ***Eurystomina mirabilis*** (Allgén, 1959), *species dubia*

Eurystomatina mirabile Allgén, 1959, pp. 93–94. Figs. 88, *a–c*.

LOCALITIES. South Georgia and the Falkland Islands.

See p. 213. The accuracy of fig. 2, *f* is doubtful since Allgén (1959) refers to a "denticulated posterior edge" to the gubernaculum which is not shown in his figure.

21. ***Eurystomina norvegica*** (Allgén, 1947*a*), *species inquirenda*

Eurystomatina norvegicum Allgén, 1947*a*, pp. 54–55. Figs. 4, *a–b*.
Eurystomina norvegicum Wieser, 1953*a*, p. 135.

LOCALITY. Storfosen Island, Norway.

The description of this species is insufficient to establish its systematic validity even although males were found and described. The figures which Allgén gives are much too small to be of any value (see Text-fig. 32, *h* which is the gubernaculum of this species redrawn from Allgén's figure).

22. ***Eurystomina opthalmophora*** (Steiner, 1922)

Eurystomina terricola var. *opthalmophorus* Steiner, 1922, pp. 215–217. Pl. 11, figs. 4, *a–d*.
? *Eurystomina ornatum* var. *indicum* Micoletzky, 1930, pp. 285–288. *Figs*. 9, *a–b*.
Eurystomina opthalmophorus, Wieser, 1953*a*, p. 136.
Eurystomina ornatum of Wieser, 1955, pp. 161–163. Fig. 1; of Chitwood, 1960, pp. 377–378. Pl. 4, figs. F–G.
non *Eurystominum terricolum* var. *opthalmophorum* of Allgén, 1947, p. 127. Figs. 33, *a–b* (= *species inquirenda*).

LOCALITIES. Port Arthur, Russia, Eastern Asia (type locality); (?) Shira-hamo-tyo, Wakayama-ken, Japan; (?) many localities in the Sunda Islands (see Micoletzky for details (1930)); La Jolla and Dillon Beach, California, U.S.A.

Filipjev (1927), Micoletzky (1930) and Wieser (1953*a*) consider the variety described by Steiner (1922) to be a distinct species but later Wieser (1955) and Chitwood (1960) consider it indistinguishable from *E. ornata*. The species described by Wieser (1955) and by Chitwood (1960) is clearly not *E. ornata* as a comparison of Wieser's figure of the gubernaculum (see Text-fig. 32, *a*) with those of Eberth (Text-fig. 31, *n*) and Filipjev (Text-fig. 31, *b*) clearly demonstrates. On the other hand Wieser, after studying the Japanese specimens concludes that "The present specimens make it clear beyond all doubt that Steiner's *E. terricola* var. *opthalmophora* is also synonymous with *E. ornata* (compare the present figure with those of Steiner, 1922 and Filipjev, 1918)". Thus Wieser considers his specimens to be conspecific with those on which Steiner (1922) based his description of *E. opthalmophora* and I think this is very probably correct, but I cannot accept that *E. opthalmophora* is conspecific with either of the species on which Filipjev (1918) based his redescription of what he called *E. assimilis* (see above under *E. filiformis* and *E. ornata*). *E. opthalmophora* is, therefore, a good species which is distinguishable by the shape and structure of the gubernaculum. Chitwood (1960) stresses the similarity between his specimens and the description given by Wieser (1955) and it is clear that he also studied *E. opthalmophora*.

The status of *E. ornata* var. *indica* Micoletzky, 1930 is uncertain but it appears probable that it is also a synonym of *E. opthalmophora*. As Wieser (1955) points out the lack of wings to the pre-cloacal supplements may be of some systematic importance although it is already known that they may not be developed in some specimens. In fact, as in the case of *E. pettiti*, one of the supplements, at least, may completely fail to develop. Nevertheless the full synonymy of *E. o.* var. *indicum* and *E. opthalmophora* cannot be considered as wholly established and it is listed here as a doubtful synonym only.

Allgén's (1947) record of this species is almost certainly inaccurate since the structure of the gubernaculum appears to be totally different from that typical of *E. opthalmophora* (see Text-fig. 32, *b*—Allgén's (1947) figure redrawn). On the other hand it is not sufficient for Allgén's record to be referred to any other species and this record is, therefore, treated as that of a *species inquirenda*.

23. *Eurystomina ornata* (Eberth, 1863)

Enoplus ornatus Eberth, 1863, pp. 40–41. Pl. IV, figs. 13–15 ; pl. V, figs. 5–6.
Eurystoma ornatum, Filipjev, 1918, p. 156.
Eurystomatina ornatum, Micoletzky, 1924, pp. 248–251 (in part since Micoletzky lists as synonyms several species here treated as distinct).
Eurystoma assimile of Filipjev, 1918, pp. 157–161. Fig. 29*c* (in part).
non *Oncholaimus ornatus*, Daday, 1901, pp. 442–444. Pl. xxii, figs. 1–3 (= *species dubia*).
non *Eurystomina ornatum* var. *indicum* Micoletzky, 1930, pp. 285–288. Figs. 9, *a–b* (= *E. opthalmophora*).
non *Eurystomina ornatum* of Gerlach, 1952, p. 519 (= *species dubia*) ; of Wieser, 1955, pp. 161–163. Fig. 1 (= *E. opthalmophora*) ; (?) of Luc & De Coninck, 1959, pp. 112–114. Figs. 14–15 ; of Chitwood, 1960, pp. 377–378.
non *Eurystomatina ornatum* of Allgén, 1957 (= *species dubia*). Pl. 4, figs. F–G (= *E. opthalmophora*).
non *Eurystomina ornatum* var. *indicum* of Timm, 1961, pp. 39–40. Figs. 16, *a–b* (= *species dubia*).

The following records of this species are not accepted since it is impossible to know whether they apply to this species or not since most of the authors giving the records treat *E. ornata* and *E. filiformis*, at least, as indistinguishable and with none of them is there a description adequate to establish to which species the record applies ; Villot, 1875 ; Southern, 1914 ; Allgén, 1940, 1943*a*, 1947, 1951 ; Schuurmans Stekhoven, 1950, pp. 74–76. Figs. 36, A–B. Although Schuurmans Stekhoven gives a description he only studied one female and his description is insufficient to allow the species he studied to be identified.

LOCALITIES. Mediterranean and Black Seas ; (?) Atlantic Ocean.

E. assimilis, *E. tenue* and *E. filiformis* have been treated as indistinguishable from this species at various times (e.g. Villot, 1875 ; Filipjev, 1918 ; Micoletzky, 1924 ;

Wieser, 1953—with some reservations ; Allgén, 1959) but *E. assimilis* is based on females only and is treated above as a *species dubia* (see p. 243) ; *E. tenue* is probably a synonym of *E. spectabilis* (see p. 251) and *E. filiformis* is a distinct species which differs from *E. ornata* in the form of the gubernaculum (see p. 245). The synonymy of this species is very complicated since, although the species has been recorded on many occasions, many of the records are based on female or juvenile specimens and many of the authors accept the synonymity of *E. ornata* and *E. filiformis.* As explained above I feel that records based on female specimens only should be treated with the greatest reservation and, in this case, I will not accept records which are not accompanied by adequate illustrations. The dangers of doing so are exemplified by the record of *E. assimilis* of Filipjev (1918) in which he has in fact recorded *E. ornata* and *E. filiformis* as the same species (see discussion under *E. filiformis*).

E. ornata is characterized by a gubernaculum which is massive and squarish in outline distally while it constricts fairly sharply about half-way along its length so that the proximal half of its length is narrow and even in width, except for the extreme proximal end which is swollen into two rounded knobs (see Text-figs. 31, *b* and *n*).

The gubernaculum of *E. ornata* var. *indica* is totally different from this, as is the gubernaculum of *E. ornata* of Wieser (1955) and of Chitwood (1960). These records are considered to represent *E. opthalmophora* (see immediately above). *E. ornatum* var. *indicum* of Timm, 1961, is based on females only and is treated as the record of a *species dubia.*

The status of *E. ornata* of Luc & De Coninck (1959) is doubtful since the male genital apparatus is not figured.

24. ***Eurystomina paralittorale*** Timm, 1951, *species dubia*

Eurystomina parallittorale Timm, 1951, pp. 15–16. Figs. 19–20.

LOCALITIES. Plum Point and Chesapeake Beach, Maryland, U.S.A.

This species is based on one (?) juvenile worm and it is impossible to come to any decision as to its validity or relationships. I, therefore, propose to treat it as a *species dubia.*

25. ***Eurystomina pettiti*** sp. nov.

See above, p. 234.

26. ***Eurystomina propinqua*** (Allgén, 1947), *species dubia*

Eurystomatina propinquum Allgén, 1947, pp. 129–130. Figs. 36, *a–b* ; Allgén, 1959, p. 89.

LOCALITIES. San Diego, West Coast of the U.S.A. (type locality) ; Falkland Islands, Port Louis and Greenpatch, Antarctica.

The original description of this species is based on one juvenile specimen which was clearly in a very poor state of preservation. Allgén in fact states on p. 66 of his paper that all the specimens were, in general, poorly preserved. The second record (Allgén, 1959) is based on two female specimens, and in the same report Allgén rejects Wieser's (1953*a*) treatment of *E. californica* and *E. propinqua* as doubtful species. I, however, agree wholly with Wieser and must insist that the poor description of badly-preserved female or juvenile specimens as new species must inevitably lead to their rejection as *species dubiae*, as I do with *E. propinqua*.

27. ***Eurystomina repanda*** Wieser, 1959

Eurystomina repanda Wieser, 1959, p. 30. Pl. XII, figs. 27, *a–b*.

LOCALITIES. Vashon Island and Alki Point, Puget Sound, U.S.A.

This species is characterized by a simple, relatively stout gubernaculum (Text-fig. 31, *m*) and a buccal cavity bearing two rows of rods, two (or one and a half) rows of dots and a cuticular ring.

No eye spots were seen.

28. ***Eurystomina retrocellata*** Micoletzky, 1930, *species incertae sedis*

Eurystomina retrocellatum Micoletzky, 1930, pp. 289–291. Fig. 10.
non *Eurystomina retrocellatum* of Wieser, 1953*a*, p. 138. Figs. 84, *a–e* (= *E. chilensis* sp. nov.).
non *Eurystomina retrocellata* of Gerlach, 1954*b*, p. 55 (= *species dubia*) ; non Andrassy, 1959, pp. 247–248 (= *species dubia*).

LOCALITY. Kei Island, Sunda Islands.

This species is characterized by the presence of large numbers of teeth in the buccal cavity. Wieser (1953) suggests that it may be indistinguishable from *E. minutisculae* although Chitwood (1951) specifically refers to "... two transverse bands, the posterior bearing three very minute rows of denticles ", as occurring in his species. In spite of Micoletzky's description this species must be considered *incertae sedis*, at least, since no figures of the male are given and there is no description of the form of the gubernaculum—only its length relative to the spicules is given.

Gerlach (1954*b*) studied only one specimen, later lost, and, because of the great difference in geographical locality as well as because of the characters on which he bases his identification, I treat his record as that of a *species dubia*. Andrassy's (1959) record, based on one female and four juveniles, is dismissed as a *species dubia* for the same reasons.

29. ***Eurystomina sawayai*** Gerlach, 1954*a*

= *Gerlachystomina sawayai* (Gerlach, 1954*a*) (see p. 255).

30. ***Eurystomina spectabilis*** (Marion, 1870)

Eurystoma spectabile Marion, 1870, pp. 20–21. Pl. 20, figs. 1–1*b* ; Filipjev, 1918, p. 157.
Eurystoma tenue Marion, 1870, p. 21. Pl. 20, figs. 2–2*b* ; Filipjev, 1918, p. 156 (suggested synonym of *E. ornatum*).
Marionella spectabilis, Cobb, 1922, p. 509.
Eurystomina spectabilis, Baylis & Daubney, 1926, p. 115.

LOCALITY. Marseille, Mediterranean.

Filipjev (1918) and Micoletzky (1924) consider *E. tenue* to be indistinguishable from *E. ornata* while Filipjev considers *E. spectabilis*, which is the type species of the genus, to be a distinct species because of the very large pre-cloacal supplements figured by Marion on the male tail. *E. spectabilis*—accepting Marion's figure to be reasonably accurate—is apparently distinguishable from *E. ornatum*, and all the other species in the genus, in having a gubernaculum which is relatively long and narrow, with sharply pointed proximal end (Text-fig. 31, *p*). *E. tenue* has exactly the same form of gubernaculum (Text-fig. 31, *c*) and as I can find no other characters which will separate the two forms I consider *E. tenue* to be a synonym of *E. spectabilis*. It is fairly certain, in my opinion, that the apparently large size of the pre-cloacal supplements in both forms (because they are shown as large in both figures although Filipjev only comments on this with reference to *E. spectabilis*) may be attributed to artistic licence.

31. ***Eurystomina spissidentata*** (Allgén, 1947), *species inquirenda*

Eurystomatina spissidentatum Allgén, 1947, pp. 127–128. Figs. 38, *a–b*.
Eurystomina spissidentatum, Wieser, 1953*a*, p. 136 (doubtful species).

LOCALITIES. Perias Islands Bay of Panama and La. Jolla, California.

It is impossible to establish the validity or relationships of this species on the basis of the description given by Allgén (1947) who refers to the gubernaculum as being finely dentate on the anterior side of the dorsal half but figures it as a simple, curved mass (fig. 2, *c*). I agree with Wieser (1953*a*) that it is a " doubtful species ".

32. ***Eurystomina stenolaima*** (Ditlevsen, 1930)

Marionella stenolaima Ditlevsen, 1930, pp. 227–230. Figs. 42–46.
non *Eurystomatina stenolaima* of Schuurmans Stekhoven, 1950, p. 77. Fig. 37 (= *E. stenolaimoides* Wieser, 1953*a*).
non *Eurystomatina stenolaimum* of Allgén, 1951, p. 382 (= *species dubia*).
non *Eurystomatina stenolaima* of Wieser, 1953*a*, pp. 138–140. Figs. 86, *a–c* (= *E. wieseri* sp. nov.).
non *Eurystomatina stenolaimum* of Allgén, 1959, pp. 88–89. Figs. 84, *a–c* (= *species dubia*).

LOCALITY. Cape Brett, New Zealand.

This species is easily recognized by the highly characteristic gubernaculum (Text-fig. 31, *f*) which is massive distally and carries a narrow, slightly serrated process with a hooked end proximally. No eye spots are present according to Ditlevsen.

Wieser (1953*a*) describes what he considers to be this species but also points out that his "... specimens show several differences from Ditlevsen's type; some of them, as especially the structure of the buccal cavity and the number of cephalic setae are most probably due to deficiencies in the original description; ..." (Wieser, 1953*a* : 139). Wieser is probably correct in this since Ditlevsen specifically says that his specimens were in a poor condition. Nevertheless the form of the gubernaculum (Text-fig. 31, *f*) is so characteristic and so different from that figured by Wieser (Text-fig. 31, *g*) that I have no hesitation in treating Wieser's specimens as representing a new species (see *E. wieseri*).

The record of Allgén (1951) is without figures and I am not prepared to accept it as referring to this species. The same author later (Allgén, 1959) records this species again but points out that his specimens were intermediate in form between *E. stenolaima* and *E. eurylaima* but, although he describes the gubernaculum as being hooked like that in *E. stenolaima*, his figures in no way resemble the gubernaculum figured by Ditlevsen (see Text-figs. 32, *h* and *i*). For that matter his two figures do not correspond with each other and I will treat this record as representing a *species dubia*.

33. ***Eurystomina stenolaimoides*** Wieser, 1953*a*, *species dubia*

Eurystomatina stenolaima Schuurmans Stekhoven, 1950, p. 77. Fig. 37, non Ditlevsen, 1930.
Eurystomina stenolaimoides Wieser, 1953*a*, p. 135 nom. nov. pro *E. stenolaima* Schuurmans Stekhoven, 1950, pre-occupied by *E. stenolaima* Ditlevsen, 1930.

LOCALITY. Baie de Lilong, Villefranche, France.

Schuurmans Stekhoven (1950) describes a new species *E. stenolaima* from Villefranche. The specific name is pre-occupied by *stenolaima* Ditlevsen, 1930 so Wieser (1953*a*) proposes the name *stenolaimoides*. The description is based on one broken, incomplete specimen and its sex is not given. Wieser considers that it may be in fact referable to the genus *Symplocostomella* but I feel that this is unnecessary speculation and that this nominal species based on the pathetic remnants of a specimen should be decently interred as a *species dubia*.

34. ***Eurystomina tenuicaudata*** Allgén, 1931*a*

Eurystomina tenuicaudata Allgén, 1931*a*, pp. 120–122. Figs. 15, *a–c*.

LOCALITY. Campbell Island, South Pacific.

This long-tailed species is characterized by a relatively straight, slim gubernaculum which is swollen at both the proximal and the distal ends (Text-fig. 31, *s*).

35. ***Eurystomina tenuissima*** Filipjev, 1927, *species incertae sedis*

Eurystomina tenuissima Filipjev, 1927, pp. 179–180. Pl. 6, figs. 61, *a–b*.

LOCALITY. Port Catherine, Mourman.

This long-tailed species, of which only the female is known, does not appear to belong to the genus *Eurystomina* in view of the structure of the head with its massive buccal cavity. The establishment of its systematic position must await the discovery of more specimens. No eye spots are reported.

36. ***Eurystomina terricola*** (de Man, 1907), *species dubia*

Eurystoma terricola de Man, 1907, pp. 84–86. Pl. IV, figs. 17–17*a*.
Eurystomatina terricola, Schuurmans Stekhoven, 1935, p. V, b. 57. Figs. 147, A–B.
Eurystomina terricola, Filipjev, 1927, p. 179.
non *Eurystomatina terricola* ? Allgén, 1931*a*, pp. 119–120. Figs. 14, *a–b* (*species dubia*).
non *Eurystomina terricola* of Gerlach, 1954*a*, p. 55 (= *species inquirenda*).

LOCALITY. Island of Walcheren in soil soaked with brackish water.

De Man (1907) bases his description of this species on a female specimen, and although the description is good and the figure of the head excellent it is doubtful if it could ever be possible to recognize the species again. The doubtful record of Allgén (1931*a*) is based on two juvenile specimens from the South Pacific and it is extremely unlikely that they represent the same species as that studied by de Man and I dismiss the record as valueless.

37. ***Eurystomina trichophora*** (Allgén, 1959), *species dubia*

Eurystomatina trichophorum Allgén, 1959, pp. 90–92. Figs. 85, *a–b*.
Eurystomatina pilosum Allgén, 1959, p. 90. Caption to figs. 85, *a–b* (*lapsus*).

LOCALITIES. Fuegian Archipelago and South Georgia.

See p. 213. As is pointed out above the specimens reported on by Allgén (1959) were in an extremely poor condition and the descriptions of *E. trichophora* and *E. linstowi* support this argument. Thus, for example, no " V " value is given for the female of *E. trichophora* and the " Dimensions " given on p. 90 (Allgén, 1959) are not referred to either sex. Allgén refers to this species as *Eurystomatina pilosum* in the caption to the figures. This is clearly a *lapsus*.

38. ***Eurystomina trichura*** (Allgén, 1953), *species dubia*

Eurystomatina trichurum Allgén, 1953, pp. 91–92. Figs. 5, *a–b*.

LOCALITY. Gallmarfjord, west coast of Sweden.

This long-tailed species is based on one female specimen and its systematic position or validity cannot be established.

39. ***Eurystomina wieseri*** nom. nov.

Eurystomina stenolaima of Wieser, 1953*a*, pp. 139–140. Figs. 86, *a–c*, non Ditlevsen, 1930.

LOCALITIES. Islas Gueitecas, Archipielago de los Chonos and Peninsula Taitao ; Canal Moreleda, Puerto Lagunas. Chile.

The species, described by Wieser (1953*a*) as *Eurystomina stenolaima* differs from that species as described by Ditlevsen (1930) not only in the various points mentioned by Wieser (see above, *E. stenolaima*) but also in the form of the gubernaculum (Text-fig. 31, *g*) which should be compared with the gubernaculum figured by Ditlevsen (Text-fig. 31, *f*). I, therefore, consider Wieser's specimens to represent a distinct species, previously undescribed, for which I propose the name *E. wieseri* sp. nov.

GERLACHYSTOMINA gen. nov.

Eurystominae : oesophagus without posterior bulbs ; cephalic setae not extremely long ; pre-cloacal supplements rather simple in structure without massive anterior and posterior apophyses as in *Eurystomina* ; gubernaculum simple without an apophysis.

Type species : *Eurystomina filispiculum* Gerlach, 1954.

Other species : *Gerlachystomina sawayai* (Gerlach, 1954*a*) comb. nov.

GEOGRAPHICAL DISTRIBUTION. Mediterranean and coast of Brazil at Santos.

Gerlach (1954 and 1954*a*) describes two species which, although he refers them to the genus *Eurystomina*, differ markedly from all the other species referred to that genus in the form of the gubernaculum which, typically, bears a very distinct dorsal prominence, while in Gerlach's species this is lacking and the gubernaculum lies very close to the spicules (Text-figs. 32, *m* and *o*). In addition both species are characterized by pre-cloacal supplements which are much simpler than is typical of *Eurystomina* species. These characters must clearly exclude both species from the genus *Eurystomina* since it, as present constituted, forms a fairly homogenous group so far as the form of the male copulatory apparatus (spicules, gubernaculum and precloacal supplements) is concerned. Gerlach's species appear to show some resemblances to *Thoonchus ferox* Cobb, 1920, the type and only species in that genus, but appears to differ from it in the form of the pre-cloacal supplements. This difference may not in fact exist and Gerlach's species may be congeneric with that of Cobb but it is not possible to establish this on the basis of Cobb's description and I, therefore, propose to erect a new genus, *Gerlachystomina*, for both of Gerlach's species. This has been anticipated above where a diagnosis of the new genus is given. The two species which are referred to it are :

1. ***Gerlachystomina filispicula*** (Gerlach, 1954)

Eurystomina filispiculum Gerlach, 1954, pp. 97–99. Figs. 1, *a–c*.

LOCALITY. Agay, Mediterranean coast of France.

This species differs from *G. sawayai* in the form of the gubernaculum (Text-fig. 2, *o*), the extremely long spicules and in the presence of only two or three rows of denticles in the buccal cavity.

2. ***Gerlachystomina sawayai*** (Gerlach, 1954*a*)

Eurystomina sawayai Gerlach, 1954*a*, p. 15. Figs. 9, *a–d*.

LOCALITY. Santos, Brazil.

This species differs from *G. filispicula* in the form of the gubernaculum (Text-fig. 32, *m*), the short, stout spicules with slightly barbed posterior ends and in the presence of many rows of denticles in the buccal cavity.

Summary of Changes Proposed

The changes proposed are complicated and may be summarized thus :

New Species

E. chilensis = *E. retrocellatum* of Wieser, 1953*a* non Micoletzky, 1930.
E. chitwoodi = *E. americana* of Chitwood, 1951 non Chitwood, 1936.
E. gerlachi = *E. assimilis* of Gerlach, 1951 and (?) of Schuurmans Stekhoven, 1943 (in part), non de Man, 1876.

E. pettiti = new species and (?) *E. assimilis* of Schuurmans Stekhoven, 1943 (in part).

E. wieseri = *E. stenolaima* of Wieser, 1953*a* non Ditlevsen, 1930.

New Genus

Gerlachystomina, with *G. filispicula* (Gerlach, 1954)—type species -and *G. sawayai* (Gerlach, 1954*a*).

Valid Species

E. abyssalis Micoletzky, 1930 ; *E. americana* Chitwood, 1936 ; *E. eurylaima* (Ditlevsen, 1930) ; *E. fenestrella* Wieser, 1953*a* ; *E. filiformis* (de Man, 1888) ; *E. minutisculae* Chitwood, 1951 ; *E. ornata* (Eberth, 1863) ; *E. opthalmophora* Steiner, 1922 ; *E. repanda* Wieser, 1959 ; *E. spectabile* (Marion, 1870) ; *E. stenolaima* (Ditlevsen, 1930) ; *E. tenuicaudata* Allgén, 1931*a*.

Species Dubiae

E. assimilis (de Man, 1878) ; *E. californica* (Allgén, 1947) ; *E. filicaudata* (Allgén, 1959) ; *E. filicolle* (Allgén, 1959) ; *E. froyense* (Allgén, 1946) ; *E. linstowi* (Allgén, 1959) ; *E. littoralé* Allgén, 1929 ; *E. mirabile* (Allgén, 1959) ; *E. paralittorale* Timm, 1951 ; *E. propinqua* (Allgén, 1947) ; *E. stenolaimoides* Wieser, 1953*a* ; *E. terricola* (de Man, 1907) ; *E. trichophora* (Allgén, 1959) ; *E. trichura* (Allgén, 1953).

Species Inquirendae

E. bilineata Wieser, 1953*a* ; *E. lithothamnii* (Saveljev, 1912) ; *E. norvegica* (Allgén, 1947*a*) ; *E. spissidentata* (Allgén, 1947).

Species Incertae Sedis

E. retrocellatum Micoletzky, 1930 ; *E. tenuissima* Filipjev, 1927.

Species Referred to the Synonymy of Other Species

E. tenue Marion, 1870 = *E. spectabile* ; *E. minutisculae* of Timm, 1954 = *E. americana* ; *E. americana* of Chitwood, 1951 = *E. chitwoodi* nom. nov. ; *E. assimile* of Gerlach, 1951 = *E. gerlachi* nom. nov. ; *E. assimile* of Filipjev, 1918 = *E. filiformis* (in part) and *E. ornata* (in part) ; *E. assimile* of Schuurmans Stekhoven, 1943 = (?) *E. gerlachi* (in part) and (?) *E. pettiti* (in part) ; *E. ornatum* var. *indicum* Micoletzky, and of Chitwood, 1960 = (?) *E. opthalmophora* ; *E. ornatum* of Wieser, 1955 = *E. opthalmophora* ; *E. retrocellatum* of Wieser, 1953*a* = *E. chilensis* nom. nov. ; *E. stenolaima* of Wieser, 1953*a* = *E. wieseri* nom. nov.

Chromadorina demani sp. nov.

Material Studied

6 ♂, 6 ♀, 3 larvae. B.M. (N.H.), Reg. Nos. 1961.315–331. Holotype ♂, 1961.331.

	Ratios				
	a	*b*	*c*	V	Body length
Males	21·8	5·80	7·5	—	0·63
	21·6	6·28	7·3	—	0·69
	21·2	6·13	7·4	—	0·70
Females	18·1	4·5	8·7	55·1	0·58 (? late 4th stage stage larva)
	17·7	6·8	6·8	50·8	0·67
	19·9	6·3	7·2	51·4	0·72

Measurements (in mm.; in order of body lengths above)

Males. Body breadth: 0·029; 0·032; 0·033. Oesophagus length: 0·108; 0·110; 0·114. Diameter of head: 0·011; 0·009; 0·012. Lengths of cephalic setae: 0·005; 0·006; 0·006. Length of oesophageal bulb: 0·026; 0·028; 0·029. Breadth of oesophageal bulb: 0·022; 0·022; 0·024. Nerve ring from the anterior end: 0·072; 0·064; 0·068. Excretory pore not seen. Length of spicules: 0·028; 0·032; 0·034. Length of gubernaculum: 0·027; 0·028; 0·028. Tail length: 0·084; 0·094; 0·097. Cloacal diameter: 0·027; 0·028; 0·031.

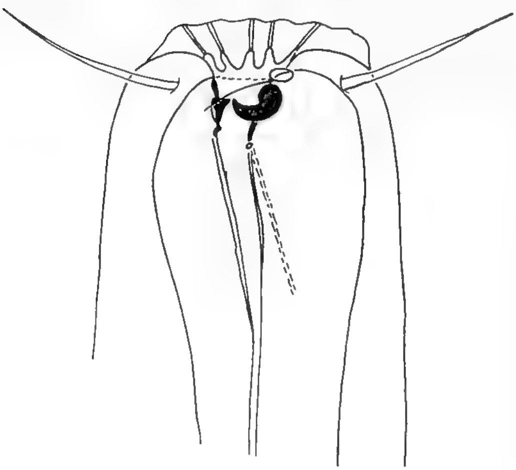
Females. Body breadth: 0·032; 0·038; 0·036. Oesophagus length: 0·133; 0·120; 0·170. Diameter of head: 0·018; 0·012; 0·016. Lengths of cephalic setae: 0·006; 0·007; 0·006. Length of oesophageal bulb: 0·024; 0·032; 0·033. Breadth of oesophageal bulb: 0·019; 0·021; 0·023. Nerve ring from the anterior end: 0·064; 0·064; 0·066. Excretory pore not seen. Tail length: 0·067; 0·099; 0·10. Anal diameter: 0·024; 0·021; 0·027. Distance of vulva from the anterior end: 0·32; 0·34; 0·37. Size of eggs: 0·051 × 0·025.

Cuticle

The cuticle is marked by rows of small punctations which appear to be restricted to the lateral field. Anteriorly these markings take the form of small dots (Text-fig. 38, *a*) which become progressively longer posteriorly until they are elongate, narrow strips (Text-fig. 38, *a* and *b*) and on the tail they are elongate oblongs (Text-fig. 38, *d*).

The Head and Oesophagus

The head appears to be relatively simple with four setae and, probably, two circles of six papillae each. The mouth opening is bounded by the usual twelve rugae and there are three solid cuticular teeth at the anterior end of the oesophagus (Text-fig. 33). There is a dorso-lateral sense organ present which is generally described as the amphid and is usually described as being spiral in this genus. I am unable to establish this in the present species and the possibility that this is in fact an amphidule (see above, p. 215) must remain. The oesophagus has a distinct posterior bulb with two conspicuous plasmatic interruptions (Text-fig. 39). No eye spots have been



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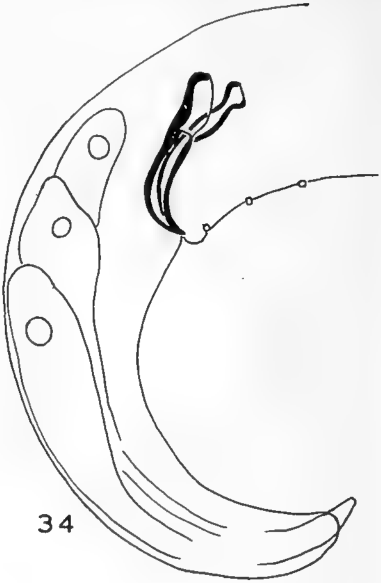

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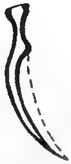

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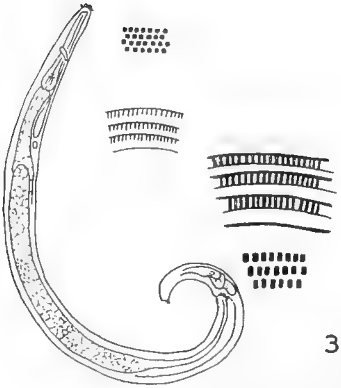

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seen but any pigment which may have been present has almost certainly been washed out since, although the eye spots could be seen in some of the other species considered in this report, in very few cases was pigment present.

Tail

The tail is relatively long and narrow with a prominent spinerette. The caudal glands are located at the level of or posterior to the cloacal or anal openings (Text-figs. 34, 38 and 40).

Male

The spicules are equal in length and identical in structure, sickle-shaped, with relatively stout anterior ends followed by a constriction from which they evenly expand again and then taper evenly to fine sharp posterior ends (Text-figs. 34, 35 and 37). There may be alae but I cannot be sure (see Text-fig. 35). The spicules show some variation in their outline, the most usual shape being as in Text-fig. 35, but there is a tendency for the anterior swelling to be more pronounced. The most extreme example of this is shown in Text-fig. 37. The gubernaculum consists of at least two lateral pieces of which the distal ends are strongly cuticularized and appear at first glance to represent pieces distinct from the rest of the gubernaculum (Text-fig. 34). When viewed from the ventral aspect their greater cuticularization is clearly seen (Text-fig. 36) and the effect is due to the more proximal parts of the gubernaculum being very much less strongly cuticularized ventrally than is the case with the distal parts. I am unable to establish the presence of a median piece to the gubernaculum. There are three small median, ventral supplements anterior to the cloacal opening (Text-figs. 34 and 36) and there is a single testis (Text-fig. 38).

Female

The reproductive system consists of two opposed uteri with associated opposed, reflexed ovaries without obvious oviducts. The vulva opens almost exactly at the middle point of the body length (Text-fig. 40).

Discussion

This species is very similar to what Daday (1901), Micoletzky (1924) and Wieser (1954*b*) call *Chromadora* or *Chromadorina laeta* (de Man, 1876) and keys out to this species in Wieser's (1954*b*) key. Micoletzky (1924) considers *Chromadorina obtusa* Filipjev, 1918, the type species of *Chromadorina*, to be indistinguishable from *Chromadora laeta* so that *C. laeta* becomes the name of the type species. However, de Man's figures and description of *C. laeta* leave much to be desired; the figure of the male tail showing the gubernaculum and (?) the spicules is particularly poor.

FIGS. 33–40. *Chromadorina demani* sp. nov. Fig. 33. Lateral view of head with the dorsal surface to the right. Fig. 34. Male tail from the lateral aspect. Fig. 35. Typical spicules from the right. Fig. 36. Ventral view of spicules and gubernaculum showing the three pre-coacal supplements. Fig. 37. An extreme variant of the spicule form, from the right. Fig. 38. Entire male from the right. *a, b, c, d*—detail of cuticular structure: *a*—just posterior to the head; *b*—just posterior to the posterior end of the oesophagus; *c*—about the middle of the body; *d*—on the tail. Fig. 39. Lateral view of the oesophagus. Fig. 40. Entire female from the left.

In fact, I cannot accept that if there should be, as I believe there are, at least two very similar species that either could possibly be referred to *C. laeta* on the basis of the description given by de Man. I therefore propose that *Chromadora laeta* de Man, 1876, be treated as a *species dubia*. This action leaves *Chromadorina obtusa* as the name for the species described by Filipjev, a species which Micoletzky (1924) believed he had found, and redescribed as a synonym of *C. laeta*. However, the shape of the spicules and the gubernaculum in Micoletzky's figure of the male tail does not correspond with that shown by Filipjev and I cannot accept that the species described by the former author is the same as that studied by the latter. *C. obtusa* is, according to Filipjev's figure, characterized by spicules which are roughly the same width along their entire lengths and which end posteriorly in rather massive points while in *C. laeta* of Micoletzky the spicules narrow evenly along their lengths and end posteriorly in sharp, fine points. In addition, the shape of the gubernaculum, viewed from the lateral aspect, is totally different. In *C. obtusa* it is roughly the same width all along its length and is composed of one distinct plate while in *C. laeta* of Micoletzky it is drawn as very much thinner proximally than it is distally. Both these figures could be inaccurate (that of Micoletzky almost certainly is, since I suspect that he has failed to see the poorly cuticularized ventral sheet which is developed on the proximal end of the gubernaculum in *C. demani*) but the differences in the shape of the spicules appear to be valid.

C. demani differs from both these species, particularly, in the shape of the spicules in which the swelling near the proximal end is very characteristic and also, although this may be less reliable, in the shape of the gubernaculum. This means that the species reported and described by Micoletzky (1924) is left without a name and I propose for it the name *C. micoletzkyi* nom. nov. pro *Chromadorina laeta* of Micoletzky, 1924. *C. laeta* of Daday (1901) is very similar to *C. demani* at least in the form of the spicules but the spicule is shown to be relatively wide distally. The gubernaculum, however, as figured is totally different in outline from that in *C. demani* but, in view of the poor description, I propose that *C. laeta* of Daday, 1901, be treated as a *species dubia*. *C. laeta* of Wieser, 1954*b*, is also generally like the species considered here but the form of the gubernaculum, as figured, is totally different from that shown for all the other records and I propose to treat *C. laeta* of Wieser, 1954*b*, as a *species inquirenda*.

Euchromadora gaulica sp. nov.

Material Studied

3 ♂, 5 ♀, B.M. (N.H.), Reg. Nos. 1961.227–236. Holotype ♂, 1961.235.

	Ratios				
	a	*b*	*c*	V	Body length
Males . .	26·5	6·4	8·8	—	1·67
	32·9	6·6	8·7	—	1·58
	26·1	5·3	8·5	—	1·33
Females . .	36·6	6·0	9·4	51·2	2·34
	35·8	5·9	9·2	49·2	2·50
	40·0	6·4	11·6	48·9	2·80

Measurements (in mm.; in order of body lengths)

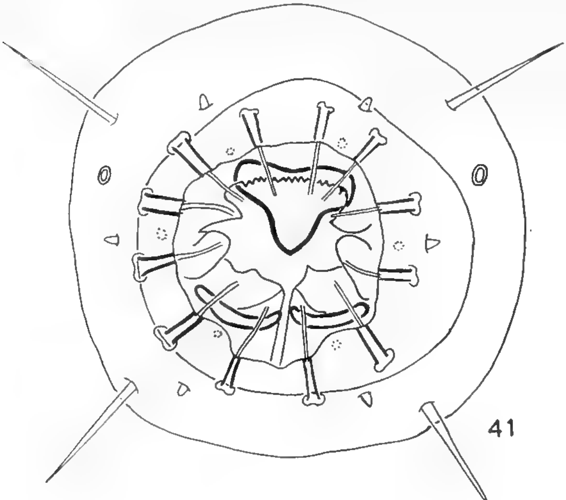
MALES. Body breadth: 0·063; 0·048; 0·051. Oesophagus length: 0·26; 0·24; 0·25. Diameter of head: 0·021; 0·028; 0·025. Nerve ring from anterior end: ... ; 0·110; 0·098. Excretory pore not seen. Tail length: 0·19; 0·18; 0·15. Cloacal diameter: 0·038; 0·034; 0·040. Length of spicules: 0·048; 0·053; 0·058. Length of gubernaculum: 0·031; 0·035; 0·032. Length of gubernaculum as a percentage of the length of the spicules: 67; 66; 67. Width of lateral fields at mid-point of body: 0·039; 0·036; 0·037. The striations on the 1·33 mm. long specimen are 0·003 mm. apart immediately posterior to the head, 0·004 mm. apart at the mid-point of the body length and 0·003 mm. apart at the cloaca.

FEMALES. Body breadth: 0·064; 0·067; 0·070. Oesophagus length: 0·39; 0·41; 0·44. Diameter of head: 0·032; 0·034; 0·035. Nerve ring not seen. Excretory pore not seen. Tail length: 0·25; 0·26; 0·24. Anal diameter: 0·055; 0·052; 0·055. Vulva from anterior end: 1·20; 1·18; 1·37. Width of lateral fields at the mid-point of body: 0·054; 0·056; 0·057. The striations on the 2·34 mm. specimen are 0·003 mm. apart immediately posterior to the head, 0·004 mm. apart at the level of the posterior end of the oesophagus, 0·005 mm. apart at the level of the vulva and 0·004 mm. apart at the level of the anus. The greatest number of eggs present in one specimen is twenty-three.

Cuticle

The structure of the cuticle in the genus *Euchromadora* has been discussed at some length by de Man (1886) and by Steiner & Hoeppli (1926). It is highly modified with a complex series of blocks and rods which vary from one part of the body to another in shape and distribution. Anteriorly the markings in *E. gaulica* are large hexagonal blocks separated by striations (Text-fig. 44) which show a distinct double effect so that more than one layer appears to be present when the cuticle is studied in optical section. In addition the blocks appear to be linked together by a network of narrow markings. More posteriorly the markings become more elongate and, about the level of the posterior end of the oesophagus become restricted to the lateral, dorsal and ventral surfaces only. The zones of markings dorsally and ventrally become increasingly narrow until they disappear completely about one-third along the body (see also de Man, 1886). The zone of markings laterally continues along the entire length of the body. The markings are continuous around the body at the posterior end as they are anteriorly.

In addition to the block-like markings there are what I propose to call " Lateral Plates " which occur on the lateral sides of the body from about the posterior end of the oesophagus posteriorly. These plates, which lie deep within the cuticle, are straight on their posterior edges and convex on their anterior edges, along the anterior half of the body. They lie one between each pair of cuticular striations and correspond to each row of large block-like cuticular markings (Text-figs. 46 and 47). (The double markings shown represent an attempt to demonstrate the appearance produced by the two layers of cuticular block-like markings.) They



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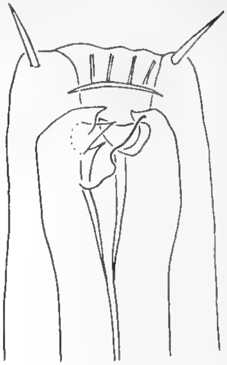

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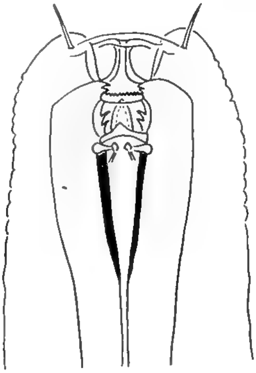

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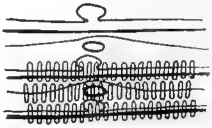

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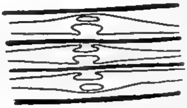

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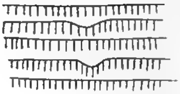

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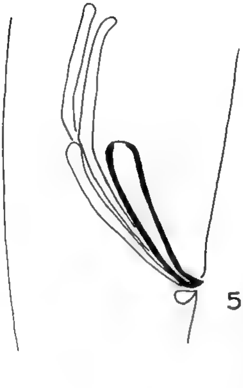

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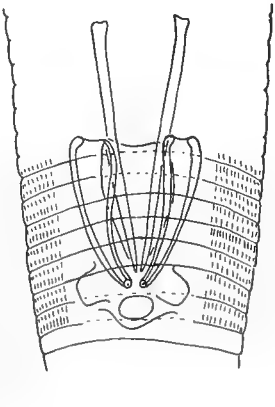

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are pierced by a small, oval hole anteriorly and posteriorly they bear a similar opening which is, however, incomplete along its posterior edge (Text-fig. 47). On the posterior half of the body the conditions are reversed (Text-fig. 47). That is, the convex edge of the lateral plate is directed posteriorly and the straight edge is directed anteriorly. The change from one form of lateral plate to the other occurs almost exactly at the mid-point of the body length where one lateral plate is convex on both edges, carries two open holes and has no completely enclosed holes (Text-fig. 47). In the females this change occurs almost exactly opposite the vulvar opening.

Head and Oesophagus

The head is very blunt and bears four longish setae and six sessile papillae. There may be an inner circle of six smaller sessile papillae but I cannot be certain of their occurrence (Text-fig. 41). The amphids are elongate, lateral slits which lie slightly posterior to the origins of the cephalic setae (Text-fig. 42). There are in addition dorso-lateral terminal pore-like structures, the amphidules, which are discussed above (p. 215). The mouth opening is surrounded by the usual fringe of cuticle which is supported by twelve rugae. There is a very complicated arrangement of tooth-like structures within the buccal cavity. Dorsally there is a very large, wholly cuticular tooth with a massive base which expands laterally when viewed *en face* (Text-fig. 41). This large tooth is set fairly far posteriorly within the buccal cavity (Text-figs. 42 and 43) and the extreme anterior dorsal edge of the oesophagus carries a series of small denticle-like structures (Text-figs. 41 and 43). Laterally, viewed *en face*, at the extreme anterior end the oesophagus is modified into two pairs of cuticular tooth-like structures while ventrally there is a single pair of long, wholly cuticular, curved bars below (i.e. posterior to) which is a further pair of cuticular tooth-like structures. The distribution of these various structures is shown in Text-figs. 41, 42 and 43.

The oesophagus expands slightly posteriorly but there is no definite bulb.

Tail

The tail in both sexes is rather long and narrow with a distinctly set-off spinerette. The caudal glands lie posterior to the cloacal opening or anus.

Male

The spicules are equal in length, identical in structure, non-alate and rather sharply curved so that they are slightly elbow-like when viewed from the lateral aspect

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FIGS. 41–51. *Euchromadora gaulica* sp. nov. Fig. 41. *En face* view of head. Note the amphidules and the elaborate arrangement of teeth and cutting blades at the anterior end of the oesophagus. Fig. 42. Lateral view of head with the dorsal surface to the right. Fig. 43. Dorsal view of head. Figs. 44–49. Detail of the structure of the lateral cuticle. Fig. 44: just posterior to the head; Fig. 45: about the level of the posterior end of the oesophagus; Fig. 46: just anterior to the middle of the body; Fig. 47: the point of change where the lateral plates become directed posteriorly; Fig. 48: about the level of the anus or the cloacal opening; Fig. 49: on the tail. Fig. 50. Lateral view of spicules and gubernaculum. Fig. 51. Ventral view of spicules and gubernaculum.

(Text-fig. 50). The gubernaculum is slightly more than half the length of the spicules. The lateral flanking pieces of the gubernaculum are bluntly rounded proximally and narrow evenly toward the distal ends where they are very slightly turned ventrally (Text-figs. 50 and 51). There is only one testis.

Female

The reproductive tract is double with opposed, non-reflexed, ovaries which lead into large uteri containing relatively large numbers of eggs. The eggs are spherical, about 0·060 mm. in diameter.

Discussion

This species falls into the group mentioned by Brunetti (1952) and by Wieser (1955) which is characterized by an oesophagus which has no posterior bulb and with equal and identical spicules in the male. There are currently four species which fall into that group, *E. striata* (Eberth, 1863), *E. africana* Linstow, 1908, *E. permutabilis* Wieser, 1954 and *E. tokiokai* Wieser, 1955. Of these species *E. striata* is characterized by stout spicules, such as are figured by Eberth (1863), Filipjev (1918) and by Brunetti (1952) but not by Wieser (1952 and 1954), and a gubernaculum with a long, sharply-pointed, markedly bent, non-dentate distal end. *E. africana*, although recorded since the original description (Schuurmans Stekhoven, 1950 ; Steiner, 1918), cannot really be identified from the very poor description given by Linstow (1908) nor, with certainty, from either of the later redescriptions. I therefore propose to treat *E. africana* as a *species dubia*. *E. permutabilis* appears to be characterized by a gubernaculum in which the lateral pieces are evenly pointed proximally and sharply pointed and markedly bent distally, while *E. tokiokai* has lateral pieces to the gubernaculum which are blunt proximally and sharp-pointed with very little curvature distally. In both the latter species the gubernaculum is about 66% of the lengths of the spicules while in *E. striata* it is about 50%. *E. gaulica* is, therefore, characterized by equal and identical spicules, a gubernaculum which is about 60% of the length of the spicules and is only very slightly curved at the distal end. In addition the form of the lateral plates with the two pore-like holes appears to be distinctive. This latter character may be of the greatest systematic importance but it is impossible to be sure on the basis of the available descriptions (see the description of *E. tyrrenica* which follows). The *E. africana* of Schuurmans Stekhoven (1950) may be conspecific with *E. gaulica* but the poverty of the description is such that this cannot be established and I treat this record as that of a *species dubia*.

Euchromadora tyrrenica Brunetti, 1952

Material Studied

1 ♂ which was later lost.

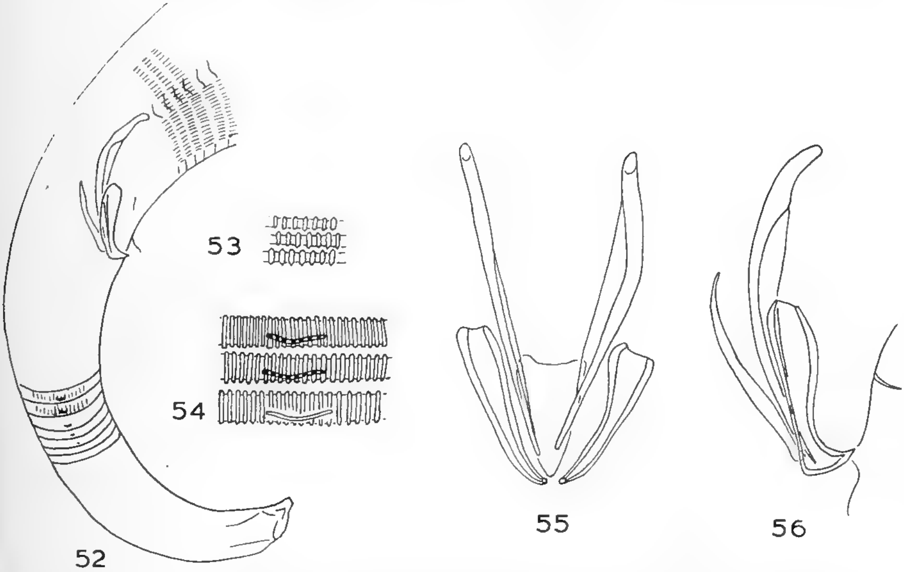
Ratios			
a	*b*	*c*	Body length
25·8	5·5	8·1	1·54

Measurements (in mm.)

Oesophagus length: 0·28. Head diameter: 0·032. Length of cephalic setae: 0·009. Nerve ring from anterior end: 0·114. Excretory pore from anterior end: 0·140. Tail length: 0·19. Cloacal diameter: 0·046. Spicule length: 0·053. Gubernaculum: 0·031. Width of lateral fields: at head, 0·003; at posterior end of oesophagus, 0·005; at middle of body, 0·005; at anus, 0·004; on tail, 0·003.

Cuticle

The cuticular markings are almost exactly the same as those on *E. gaulica* (Text-figs. 53 and 54) but there are no distinct lateral plates although there are what appear to be homologous, slightly curved structures present. These are apparent as slightly curved rods (? thickened plates in optical section) which are directed anteriorly over the anterior half of the body and posteriorly over the posterior half (Text-fig. 54). There are no distinct lateral holes associated with these rods/plates as in *E. gaulica*.



FIGS. 52–56. *Euchromadora tyrrenica* Brunetti, 1952. Fig. 52. Male tail from the lateral aspect. Fig. 53. Cuticular pattern just posterior to head. Fig. 54. Cuticular pattern on the posterior half of the body. Fig. 55. Ventral view of spicules and gubernaculum. Fig. 56. Lateral view of spicules and gubernaculum, from the right.

Head and Oesophagus

The head appears to be identical in structure with that of *E. gaulica* but the amphids have not been seen. The oesophagus swells to form a distinct posterior bulb, without valvular structures.

Tail

The tail is relatively long and rather stout.

Male

The spicules are equal in length and identical in structure. They appear to carry very narrow alae, which are not figured by Brunetti (1952) but may have been overlooked (Text-fig. 56). The lateral pieces of the gubernaculum are stout with blunt proximal ends and rather massive distal ends which terminate in very sharp points but bear no denticles (Text-figs. 52 and 56). The gubernaculum is 58% of the spicules in length. There is a single testis.

Discussion

This specimen is very similar to *E. tyrrenica* and differs markedly from the description given by Brunetti (1952) only in the presence of narrow alae on the spicules, which could have been overlooked very easily. The slight markings on the lateral fields which probably correspond to the lateral plates of *E. gaulica* are rather characteristic although they also were probably overlooked by Brunetti.

Hypodontolaimus colesi sp. nov.

Material Studied

1 ♂, 1 ♀ (+ 1 very badly damaged ♀ used for an *en face* preparation). B.M. (N.H.), Reg. Nos. 1961.354–355. Male selected as holotype, 1961.354.

	Ratios				
	a	*b*	*c*	V	Body length
Male . .	26·5	7·3	9·2	—	0·98
Female . .	19·4	7·3	9·1	49·5	1·03

Measurements (in mm.)

MALE. Body breadth: 0·037. Oesophagus length: 0·134. Head diameter: 0·020. Oesophageal bulb, length: 0·025 (approx.); breadth: 0·022. Cephalic setae length: 0·022. Body setae: 0·031–0·047. Nerve ring from anterior end: 0·076. Excretory pore not seen. Spicule length: 0·039. Gubernaculum length: 0·026. Tail length: 0·107. Cloacal diameter: 0·030. Tail length/cloacal diameter: 3·57.

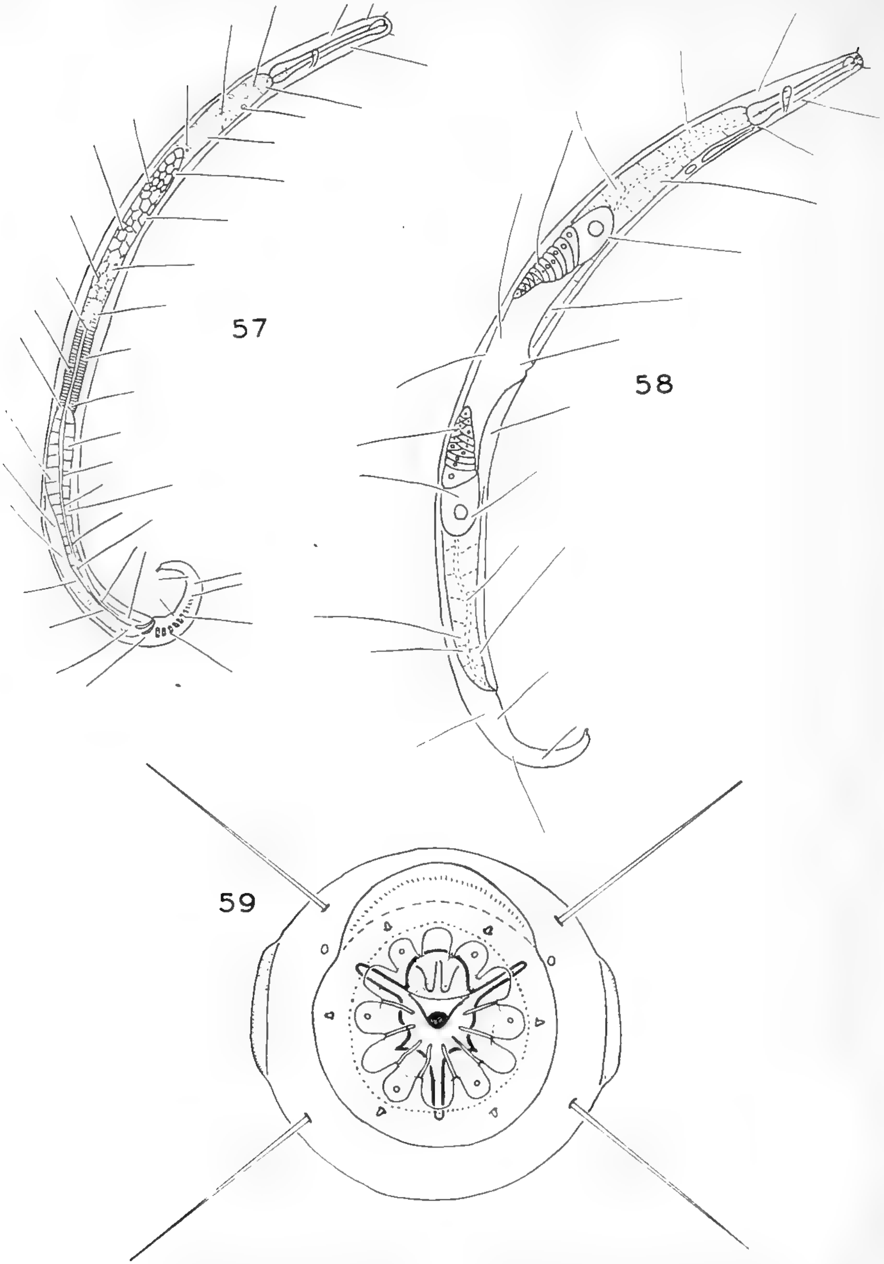
FEMALE. Body breadth: 0·053. Oesophagus length: 0·141. Head diameter: 0·021. Oesophageal bulb, length: 0·042 (approx.); breadth: 0·037. Nerve ring from the anterior end: 0·078. Excretory pore not seen. Tail length: 0·113. Anal diameter: 0·026. Tail length/anal diameter: 4·4. Vulva from the anterior end: 0·51.

Cuticle

The cuticle is differentiated laterally by two files of large dots separated by lateral bars (Text-fig. 60) which are about 0·005 mm. wide just posterior to the head, lengthening to about 0·009 mm. about the posterior end of the oesophagus and remaining about this width until just anterior to the anus or cloacal opening where they shorten, being about 0·005 mm. wide at the level of the anus or the cloacal opening. The bars are about 0·002 mm. apart antero-posteriorly. The files of large dots are flanked by rows of smaller markings which extend laterally for about the same distance as the lengths of the lateral bars, that is, the total lateral differentiation equals approximately three times the length of the lateral bars at any given level. The markings flanking the large dots are rather round in shape anterior to the posterior end of the oesophagus (Text-fig. 62) and become relatively closer together, antero-posteriorly, anteriorly until the differentiation ceases just posterior to the cephalic setae (Text-fig. 60). In the middle region of the body the rows of the lateral differentiation are relatively far apart and the markings are rather small (Text-fig. 63) while from about the level of the anus, or the cloacal opening, the rows of markings become increasingly closer together, more prominent and longer (Text-fig. 64). The zone of lateral differentiation is raised above the general surface of the body (Text-fig. 59). There are two files of very long, thin setae running almost the full length of the body. These files of setae arise from just outside the files of large markings (Text-figs. 63, 64 and 65) and some of these larger markings are replaced by the openings of lateral pores (Text-figs. 63 and 64) along the middle part of the body length. These pores are not the bases of broken setae since the setae always arise lateral to them. The lateral bars appear to be further modified by lateral plates which are directed anteriorly over the whole length of the body (Text-figs. 63, 64 and 65). These structures, which become progressively less prominent anterior to the posterior end of the oesophagus until they disappear about the level of the nerve ring, appear to be comparable to the lateral plates found in species of *Euchromadora* (see p. 00). Such plates and the lateral pores do not appear to have been reported from species of this genus before.

Head and Oesophagus

The head is rather blunt and evenly rounded and bears four long, thin setae in an outer circle, six slightly setose papillae in an intermediate circle and an inner circle of six small sessile papillae (Text-figs. 59 and 60). Thus there are only four long setae, not ten as has been reported for *H. schuurmansstekhoveni* Gerlach, 1951*a* and *H. setosa* (Bütschli, 1874). The mouth opening is large and roughly circular, surrounded by the usual fringe of cuticle which is supported by twelve rugae (Text-fig. 59). The amphids are elongate lateral slits lying about the level of the origins of the four long setae (Text-fig. 60) and there is a pair of what appear to be amphidules dorso-lateral in position (Text-fig. 59). The presence of the amphidules is quite certain but I cannot be absolutely certain about the presence of the slit-like amphids. There is a very prominent S-shaped dorsal tooth and the dorsal sector of the anterior end of the oesophagus is very strongly swollen by the muscles which



FIGS. 57–59. *Hypodontolaimus colesi* sp. nov. Fig. 57. Entire male from the right. Fig. 58. Entire female from the right. Fig. 59. *En face* view of head. Note the dorsal development of the oesophageal musculature and the presence of the amphidules.

supply it (Text-figs. 59 and 60). In optical section, *en face*, it can be seen that this dorsal swelling forms a distinct bump projecting dorsally from the circular section of the more ventral part of the oesophagus (Text-fig. 59). In addition to the large dorsal tooth there are two small, wholly cuticular denticles which are borne on the ventro-lateral sectors of the oesophagus near their anterior ends. Anterior to the large dorsal tooth is a thickened cuticular plate-like structure, in lateral view, which when studied *en face* is seen to be paired (compare Text-figs. 59 and 60). The lumen of the oesophagus at the anterior end is not simply tri-radiate but each ventro-lateral sector is partly divided into two lobes very similar in appearance to the condition in *Euchromadora* (see Text-fig. 59), but without the complex arrangement of ridges and teeth so characteristic of that genus. The oesophagus swells evenly at the posterior end but does not develop into a distinct posterior bulb such as that figured by Gerlach (1951*a*) as occurring in *H. schuurmansstekhoveni*, but there is a slight thickening of the cuticle lining the posterior lumen of the oesophagus (Text-fig. 61).

Tail

The tail is rather stout in both sexes and does not extend into a long, narrow terminal zone as in *H. schuurmansstekhoveni*. The spinerette opens through a terminal duct which projects from the ventral part of the tail (Text-fig. 65) and in this respect also it is different from *H. schuurmansstekhoveni*.

Male

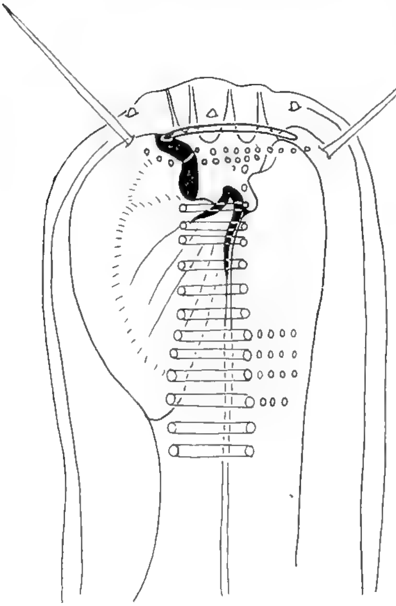
The spicules are equal in length and identical in structure, about the same width along most of their lengths. They are evenly curved and narrow very rapidly just before their posterior ends so that they terminate in long narrow points (Text-fig. 65). The gubernaculum is simple, without any apophysis, and bears slight lateral flanges just before its posterior end, flanges which slightly enfold the spicules (Text-fig. 65). There are no pre-cloacal supplements nor special setae. There is a single testis (Text-fig. 57).

Female

The reproductive apparatus is double with opposed, reflexed ovaries which lead into large uteri. The female specimen contains no eggs (Text-fig. 58).

Discussion

This species is most similar to *Hypodontolaimus schuurmansstekhoveni* Gerlach, 1951*a*, from which it differs in the form of the posterior end of the oesophagus, the shape of the terminal part of the tail, the short circle of intermediate setose papillae on the head and in the form of the spicules with a distinct swelling just anterior to the posterior end.



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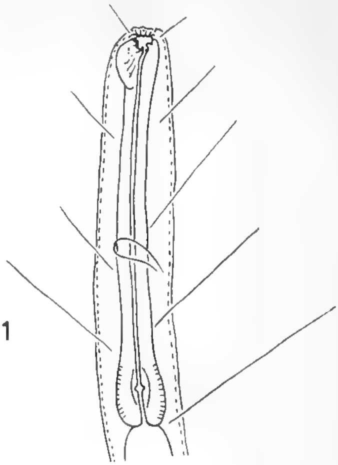

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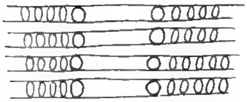

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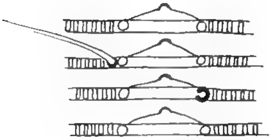

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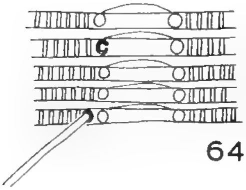

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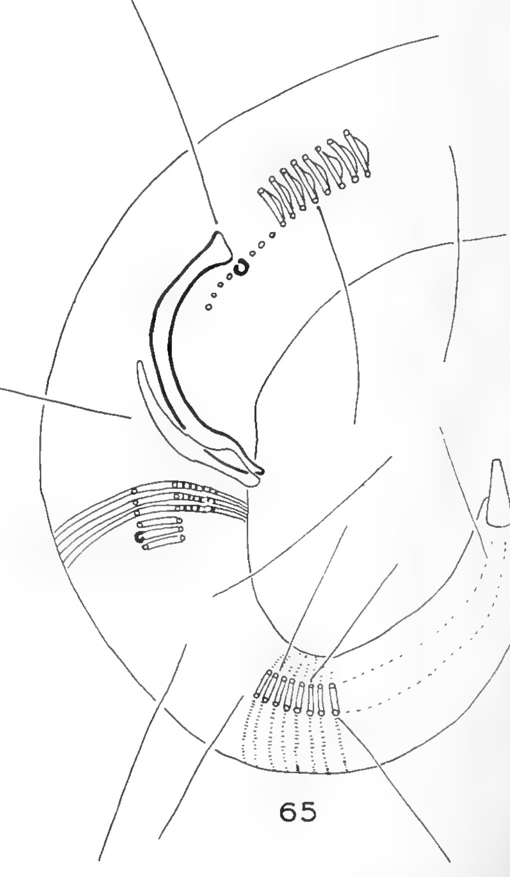

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Paracanthonchus barka sp. nov.

Material Studied

1 ♂, B.M. (N.H.), Reg. No. 1961.353. Holotype.

Ratios			
a	*b*	*c*	Body length
30·7	4·8	10·3	0·86

Measurements (*in mm.*)

Body breadth : 0·028. Oesophagus length : 0·180. Head diameter : 0·015. Length of long cephalic setae : 0·006. Length of short cephalic setae : 0·005. Diameter of amphids, left : 0·008 ; right : 0·007. Distance of amphids from anterior end : 0·005. Tail length : 0·074. Cloacal diameter : 0·025. Tail length/cloacal diameter : 3·0. Gubernaculum length : 0·018. Spicule length : 0·019. Nerve ring from anterior end : 0·089 (?). Excretory pore from anterior end : 0·024 (?).

The single specimen is in a rather poor condition but it has been possible to see all the important systematic characters. The amphids lie fairly far posterior to the anterior end of the body, the distance as measured probably does not give a true impression as the anterior end of the body appears to be somewhat invaginated (Text-fig. 66) so that the inner setae have not been seen. The right amphid has four and a half spirals and the left has five and a half. The punctations on the cuticle start slightly posterior to the bases of the cephalic setae and are larger and more prominent laterally. There are the usual rows of pores for the lateral glands. The oesophagus is relatively stout, expanding slightly towards the posterior end. The measurements given above for the positions of the nerve ring and excretory pore are open to some doubt as I am not sure that I really did see these structures.

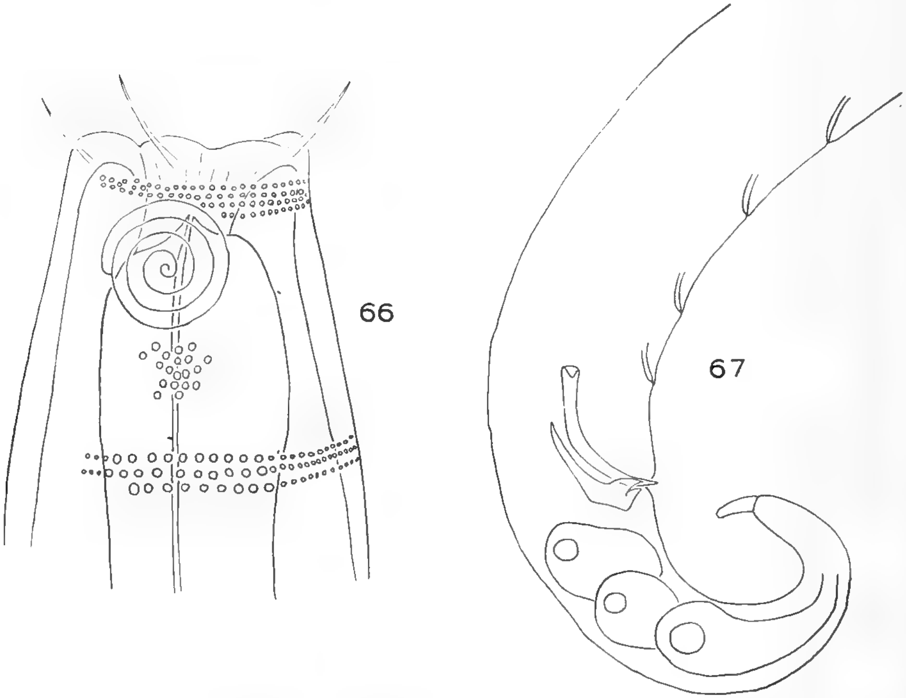
The tail is fairly stout, narrowing evenly posteriorly to terminate in a rather long spinerette. The caudal glands lie posterior to the cloacal opening. There are four pre-cloacal tubuli on the mid-ventral surface of the body anterior to the cloacal opening (Text-fig. 67).

The spicules are equal in length and identical in structure, curved, non-alate and terminate posteriorly in simple points. The gubernaculum ends distally in a rather sharp, rounded point, is bent about half-way along its length and expands very rapidly along approximately the proximal half of its length. It remains roughly the same width all along the distal half of its length and ends distally in a bluntly expanded mass which is developed on the edge nearer the spicules into two small, sharp teeth (Text-fig. 67).

FIGS. 60–65. *Hypodontolaimus colesi* (continued). Fig. 60. Lateral view of head with the dorsal surface to the left. Fig. 61. Structure of the oesophagus. Fig. 62. Cuticular pattern on the lateral surface just posterior to the head. Fig. 63. The same about the middle of the body. Fig. 64. The same posterior to the anus or cloacal opening. Note in this and the previous figure the lateral pores which are outlined by a very heavy solid black line and the way in which the lateral setae originate outside the lateral differentiating bars. Fig. 65. The male tail from the lateral aspect

Discussion

As Wieser (1954) points out, the best characters for the delimitation of genera and, to some extent, species in the subfamily Cyatholaiminae are those afforded by the structure of the gubernaculum and in this respect *P. barka* differs from all the previously described species of *Paracanthonchus*. It is most similar to the species grouped by Wieser (1954) in his group " B " (Wieser, 1954 : 16) but differs from them all in the outline of the gubernaculum and the relative simplicity of the proximal end of that structure. *P. serratus* Wieser, 1959, possesses a gubernaculum which is somewhat similar to that of *P. barka* in general outline but it differs in having the broad terminal plate-like part serrated. The gubernaculum of *P.* [=*Harveyjohnstonia*] *kartanum* (Mawson, 1953) is also a little like that of *P. barka* but also differs in having the blade-like part serrated.



Figs. 66–67. *Paracanthonchus barka* sp. nov. Fig. 66. Lateral view of head with the dorsal surface to the left. Fig. 67. Lateral view of male tail from the right.

Wieser (1959) considers *Harveyjohnstonia* Mawson, 1953 to be a synonym of *Paracanthonchus* and with this I concur.

Sphaerocephalum chabaudi sp. nov.

Material Studied

5 ♂, 9 ♀, 16 larvae. B.M. (N.H.), Reg. Nos. 1961.284–314. Holotype male, Reg. No. 1961.284.

This species is long and thin with a blunt anterior end and is easily recognized when seen alive. It is also easy to pick out when killed with heat as it coils up into a fairly tight spiral (Text-fig. 72). The cuticle is thin and bears no obvious striations.

Larva I

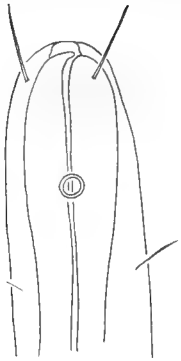
The body of the only specimen of this larval stage is 0·78 mm. long by 0·016 mm. wide; the oesophagus, which is identical with that of the adults in structure is 0·016 mm. long; the diameter of the head is 0·015 mm.; the cephalic setae are 0·008 mm. long; the amphid is 0·005 mm. in diameter and lies 0·018 mm. from the anterior end; the tail is 0·076 mm. long and the nerve ring lies 0·074 mm. from the anterior end. $a = 48{\cdot}7$; $b = 6{\cdot}0$; $c = 10{\cdot}3$.

The most startling feature of this larval stage (? second) is that the amphid is a simple circular depression without any central elevation or any indication of its being spiral and that the head bears only four long setae (Text-fig. 68). Otherwise the head is identical with that of the adult. That is, the buccal cavity is short and the extreme anterior end of the dorsal sector of the oesophagus projects over the ventro-lateral sectors (see below, p. 276). There are a few longish setae scattered over the anterior end of the body.

Larva II

In this larval stage(s) two specimens have been measured. The body is 1·04 mm. long in one and 2·61 mm. long in the other; they are 0·027 mm. and 0·048 mm. wide respectively; the oesophagus is 0·180 mm. and 0·280 mm. long; the cephalic setae are 0·008 mm. and 0·012 mm. long in the shorter and 0·009 mm. and 0·014 mm. long in the longer; the tail is 0·087 mm. and 0·160 mm. long; the head is 0·021 mm. and 0·031 mm. in diameter; the amphids are 0·006 mm. and 0·008 mm. in diameter and lie 0·015 mm. and 0·019 mm. from the anterior end; the nerve ring is 0·092 mm. and 0·149 mm. and the excretory pore is 0·058 mm. and 0·113 mm. from the anterior end; the anal diameter is 0·020 mm. and 0·041 mm. $a = 38{\cdot}5$ and $54{\cdot}4$; $b = 5{\cdot}5$ and $9{\cdot}3$; $c = 12{\cdot}0$ and $16{\cdot}3$.

It is probable that these specimens represent different larval stages, the third and the fourth (?). Structurally, however, they are identical. The head bears two circles of longish setae and there are several long setae scattered over the anterior end of the body. The amphid is circular with a distinct central elevation (Text-fig. 69). The structure of the oesophagus and the tail is identical with that found in the adults.



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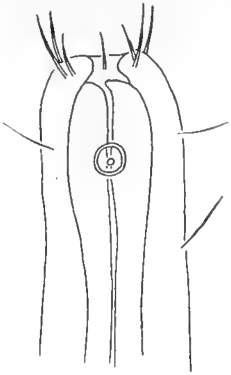

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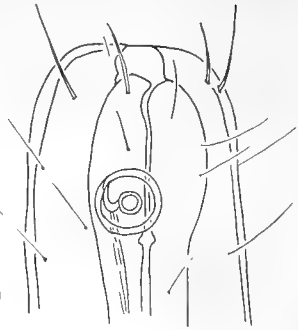

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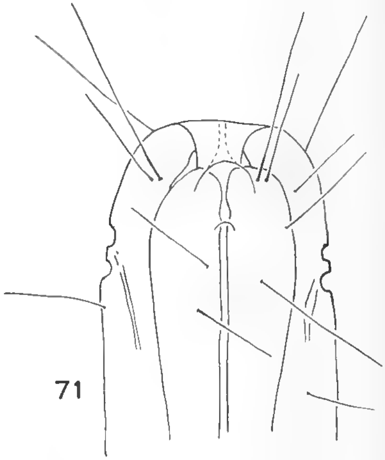

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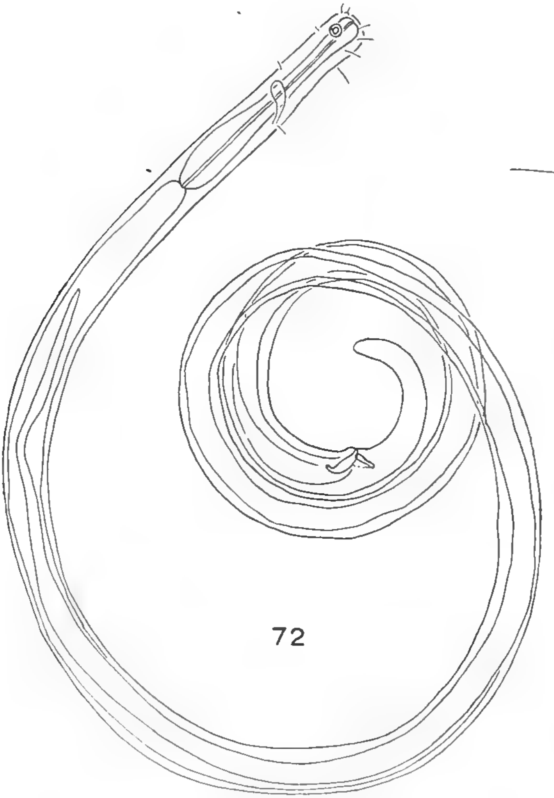

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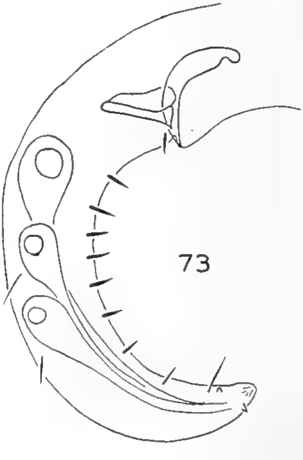

73

Adult

	Ratios				
	a	*b*	*c*	V	Body length
Males . .	73·1	11·4	18·8	—	2·85
	74·1	12·2	18·5	—	3·04
	82·1	15·2	19·6	—	3·20
Females . .	66·7	9·5	16·6	45·5	2·66
	59·1	10·8	20·3	49·8	3·13
	65·5	12·3	26·8	44·7	3·80

Measurements (in mm. ; in order of body lengths above)

MALES. Body breadth : 0·039 ; 0·041 ; 0·039. Oesophagus length : 0·25 ; 0·25 ; 0·21. Diameter of head : 0·026 ; 0·032 ; 0·032. Diameter of amphid : 0·012 ; 0·010 ; 0·011. Nerve ring from the anterior end : 0·126 ; 0·120 ; 0·123. Excretory pore from the anterior end : 0·101 ; 0·097 ; 0·094. Length of spicules : 0·036 ; 0·042 ; 0·041. Length of gubernaculum : 0·020 ; 0·023 ; 0·022. Length of tail : 0·152 ; 0·164 ; 0·163. Cloacal diameter : 0·033 ; 0·042 ; 0·044. The extreme thinness of the cephalic setae makes them very difficult to measure but the long setae appear to be about 0·014 mm. and the short about 0·011 mm. long in all the specimens.

FEMALES. Body breadth : 0·040 ; 0·053 ; 0·058. Oesophagus length : 0·28 ; 0·29 ; 0·31. Diameter of head : 0·034 ; 0·039 ; 0·041. Diameter of amphid : 0·011 ; 0·009 ; 0·014. Nerve ring from anterior end : 0·138 ; 0·133 ; 0·137. Excretory pore from anterior end : 0·118 ; 0·102 ; 0·122. Length of tail : 0·160 ; 0·154 ; 0·142. Anal diameter : 0·036 ; 0·032 ; 0·039. Distance of vulva from anterior end : 1·21 ; 1·56 ; 1·71.

Head and Oesophagus

The head bears an inner circle of six small sessile, inconspicuous papillae and an outer circle of ten long, very thin, setae of which six are short and four are long (Text-fig. 74). Posterior to this circle of ten setae are a number of similar setae which become shorter and less prominent posteriorly and which disappear about the level of the nerve ring (Text-figs. 70 and 71). The amphids are circular but of a crypto-spiral nature with the amphidial nerve entering on the dorsal side. They are about one-third of the corresponding body width in diameter. The small mouth

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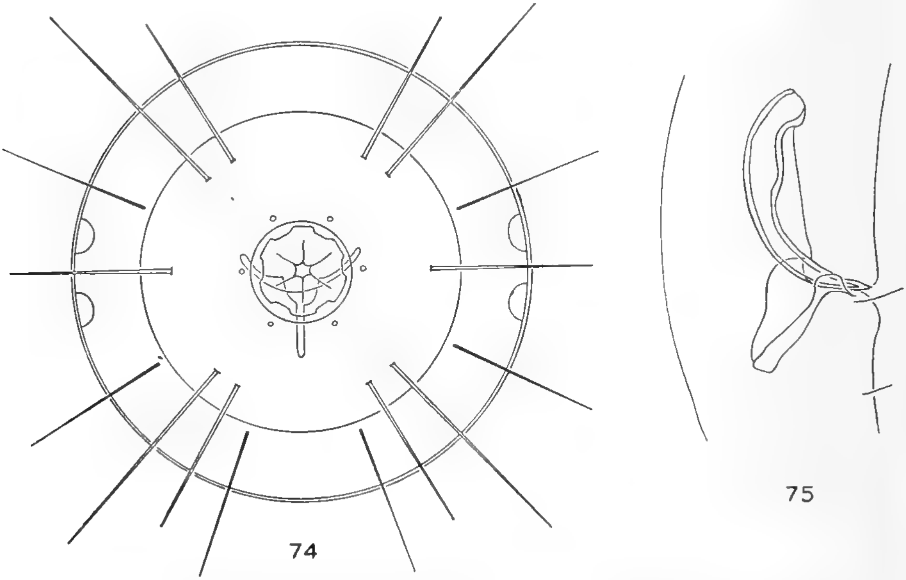
FIGS. 68–73. *Sphaerocephalum chabaudi* sp. nov. Fig. 68. Head of Larva—I with the dorsal side to the left. Note the simple pore-like form of the amphid. Fig. 69. Head of Larva—II, with the dorsal side to the right. Note the central elevation to the amphid. Fig. 70. Head of adult with the dorsal surface to the left. Note the distinctly spiral nature of the amphid with the dorsal innervation. Fig. 71. Head of adult from the dorsal aspect. Fig. 72. Entire male from the right. Fig. 73. Male tail from the lateral aspect.

opening is bounded by six thin lip-lobes which are supported by six processes developed from the anterior edge of the thin cuticular lining of the circular buccal cavity (Text-figs. 71 and 74). The spaces between these processes are very prominent, particularly when the head is studied from the dorsal aspect (Text-fig. 71) and this probably explains the rather strange structures shown by Filipjev (1918) in his figure of the head of *Sphaerocephalum crassicauda* (Filipjev's fig. 75*b*). The dorsal sector of the oesophagus is developed as a lobe which projects ventrally to lie over the paired ventro-lateral sectors and is most obvious in lateral and *en face* views (Text-figs. 70 and 74).



FIGS. 74–75. *Sphaerocephalum chabaudi* (continued). Fig. 74. *En face* view of adult head. Note the six-lobed mouth opening and the way in which the ventro-lateral sectors of the oesophagus are covered by the lobe developed from the dorsal sector. (The cephalic setae are unfilled while the cervical setae are drawn solid black.) FIG. 75. Lateral detail of the spicules and gubernaculum.

The anterior end of the oesophagus is slightly swollen and it broadens evenly from just posterior to the nerve ring but there is no distinct posterior bulb (Text-fig. 72). There is no cardia. The nerve ring lies just posterior to the excretory pore.

Tail

The shape of the tail is the same in both sexes (Text-figs. 72 and 73). It is about the same width along most of its length and ends posteriorly in a blunt tip. The three caudal glands lie posterior to the anus or cloacal opening.

Male

The spicules are equal in length and identical in structure. They are sickle-shaped with distinct swellings on their ventral surfaces over most of the anterior third to half their lengths. Posteriorly they are slightly swollen just before their extreme, sharply pointed, tips (Text-fig. 75). The gubernaculum consists of two side pieces which are directed dorso-posteriorly with blunt posterior ends and which are developed into sharply pointed heads at the ends nearer the cloacal opening (Text-fig. 75). There is a thin, lightly cuticularized plate-like median structure lying between the spicules. The tail bears up to ten pairs of long, thin setae on its ventral surface and a few similar setae are scattered generally over the remainder of its surface (Text-fig. 73). No setae have been seen anterior to the cloacal opening. There is a single testis (Text-fig. 72).

Female

There are two opposed, extended ovaries and there are no obvious oviducts. The eggs, of which up to six have been seen in a single specimen, are long and narrow, 0·113 × 0·037 mm.–0·138 × 0·041 mm. in size. The vulva opens slightly anterior to the middle of the body length, V = 45·5–49·8.

Discussion

This species is similar to *Sphaerocephalum crassicauda* Filipjev, 1918 (the type species of the genus) but differs from it in that Filipjev reported his species, based on one female only, to have only one ovary, but two uteri. This description appears improbable but the position cannot be cleared up until more specimens from the same locality have been studied. At least three further species have been referred to the genus: *S. longicaudatum* Schuurmans Stekhoven, 1935, *S. bulbiferum* Schuurmans Stekhoven, 1943 and *S. hirsutum* Gerlach, 1954. The first two species are described as having distinct cardia (elongate oesophageal-intestinal valves) and such structures are definitely not present in *S. chabaudi*. Of Schuurmans Stekhoven's species the first was described from one female specimen and the second from one juvenile. From the descriptions it is impossible to be sure whether or not these species are congeneric with *S. crassicauda* and *S. chabaudi*. Schuurmans Stekhoven (1935) expresses doubt as to the accuracy of Filipjev's (1918) description and infers that a cardia might have been present but such a structure is definitely not present in my specimens, nor is it mentioned by Gerlach (1954), and I am prepared to accept Filipjev's description as accurate. Further neither of Schuurmans Stekhoven's specimens appears to have the same arrangement of long setae posterior to the head as that found in the other species and I am of the opinion that both *S. longicaudatum* and *S. bulbiferum* should be treated as species *incertae sedis*, at least, and more probably warrant treatment as *species dubiae*.

Gerlach (1954) describes *S. hirsutum* sp. nov. from Banyuls-sur-Mer but he only studied female specimens. His specimens had only four long cephalic setae and he suggests that Filipjev (1918) may have been in error in describing ten on *S. crassicauda* but ten are present on the adults of *S. chabaudi*. The structure of the anterior end of the oesophagus and the buccal cavity also appears to be different in *S. hirsutum*, particularly the form of the dorsal sector of the oesophagus which does not appear to be lobed as in *S. chabaudi*. The two species also appear to differ in the form of the amphid, possibly a less significant character, and are markedly different in the relative lengths of the female tails.

Sphaerocephalum chabaudi is, therefore, distinct in the presence of two ovaries, the form of the head, the number of cephalic setae, the form of the amphids and the relative length of the tail. As this is the first species of the genus in which the male is known the genus *Sphaerocephalum* may be fully diagnosed, thus :

SPHAEROCEPHALUM Filipjev, 1918

Linhomoeidae : anterior end blunt ; papillae of inner circle small and sessile ; outer circles of setae lying at approximately the same level (?), with four of the circle longer than the remaining six ; mouth opening surrounded by six small lip-lobes supported by six prolongations of the lining of the buccal cavity ; dorsal sector of the oesophagus developed as a lobe overlying the ventro-lateral sectors (?) ; amphid circular with one spiral ; oesophagus without posterior bulb or cardia ; long cervical setae present ; tail fairly long and of an even breadth. MALE : spicules relatively massive ; gubernaculum composed of two posteriorly directed lateral apophyses with a plate-like central structure ; no pre-cloacal supplements or setae.

Type species : *Sphaerocephalum crassicauda* Filipjev, 1918.

GEOGRAPHICAL DISTRIBUTION. Mediterranean and Black Seas.

ACKNOWLEDGEMENTS

I wish to express my thanks to the Directeur, M. le Professeur G. Pettit, the Sous-directeur, M. le Dr. (now Professeur) C. Delamare Deboutteville, and the staff of the Laboratoire " Arago ", Banyuls-sur-Mer for the assistance they afforded me during my stay in the laboratory during September, 1959. Without the help and kindness of M. le Professeur Alain G. Chabaud and his family my visit to Banyuls could not have been as valuable as it was and I wish to acknowledge my deep indebtedness to them.

LIST OF NOMENCLATORIAL CHANGES PROPOSED

Chromadora laeta de Man, 1876 = *species dubia.*
Chromadora laeta of Daday, 1901 = *species dubia.*
Chromadorina laeta of Micoletzky, 1924 = *Chromadorina micoletzykyi* nom. nov.
Enoplostoma [= *Enoplus*] *hirtum* Marion, 1870 = *Enoplus quadridentatus* Berlin, 1853.
Enoplus tridentatus Dujardin, 1845 = *species dubia.*
Euchromadora africana Linstow, 1908 = *species dubia.*
Euchromadora africana of Steiner, 1918 = *species dubia.*
Euchromadora africana of Schuurmans Stekhoven, 1950 = *species dubia.*

Eurystomina Filipjev, 1921.
  americana of Chitwood, 1951 = *E. chitwoodi* nom. nov.
  assimile of Gerlach, 1951 = *E. gerlachi* nom. nov.
  assimile of Filipjev, 1918 = *E. filiformis* (in part) and *E. ornata* (in part).
  assimile of Schuurmans Stekhoven, 1943 = (?) *E. gerlachi* (in part) and (?) *E. pettiti* (in part).
  assimilis of Gerlach, 1951 = *E. gerlachi* nom. nov.
  assimilis (de Man, 1876) = *species dubia.*
  bilineata Wieser, 1953 = *species inquirenda.*
  californica Allgén, 1947 = *species dubia.*
  filicaudata Allgén, 1959 = *species dubia.*
  filicolle Allgén, 1959 = *species dubia.*
  filispiculum Gerlach, 1954 = *Gerlachystomina filispiculum* comb. nov.
  froyense Allgén, 1946 = *species dubia.*
  linstowi Allgén, 1959 = *species dubia.*
  lithothamnii Saveljev, 1912 = *species inquirenda.*
  littorale Allgén, 1929 = *species dubia.*
  minutisculae of Timm, 1954 = *E. americana* Chitwood, 1936.
  mirabile Allgén, 1959 = *species dubia.*
  norvegica Allgén, 1947 = *species inquirenda.*
  ornatum of Wieser, 1955 = *E. opthalmophora* (Steiner, 1922).
  ornatum of Chitwood, 1960 = *E. opthalmorphora* (Steiner, 1922).
  ornatum var. *indicum* Micoletzky, 1930 = (?) *E. opthalmophora* (Steiner, 1922).
  paralittorale Timm, 1951 = *species dubia.*
  propinqua Allgén, 1947 = *species dubia.*
  retrocellatum of Wieser, 1953 = *E. chilensis* nom. nov.
  sawayai Gerlach, 1954 = *Gerlachystomina sawayai* comb. nov.
  spissidentata Allgén, 1947 = *species inquirenda.*
  stenolaima of Wieser, 1953 = *E. wieseri* nom. nov.
  stenolaimoides Wieser, 1953 = *species dubia.*
  tenue Marion, 1870 = *E. spectabilis* (Marion, 1870).
  tenuissima Filipjev, 1927 = *species incertae sedis.*
  terricola de Man, 1907 = *species dubia.*
  trichophora Allgén, 1959 = *species dubia.*
  trichura Allgén, 1953 = *species dubia.*
Oncholaimus bollonsi Ditlevsen, 1930 = *species inquirenda.*
Oncholaimus dujardini of Wieser, 1953 and 1955 = (?) *O. steineri* Schuurmans Stekhoven, 1950.
Oncholaimus dujardini of Mawson, 1958 = (?) *O. steineri* Schuurmans Stekhoven, 1950.
Oncholaimus exilis Cobb, 1889 = *species dubia.*
Sphaerocephalum longicaudatum Schuurmans Stekhoven, 1935 = *species incertae sedis.*
Sphaerocephalum bolbiferum Schuurmans Stekhoven, 1943 = *species incertae sedis.*

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ON A COLLECTION OF FRESHWATER GASTROPOD MOLLUSCS FROM THE ETHIOPIAN HIGHLANDS

C. A. WRIGHT AND D. S. BROWN

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LONDON: 1962

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Pp. 285–312 ; *Plates* 8–9 ; *Map* ; 33 *Text-figures*

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ON A COLLECTION OF FRESHWATER GASTROPOD MOLLUSCS FROM THE ETHIOPIAN HIGHLANDS

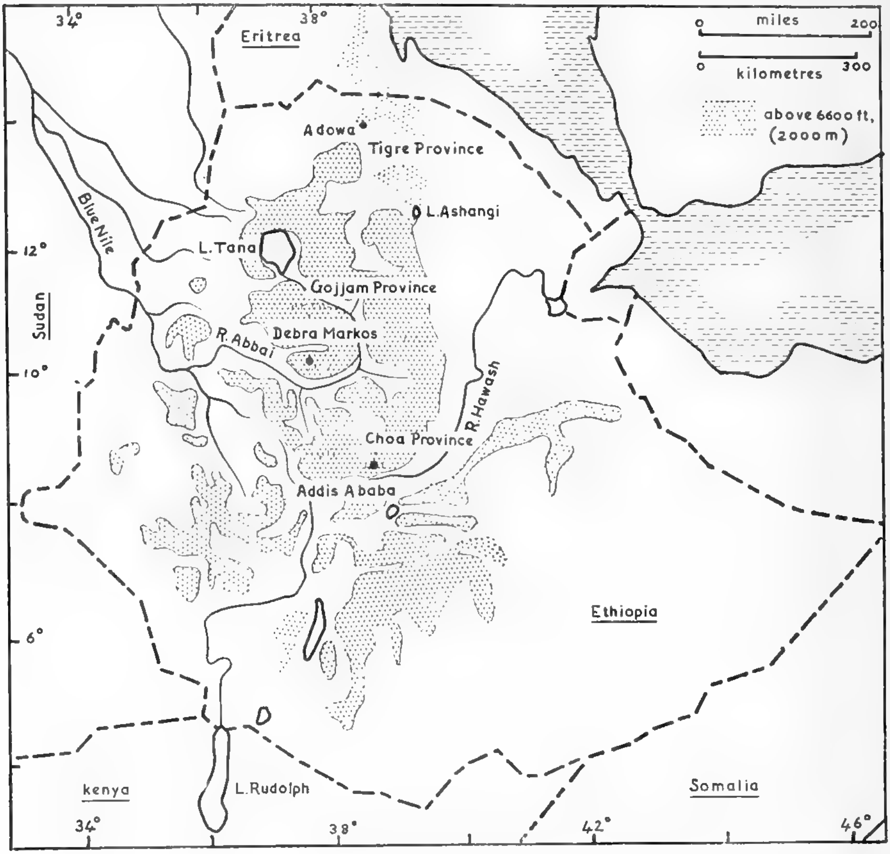
By C. A. WRIGHT & D. S. BROWN

In 1957 the Chokke Mountains which lie to the south of Lake Tana in Gojjam Province, Ethiopia, were visited by a Cambridge botanical expedition, and a zoologist accompanying the expedition, Mr. W. J. Ballantine, undertook to make a collection of land and freshwater molluscs from the area with particular regard to the altitudinal limits of the distribution of *Bulinus forskali*. He brought back an excellent collection of well-preserved specimens, although *B. forskali* was not found, and the freshwater gastropods from that material are the subject of this paper.

The areas covered by the expedition lie to the north-east and south of Debra Markos (37° 43′ E. 10° 20′ N.), the provincial capital, within twenty-five miles of the town which is situated at 8,100 ft. This part of the Ethiopian Highlands is bounded to the east and south by the River Abbai which flows southward out of Lake Tana and further downstream becomes the Blue Nile (Map 1). Collections were made between 7,000 and 12,000 ft. and a list of stations relevant to this part of the collection is given in an appendix to this paper, together with some data on the climate of the area. Locality numbers given in the text refer to this list. The freshwater gastropods collected belong to two families only, the Planorbidae and the Lymnaeidae. The list of synonyms given for each species is primarily a regional one and is not intended to be complete for the whole of Africa.

HISTORICAL

The major work on the Mollusca of Ethiopia is Jickeli's account of the non-marine molluscs of North-east Africa published in 1874. Before this date the eastern part of the highland region had been visited by Blandford (1870) who included descriptions of some molluscs in the general account of his journey. Subsequent authors who have described species or provided records of already known forms from Ethiopia are Bourguignat (1883 and 1885), von Martens (1897), Pollonera (1898), Neuville & Anthony (1906), Piersanti (1940) and Verdcourt (1956 and 1960). There are many accounts of the Mollusca of neighbouring Italian and French Somaliland of which that of Germain (1904) may be specially mentioned. Bacci (1951) has compiled a list of both terrestrial and aquatic species for Abyssinia (Ethiopia and Eritrea) and Italian Somaliland and provides a comprehensive list of references. For this reason only those papers published prior to 1951 which are strictly relevant to the material described are mentioned in the present paper, although an attempt has been made to provide a complete list of work published since that date. A great deal of information concerning the freshwater gastropods of the area is provided by Ayad (1956) who carried out a survey, under the auspices of the World Health Organization, to determine the incidence and mode of transmission of human schistosomiasis.



MAP 1. Ethiopia and surrounding territories (redrawn from Ayad, 1956).

Family PLANORBIDAE

Bulinus sericinus (Jickeli, 1874)

Isidora sericina Jickeli, 1874.
Isidora shackoi Jickeli, 1874.
Isidora sericina var. *harpula* Pollonera, 1898.
Isidora shackoi mut. *minima* Pollonera, 1898.
Bullinus (*Isidora*) *mussolinii* Piersanti, 1940.

LOCALITIES (figures in brackets indicate the numbers of individuals in the samples) 1 (296); 2 (48); 3 (21); 4 (6); 5 (5). Most of the specimens were collected at the margins of streams on vegetation and mud.

There is a good deal of variation in the shell characters both between different population samples and within the same sample. The shells from locality 1 (Pl. 8) have the whorls not markedly inflated or ribbed and the majority are thickly coated with a black deposit. The degree of exsertion of the spire is variable, the more elongated shells (Pl. 8) resembling *Bulinus shackoi*. The ratio of shell length (*l*) to aperture length (*ml*) is plotted against shell length in Text-fig. 1 ; this illustrates that there is a tendency for the ratio to increase with the size of the shell although at any particular size there is a wide variation in the actual values. The aperture is ovate and the columellar margin is widely reflexed, almost closing the umbilicus. From locality 2 the majority of the specimens are empty shells of a reddish-brown colour and more globular in appearance (Pl. 8) than those from locality. 1 The whorls are inflated and, in some of the smaller specimens, there is a marked " shoulder " on the upper part of the whorls. The values of the ratio *l/ml* are included in Text-fig. 1, and are generally smaller than those obtained from locality 1, although there is

TABLE I.—*The Variation in the Ratio Total Length/Aperture Length (l/ml) in Shells of* Bulinus sericinus *from Three Localities*

Locality	Size group* (mm.)	Number of specimens	Mean *l/m*	Range *l/ml*
1	11	2	1·64	1·55–1·74
	10	3	1·49	1·42–1·61
	9	17	1·49	1·37–1·36
	8	26	1·49	1·29–1·78
	7	25	1·46	1·30–1·68
	6	53	1·46	1·30–1·78
	5	66	1·35	1·21–1·61
	4	63	1·32	1·21–1·52
	3	27	1·32	1·21–1·52
	2	1	1·32	—
2	11	1	1·51	—
	10	1	1·49	—
	9	3	1·41	1·30–1·52
	8	8	1·39	1·29–1·48
	7	17	1·35	1·21–1·44
	6	12	1·34	1·27–1·45
	5	1	1·33	—
	4	3	1·23	1·19–1·27
	3	1	1·30	—
3	8	4	1·28	1·22–1·32
	7	2	1·29	1·29–1·30
	6	6	1·36	1·30–1·44
	5	4	1·28	1·21–1·35
	4	4	1·22	1·18–1·25

* Shells grouped according to total length, i.e., 10 mm. group contains individuals of 10·0–10.9 mm. length.

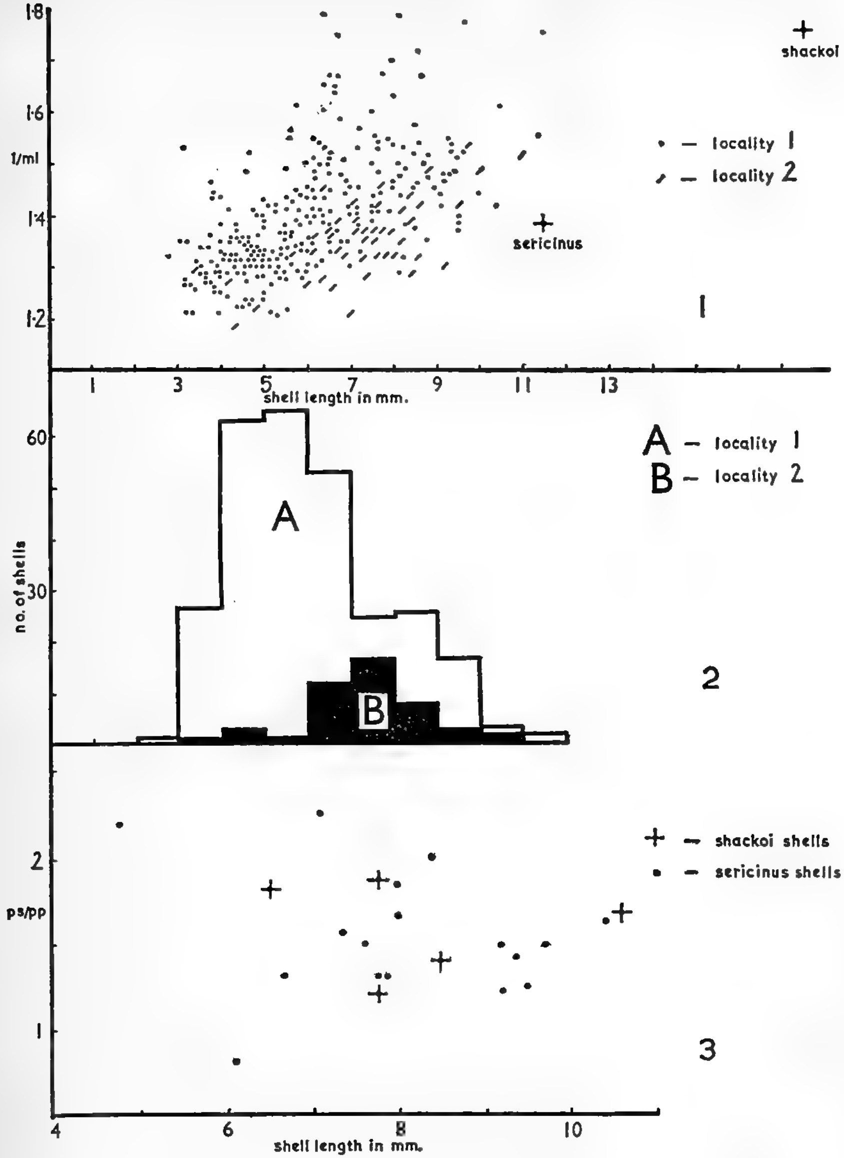
extensive overlapping between the two populations. Many of the shells have fine, regularly spaced ribs whose size is increased by frayed folds of periostracum. In some specimens these ribs are confined to the upper whorls but in others up to 8 mm. shell length they are present over the whole shell. The shells from locality 3 show a degree of inflation that is intermediate between the preceding populations, and ribs are present on the upper whorls of most of them (Pl. 8). In order to show the change of form with size, the variation at a particular size, and the variation between different populations, the mean values of *l/ml* have been calculated for shells from localities 1–3 which have been divided into millimetre size groups (Table I). In the sample from locality 4 there is a single specimen with inflated whorls and a rounded aperture while the remaining shells resemble the more slender specimens from locality 1 and lack ribs. The five specimens from locality 5 have reddish-brown shells with inflated whorls and widely reflexed columellar margins and no ribs. Besides the differences in the form of the shells there appear to be differences in the size composition of the two largest collections (localities 1 and 2, Text-fig. 2).

There is great variation in the intensity of pigmentation of the external surface of the mantle. The least and most heavily pigmented mantles from localities 1 and 2 are illustrated in Text-figs. 8 and 9. The epithelium overlying the visceral hump is evenly and relatively deeply pigmented. There is no trace of a ridge on the kidney, but between the kidney and the rectum is an intermediate mantle ridge running across the roof of the pallial cavity parallel to the rectum, extending from a point approximately level with the proximal end of the kidney as far as the mantle collar (Text-fig. 10).

In the male copulatory organ the relative proportions of the penis sheath and the preputium vary widely, particularly in the smaller specimens, but, with one exception, the sheath was found to be longer than the preputium. The ratio of the length of the penis sheath to that of the preputium (*ps/pp*) is plotted against shell length for some specimens from locality 1 (Text-fig. 3). In those from locality 2 the ratios lie between 1·0 and 1·88 ; a single aphallic specimen was found in this sample. The upper part of the penis sheath is swollen and is usually wider than the broadest part of the preputium (Text-figs. 6 and 7). A short epiphallus is followed by the thick-walled eversible part of the penis which occupies almost the whole of the upper part of the lumen of the sheath. Four stages in the development of the accessory genital glands and the distal genitalia are shown in Text-figs. 4–7, from which it can be seen that the male copulatory organ is relatively larger in the smaller specimens. Both the male and female genitalia increase rapidly in size between a shell length of 7 and 8 mm. and full hermaphrodite maturity is probably reached at a length of about 8 mm. In mature specimens the spermatheca is subspherical in shape and the spermathecal duct is about equal to its longest axis.

The seminal vesicle is formed by a thickened coiled part of the hermaphrodite duct that bears numerous papillae. In the ovotestis of a specimen of 7 mm. there are about 40 acini arranged regularly in three rows.

There are 23–25 teeth in each half-row of the radula. The shape of the mesocone of the lateral teeth (Text-fig. 11) is neither sharply conical as illustrated by Mandahl-Barth (1957*b*) or bluntly arrow-headed (Mandahl-Barth, 1960). Transition from

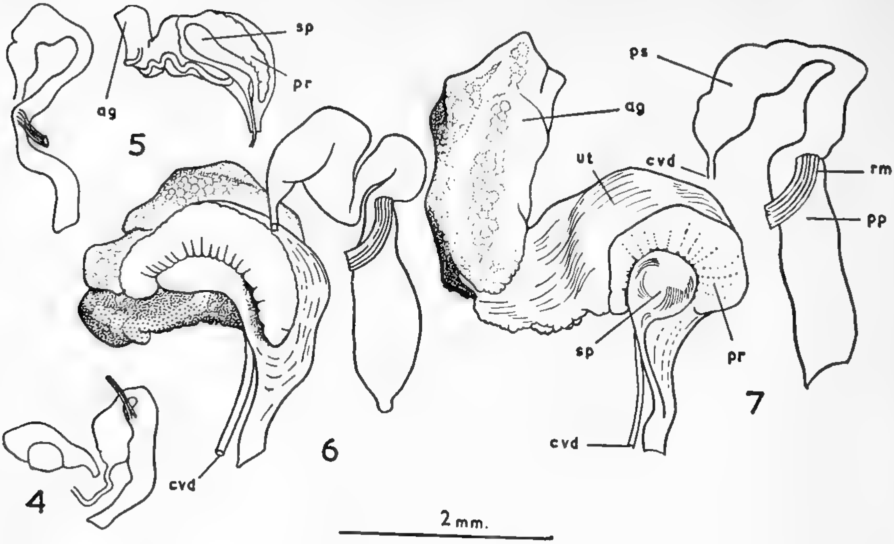


Bulinus sericinus (Jickeli)

FIG. 1. The ratio of shell length/aperture length (*l/ml*) plotted against shell length for shells from localities 1 and 2.

FIG. 2. Size frequency histogram for the samples from localities 1 and 2.

FIG. 3. The ratio of length of penis sheath to length of preputium *ps/pp*) plotted against shell length for specimens from locality 1.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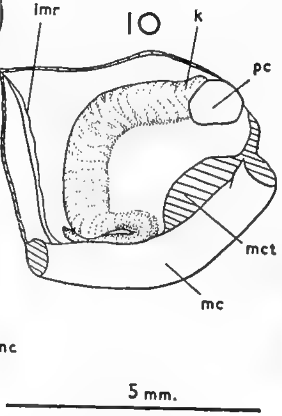
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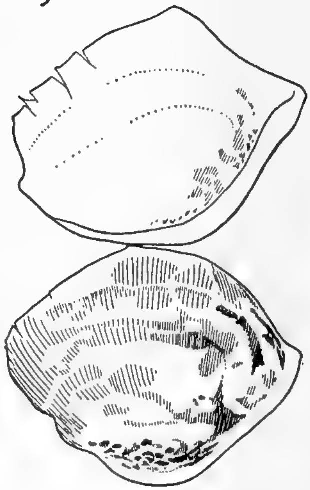

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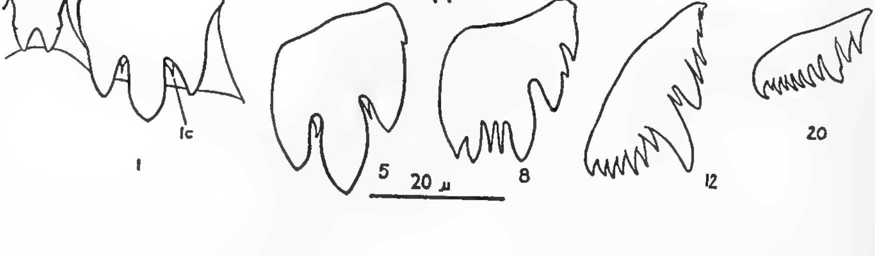
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lateral to marginal teeth takes place between longitudinal rows 6 and 8. Two small interstitial cusps which do not appear to have been described previously in any bulinid snail are present on either side of the mesocone in the majority of lateral teeth.

In his description of *Isidora sericina* Jickeli gives the type locality as the River Toquor at Mekerka in Hamasen Province. The precise position of this locality is uncertain but it probably lies near Asmara in what is now Eritrea. Jickeli described four specimens with markedly exserted spires from the same place as a separate species, *Isidora shackoi*. He could find no difference between the radulae of the two forms and considered the possibility that they might in fact be no more than variants of the same species but rejected this idea because of the marked differences between the shells. The ratios of l/ml plotted in Text-fig. 1 provide an index of the degree of exsertion of the spire and included in this figure are the ratios calculated from Jickeli's measurements of *sericinus* and *shackoi*. Although the largest specimen from the Debra Markos area is only 11·5 mm. in length, while the type of *shackoi* is 17 mm. long, the value of l/ml for *shackoi* (1·75) lies within the range of variation present in the Debra Markos material, which includes a complete gradation of form between *shackoi* and typical *sericinus*. Dissections have been made of specimens with shells of *shackoi* proportions (for this purpose regarded as having the ratio l/ml greater than 1·6) and no anatomical differences have been found between them and typical *sericinus* (Text-fig. 3). It appears that the two species were originally described from extreme variants from a single population.

The strongly ribbed forms found in some of the samples from the Debra Markos area correspond to *Isidora sericina* var. *harpula* of Pollonera from Asmara and Debaroa. Pollonera also described some specimens of 7 mm. shell length as a mutant *minima* of *I. shackoi*; many smaller specimens having shells of *shackoi* proportions occur in the present material. Piersanti (1940) illustrated a very inflated form with a shouldered body whorl and depressed spire as *Bullinus sericinus* (Jickeli) and figured and described another form which appears to be identical with typical *sericinus* as *Bullinus* (*Isidora*) *mussolinii*. Re-examination of the material described by Wright (1956) as *B. sericinus* from Senegal indicates that it should not have been referred to this species but to *B. truncatus rohlfsi* (Clessin).

The relationships of *B. sericinus* are not easy to determine. Haas (1935) suggested that it is a form of *B. truncatus* while Mandahl-Barth (1957*b*) placed it in the *tropicus*

Bulinus sericinus (Jickeli)

FIGS. 4–7. Stages in the development of the accessory genital glands and male copulatory organ—

4. at 6·1 mm. shell length; 5. at 7·1 mm. shell length; 6. at 8 mm. shell length; 7. at 9·2 mm. shell length.

FIGS. 8 and 9. Examples of mantles showing the variation in the degree of pigmentation of the outer surface—

8. Lightly and deeply pigmented specimens from locality 1. 9. Lightly and deeply pigmented specimens from locality 2.

FIG. 10. Inner surface of mantle.

FIG. 11. Radula teeth.

group but mentioned that intermediates between *sericinus* and both *truncatus* and *tropicus* had been seen. The differences between the *truncatus* and *tropicus* groups are not well defined and it is possible that they are not really distinct. According to Mandahl-Barth the members of the *tropicus* group have triangular mesocones on their lateral radula teeth, they are rarely aphallic, and none of the species are known to act as intermediate hosts of *Schistosoma haematobium* ; the species of the *truncatus* group have arrow-headed shaped mesocones, are frequently aphallic and *B. truncatus* is the principal snail host for urinary schistosomiasis in North Africa and the Middle East. The mesocones of the lateral teeth in the Debra Markos material are more arrow-headed than triangular and a single aphallic specimen was found in one of the samples. These characteristics indicate a closer affinity with the *truncatus* rather than the *tropicus* group. This is the conclusion reached by Mandahl-Barth (1960) after examination of material from Lake Tana, and he has reduced *sericinus* to a subspecies of *B. truncatus*. In the present paper the specific status of *sericinus* has been preserved for reasons which are given in the general discussion. It has not been proved that *B. sericinus* can act as a host of *Schistosoma*, but this seems likely to be the case as there are extensive highland areas in Ethiopia from which *S. haematobium* has been reported and in which no other species of *Bulinus* has been found (Ayad, 1956).

Until living material of *B. sericinus* becomes available for further study it is perhaps best to retain this name for the *Bulinus* from the highland regions of Ethiopia although subsequent work may well prove that it is not a distinct species.

Biomphalaria rueppelli (Dunker)

Planorbis rüppellii Dunker, 1848.
Planorbis adowensis Bourguignat, 1879.
Planorbis herbini Bourguignat, 1883.
Planorbis cecchii Pollonera, 1887.
Planorbula boccardi Pollonera, 1898.
Planorbis bozasi Rochebrune & Germain, 1904.

LOCALITIES : 2 (69) ; 3 (61). The specimens were collected from broad-leaved vegetation in the shallows (2) and from floating weeds and rocks in a small pool overhung by undergrowth (3).

There is no difference in the appearance of the shells from the two localities. The largest specimens have a diameter of 10–11 mm. and consist of 4–4½ whorls which are rounded on the upper surface except for the last one which is flattened toward the aperture (Pl. 9). In the majority the first two whorls are more deeply sunk on the upper side, and there is a blunt angulation on the under surface of all the whorls near the suture. There is no sculpture apart from fine irregular growth lines. The mean ratios of maximum diameter to height (d/h), maximum diameter to diameter of umbilicus (d/ud), and diameter of umbilicus to height (ud/h) are given for the individuals of both populations grouped according to their diameter into size groups of 1 mm. (Table II). As the last whorl was deflected to a variable extent towards the aperture the height of the last whorl only, and not the total height of the shell, was measured. The ratios d/h and d/ud for specimens from locality 3 are plotted against

TABLE II.—*The Variation in the Proportions of the Shells of* Biomphalaria rueppelli *from Two Localities*

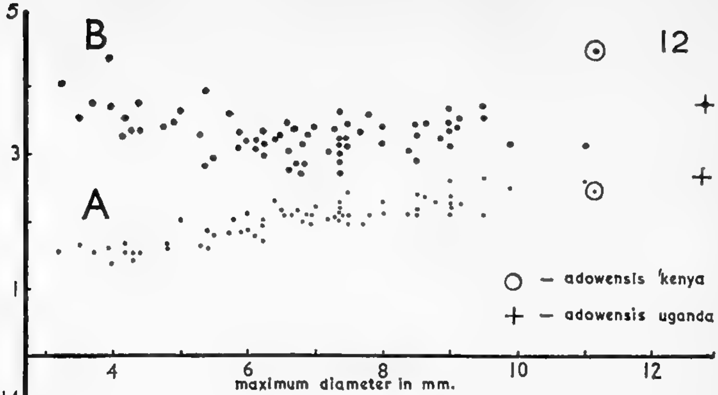
Locality	Size group* (mm.)	Number of specimens	Mean *d/h*	Mean *d/ud*	Mean *ud/h*
2	10	1	2·64	3·00	0·88
	9	13	2·64	3·08	0·72
	8	16	2·14	3·04	0·71
	7	22	2·15	3·13	0·69
	6	4	2·00	3·13	0·64
	5	3	1·89	3·23	0·58
	4	3	1·60	2·67	0·60
3	11	1	2·56	3·08	0·84
	10	—	—	—	—
	9	9	2·33	3·40	0·69
	8	8	2·22	3·23	0·69
	7	14	2·12	3·22	0·67
	6	17	1·99	3·10	0·64
	5	8	1·83	3·30	0·56
	4	8	1·51	3·44	0·44
	3	4	1·54	3·89	0·40

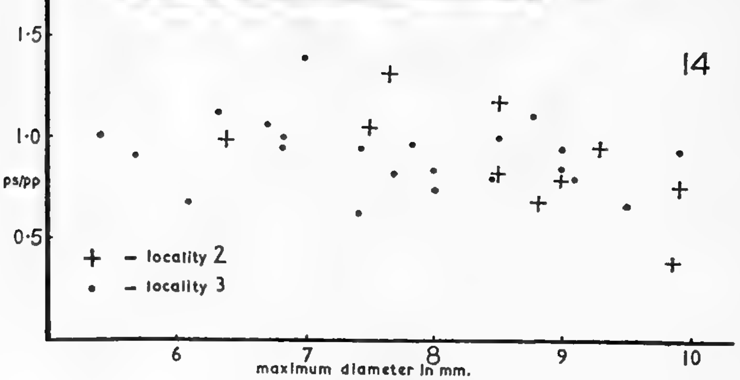
* Shells grouped according to maximum diameter, e.g., 10 mm. group contains individuals of 10·0–10·9 mm. diameter.

diameter in Text-fig. 12 and it is evident that all vary according to the size of the shell; *d/ud* is largest in the smallest specimens and decreases to remain at a relatively constant level in the larger specimens; *d/h* increases steadily over the whole of the size range present in the sample.

A light grey pigmentation on the outer surface of the mantle is concentrated at the borders of the kidney. The disposition of ridges within the pallial cavity and the structure of the pseudobranch and the pulmonary siphon closely resemble that described in *Biomphalaria pfeifferi* by Schutte & van Eeden (1957*b*) and their terminology will be followed. Between the kidney (on which there is no ridge) and the rectum is an intermediate mantle ridge (IMR) which extends from the ventral surface of the mantle collar to the level of the pericardium (Text-fig. 19). On the left side of the rectum is a very large lateral rectal ridge (LRR) which is highly convoluted with a thickened free edge. A median rectal ridge (MRR) runs from the edge of the pulmonary opening along the right side of the rectum for a short distance. A continuation of the lateral rectal ridge runs along the entire length of the anal lobe.

There is considerable variation in the ratio of the length of the penis sheath (*ps*) to that of the preputium (*pp*), the extremes of *ps/pp* being 1·5 in a shell of diameter 7 mm. and 0·5 in one of 9·5 mm. (Text-fig. 14). The tip of the penis lies either immediately proximal or immediately distal to the junction between the sheath and the preputium. The preputium is the most deeply pigmented part of the copulatory organ and longitudinal concentrations of pigment can usually be detected which overlie the muscle pillars on the inner wall. These muscle pillars are opposed to each





Biomphalaria rueppelli (Dunker)

FIG. 12. The ratio of (A) maximum diameter of shell to shell height (*d*/*h*), and (B) maximum diameter to umbilicus diameter (*d*/*ud*) plotted against maximum diameter for shells from locality 3.

FIG. 13. Size frequency histogram for the sample from locality 2.

FIG. 14. The ratio of length of penis sheath to length of preputium (*ps*/*pp*) plotted against maximum diameter of shells from localities 2 and 3.

other, that on the right side of the preputium being larger than that on the left and in some specimens the left pillar may be absent (Text-fig. 20). Two muscles are inserted at the junction between the penis sheath and the preputium (Text-fig. 17), the larger (*rm* 2) passes ventrally and is attached to the columellar muscle, and the smaller (*rm* 1) originates on the dorsal wall of the head region. In addition fine fibres are inserted in rows on each side of the preputium (*rm* 3 and 4) and are also attached beneath the dorsal wall of the head. The structure of the prostate is difficult to make out because of the retracted condition of the specimens, it closely resembles that of *B. pfeifferi* as described by Schutte & van Eeden (l.c.) although there appear to be at least 12 rather than 9–12 primary diverticula. The majority of the diverticula are branched and some bear tertiary diverticula.

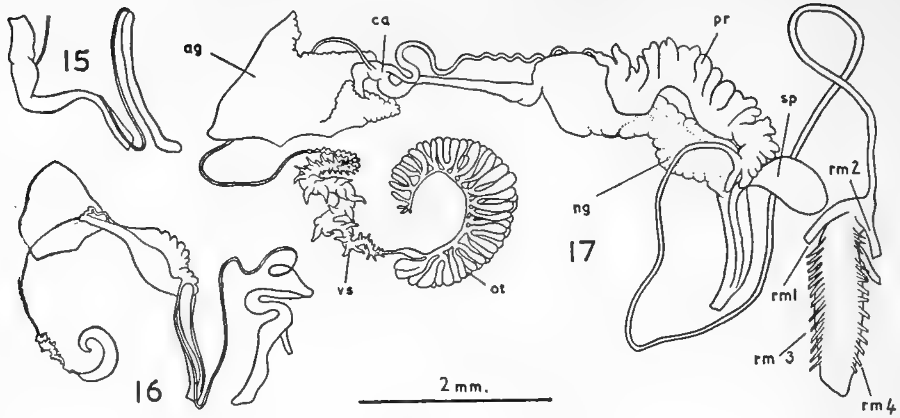
The female system of *B. rueppelli* resembles that described for other *Biomphalaria* and appears to be of little taxonomic importance. In mature specimens the spermatheca is flattened against the other organs and its periphery is more or less circular. The spermathecal duct is relatively long and opens into the vagina near the female genital pore (Text-fig. 17).

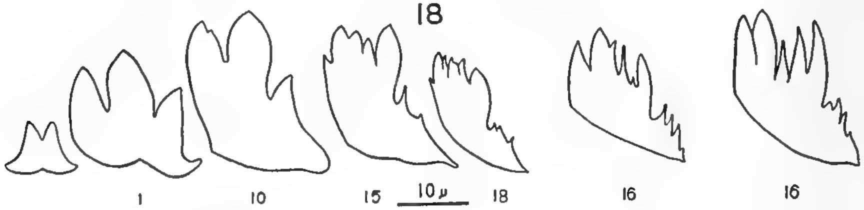
The ovotestis consists of a variable number of pairs of branched acini ; the hermaphrodite duct is dilated close to the bases of the first pair of diverticula (Text-fig. 17). The dilatation of the hermaphrodite duct that forms the vesicula seminalis begins close to the ovotestis and the thickness of the coiled duct increases rapidly and decreases again distally. This part of the duct bears finger-like processes which are replaced anteriorly by more translucent rounded vesicles.

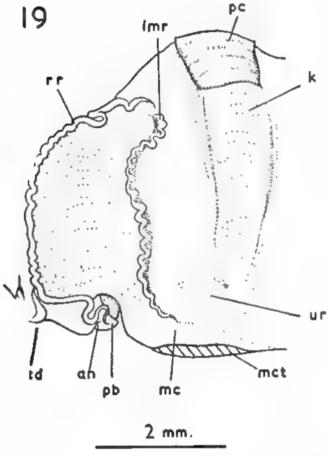
Three stages in the development of the accessory genital glands and the male copulatory organ are shown in Text-figs. 15–17. These organs increase in size rapidly between a shell diameter of 6 and 8 mm. and though protandry is not so marked as in *Bulinus sericinus* the male system appears to be better developed at a smaller size. Full sexual maturity is probably reached between a shell diameter of 7 and 8 mm.; there is no apparent change in shell form correlated with this.

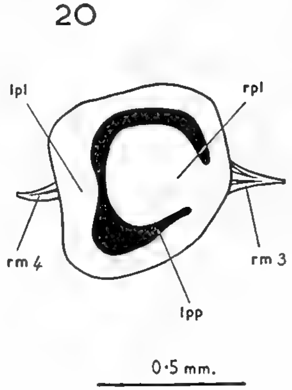
In most of the radulae examined there are 22 teeth present in each half-row. The ectocones of the laterals are triangular and the endo- and mesocones are more or less lanceolate ; no interstitial cusps were observed (Text-fig. 18). In a few specimens bifurcation of the endocone occurs in the 10th longitudinal row of teeth, and in general the transition between the lateral and marginal teeth takes place between the 12th and 15th rows. There is great variation in the form of the lateral teeth and the ectocone is not always divided into four cusps as described by Mandahl-Barth (1957*a*) ; although in no case was it undivided as is the typical condition in S. African *B. pfeifferi*. In one radula the whole longitudinal row of 5th lateral teeth is bicuspid resembling the centrals.

Bourguignat (1879) described *Planorbis adowensis* from a shell of *Planorbis rueppelli* Dunker, with rapidly increasing whorls and a relatively small umbilicus, illustrated by Jickeli (1874). The internal anatomy of *rueppelli* and *adowensis* was first described by Ranson & Cherbonnier (1952) from material collected at great distances from the type localities. Mandahl-Barth (1957*a*) observed that populations usually consist of either typical *rueppelli* or *adowensis*, but concluded from the occurrence of mixed populations with some specimens intermediate between the two that *adowensis* should









Biomphalaria rueppelli (Dunker)

FIGS. 15–17. Stages in the development of the accessory genital glands and the male copulatory organ—
15. at 5·8 mm. shell diameter; 16. at 6·5 mm. shell diameter; 17. at 7·7 mm. shell diameter.

FIG. 18. Radula teeth.

FIG. 19. Pneumostome cut through on right side and mantle turned to the left to show pseudobranch, kidney and pallial ridges.

FIG. 20. Transverse section through preputium.

be regarded as a form of *rueppelli* having no ecological significance. Mandahl-Barth gives measurements of the shells of the *adowensis* form from Uganda and Kenya and these are included in Text-figs. 12 and 14. The Uganda specimens are considerably larger than the Ethiopian shells from the known pattern of variation. However, the *d/ud* ratio for the Kenya sample does appear to lie outside the Ethiopian range of variation ; although *d/ud* increases slowly with size it is unlikely that any individuals of the Ethiopian populations reach the proportions of the Kenya *adowensis*. The anatomy of the Ethiopian specimens also corresponds more closely to *rueppelli* ; the ratio *ps/pp* lies between 0·75 and 1·25 for the majority of the specimens dissected, but it is of interest that in several specimens the sheath is only about half as long as the preputium, a feature which is described as diagnostic of *adowensis* by Mandahl-Barth. A shell from the Debra Markos collection that resembles *adowensis* in the relatively small size of the umbilicus is shown in Pl. 9. It seems likely that future collecting will reveal a complete intergradation between *adowensis* and typical *rueppelli*.

There are several differences between the morphology of the Ethiopian *rueppelli* and that illustrated by Ranson & Cherbonnier (l.c.). These authors depict one retractor muscle at the junction of the penis sheath and preputium instead of two ; the seminal vesicle is different in their material and a posterior thickly coiled part is omitted ; the spermathecal duct is far thicker than in the Ethiopian material ; the diverticula of the ovotestis do not resemble those of the Ethiopian specimens and are depicted as arranged in a single row. In addition the radula teeth illustrated appear to be very worn and thus of little value for comparative purposes.

Schutte & van Eeden (1959*a* and *b*) and Azevedo *et al.* (1957) have made anatomical studies of *Biomphalaria pfeifferi* based on material from South Africa and Mozambique respectively. A comparison of the measurements made on Ethiopian *rueppelli* with those made by Schutte & van Eeden reveals a difference from *pfeifferi* in the relative proportions of the penis sheath and preputium. In *pfeifferi* the preputium is between 0·71 and 1·60 times the length of the sheath and in *rueppelli* between 1·25 and 2·0 times the length of the sheath. Mandahl-Barth (1957*a*) considered *rueppelli* to be a subspecies of *pfeifferi* but more recently (1960) has suggested that the differences between the subspecies of *pfeifferi* are not sufficiently constant to justify their retention and he therefore regards *rueppelli* as a synonym of *pfeifferi*. The observations reported above suggest that it is perhaps premature to treat *rueppelli* as identical with *pfeifferi* and it is therefore regarded here as a separate species.

Gyraulus costulatus (Krauss)

Planorbis costulatus Krauss, 1848.
Planorbis costulatus Jickeli, 1874.
Planorbis stelzneri Dohrn, E. v. Martens, 1869.
Planorbis aethiopicus Bourguignat, 1883.
Caillaudia angulata Bourguignat, 1883.

LOCALITIES : 3 (3).

The specimens were collected with large numbers of *Anisus natalensis* (Krauss) from which they can be readily distinguished by the presence of a carination on the periphery of the shell and more rapidly widening whorls (Pl. 9). The underside of the shell is concave with the lower surface of the whorls more rounded than the upper. Coarse, regularly spaced ribs are present, and in one specimen areas of both coarse costulation and fine irregular striation are present. This variation of the ornamentation present on a single shell raises doubts about the validity of using sculptural characters for the differentiation of subspecies of *Gyraulus costulatus* as Mandahl-Barth (1954) has done.

Only one shell contained an animal and the condition of this did not allow a detailed anatomical examination. The structure of the penis is like that of other gyraulid snails which have been described ; at the tip there is a grooved stylet with a bulbous base proximal to which lies the opening of the vas deferencs.

Planorbis aethiopicus was described by Bourguignat from one of Jickeli's drawings of *P. costulatus* and is only tentatively included in the list of synonyms given above. It must be mentioned that Ranson (1955) regards it as a distinct species.

Anisus natalensis (Krauss)

Planorbis natalensis Krauss, 1848.
Planorbis abyssinicus Jickeli, 1874.
Planorbis abyssinicus var. *gravieri* Germain, 1904.

LOCALITIES : 3 (45) ; 4 (43) ; 5 (30).

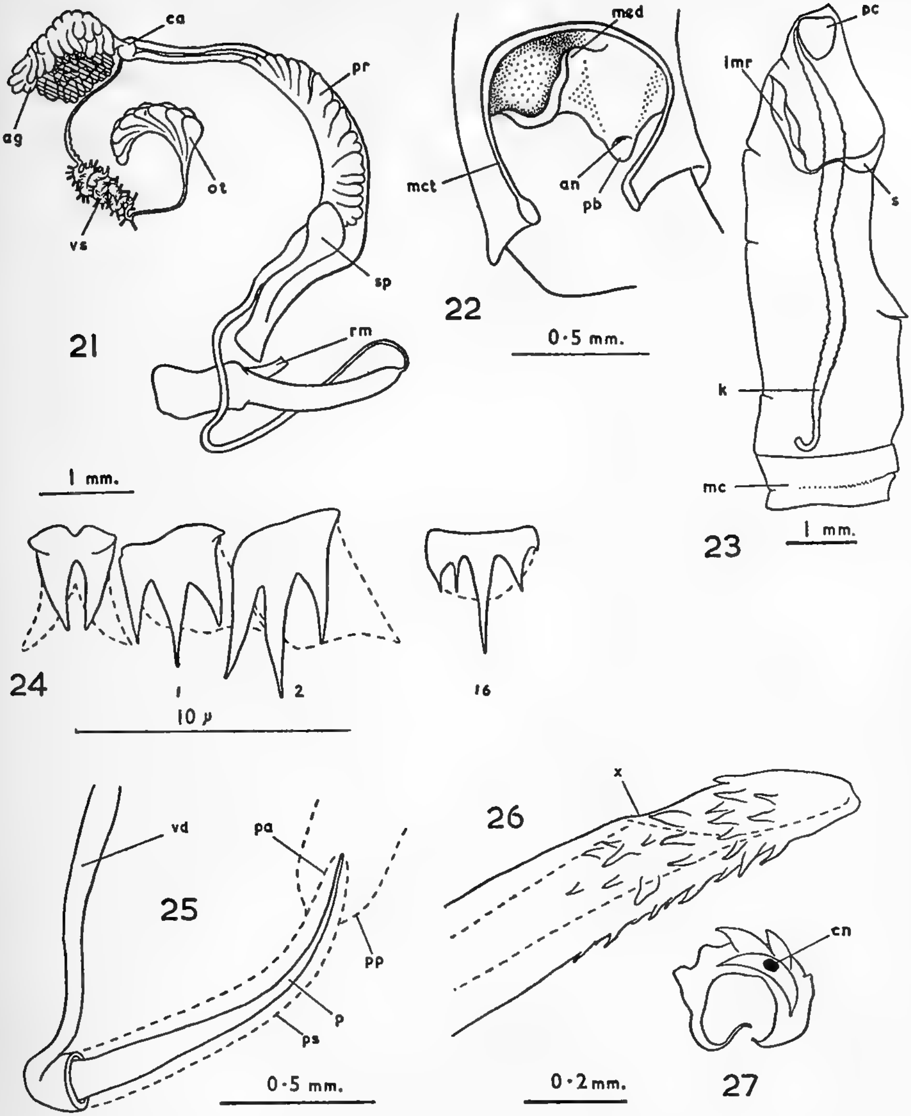
The specimens were collected from small shallow pools overhung by vegetation.

The whorls of the reddish-brown shell increase slowly in width and are separated by a deep suture ; they are slightly flattened on the upperside but are otherwise rounded with a slight angulation towards the underside in some specimens (Pl. 9). No trace of a carination is present. The degree of concavity of the upper surface of the shell is variable but is usually considerably less deep than on the underside. The coiling of many of the shells is loose and irregular, and as a result of the friability of the shells the whorls easily become detached from each other. The aperture is large, and slightly deflected ventrally. Transverse sculpture consisting of numerous, irregular, fine striations is present, and a fine spiral sculpture is usually visible on the under surface. The mean measurements from 10 of the largest shells are as follows :

Diameter : 4·7 mm. Diameter of umbilicus : 2·0 mm. Height : 1·4 mm. Ratio of diameter/diameter of umbilicus : 1·97.

The measurements of the largest specimen are : *d* 5·5 mm.; *ud* 2·3 mm. ; *h* 1·5 mm.; *d*/*ud* 2·39 mm.

The mantle wall is translucent with hardly any pigmentation. The pseudobranch is rudimentary (Text-fig. 22). There is no ridge on the long and narrow kidney (Text-fig. 23) but a conspicuous ridge (IMR) is present on the left-hand side of the roof of the pallial cavity extending from the cardiac end of the kidney to about one-third of its length, and continuous distally with an incomplete septum lying across the mantle cavity. This ridge appears to correspond to the intermediate mantle ridge of *Biomphalaria pfeifferi*.



Anisus natalensis (Krauss)

FIG. 21. Genital system.
FIG. 22. Mantle cut away to show pneumostome and pseudobranch.
FIG. 23. Inner surface of mantle.
FIG. 24. Radula teeth.
FIG. 25. Distal part of vas deferens and penis (penis sheath and preputium shown in broken outline).
FIG. 26. Tip of penis (course of vas deferens in broken outline).
FIG. 27. Transverse section of penis tip at position *x* in Fig. 26.

The size of the male copulatory organ is large in relation to the other reproductive organs (Text-fig. 21), for example, in a shell of diameter 3·5 mm. the length of the preputium is 0·7 mm. and of the penis sheath 0·9 mm. The tip of the penis projects into the preputium and is surrounded by a continuation of the wall of the penis sheath (this has been described by Baker (1945) from European species of *Anisus* and called a papilla). A single retractor muscle is inserted at the junction between the penis sheath and the preputium and has a ventral origin on the columellar muscle. The structure of the penis (Text-figs. 25 and 26) differs from that described in other planorbid genera ; it was examined both in serial sections cut at 6 μ, and by direct dissection. There is no separate stylet but from approximately the mid-point in its length the colour of the penis changes through pale yellow to light brown and the organ becomes increasingly stiff towards the tip. Transverse sections show that this is due to a substance resembling sclerotized arthropod cuticle which is formed at the periphery of the wall as well as internally lining the vas deferens which extends right to the tip of the penis. The size and number of cells in the penis wall decrease progressively towards the tip so that near the opening of the vas deferens there are only a few cells embedded in a solid matrix (Text-fig. 27). The opening of the vas deferens is situated slightly to one side of the penis tip from which project numerous backwardly pointing spines.

The prostate consists of 14–17 lobes (Text-fig. 21), some of which may be subdivided ; they open into a prostatic duct, the lumen of which is separate from that of the vas deferens, although the two ducts are fused together by their walls and are closely wrapped around the uterus and nidamental gland. The lumen of the prostatic duct opens into the vas deferens a short distance below the base of the most distal lobe of the prostate. In smaller specimens the acini of the ovotestis are arranged in two alternating rows as depicted by Baker for other species of *Anisus* and *Gyraulus*, but in larger specimens this arrangement is disturbed by the proliferation of acini at the base of the gland. The seminal vesicles consist of a thick part of the hermaphrodite duct from which project large numbers of small papillae.

The radula consists of 17 marginal and lateral teeth (Text-fig. 24) in each half-row ; the cusps are long and sharp and resemble those of *Anisus* and *Gyraulus* species depicted by Baker. Transition from marginal to lateral teeth takes place in the 13th and 14th longitudinal rows with the appearance of a cusp between the endocone and the mesocone and another on the outer side of the ectocone.

Apart from the few specimens that conform to *Gyraulus costulatus* (Krauss) all the small planorbid shells collected in the vicinity of Debra Markos resemble *Anisus abyssinicus* (Jickeli, 1874). Jickeli provided no information about the internal anatomy of his species and neither have subsequent authors who have recorded it from widely separated localities in Eritrea, Ethiopia and Somaliland (Germain, 1904 ; Piersanti, 1941 ; Bacci, 1951). By the narrowness of their whorls the Debra Markos specimens resemble *Anisus* more closely than *Gyraulus*, although Baker (1945) includes *abyssinicus* with *natalensis* Krauss, a widespread species in S. Africa, in *Gyraulus*. Connolly (1939) was of the opinion that all the forms of small planorbid mollusc with the shell form of *Anisus* should be regarded as a single species *natalensis* Krauss but makes no reference to *abyssinicus* Jickeli. However, there is a close resemblance between the present material, that described by Jickeli, and recently collected *Anisus natalensis* from Transvaal.

There are, to our knowledge, no published descriptions of the anatomy of the male copulatory organ of African *Anisus*. Mandahl-Barth (1954), in a description of *A. natalensis* from East Africa, merely states that the internal anatomy of *Anisus* in general resembles that of *Gyraulus*. The penis of the Debra Markos specimens differs markedly from that of *Gyraulus gibbonsi* (Nelson) as described by Binder (1958) and that of *Gyraulus costulatus* from Khartoum and Angola. The latter species possesses a grooved stylet with a bulbous base that is abruptly delimited from the soft part of the penis, and a vas deferens that opens proximally to the stylet. Such a structure is typical of the non-African species for which descriptions are available (Baker, 1945; Hubendick, 1955, 1957, 1958). Through the kindness of Dr. J. A. van Eeden specimens of *Anisus natalensis* were obtained from the Transvaal and the structure of the penis was found to be similar, if not identical, to that of the Ethiopian specimens. On the basis of the similarity in both shell and anatomy the material is assigned to *Anisus natalensis* (Krauss) of which *A. abyssinicus* (Jickeli) is provisionally regarded as a synonym. There are some small differences between the shells of the Ethiopian and South African specimens, the importance of which can only be assessed when further samples are available.

The whole question of the relationships between the planorbid genera *Gyraulus*, *Anisus*, and *Armiger* is a long way from clarification. At the present time the anatomical characteristics of *Anisus natalensis* are unique and show that the morphology of the male copulatory organ is far more heterogeneous than when Hubendick (1957) suggested the retention of only a single genus *Anisus*.

Family LYMNAEIDAE

Lymnaea truncatula (Müller)

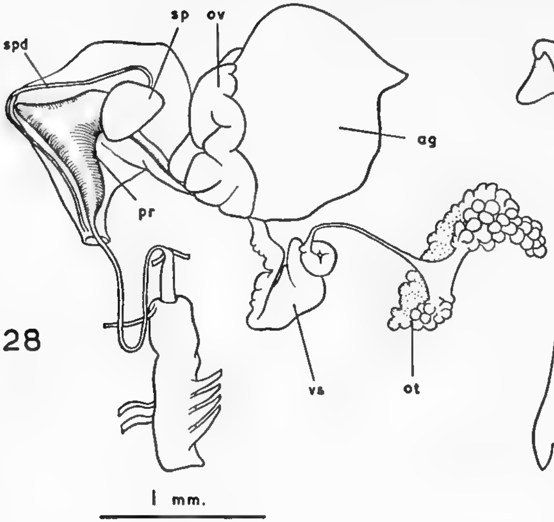
? *L. mweruensis* Connolly, 1929.
? *L. peregra* (Müller), Jickeli, 1874.

LOCALITIES: 1 (1); 2 (3); 3 (1); 4 (4); 6 (86); 7 (17); 8 (6); 9 (62); 10 (12); 11 (2).

The shells (Pl. 8) closely resemble European specimens and are ornamented to a varying extent with a microsculpture consisting of spiral tracts of fine vertical lines. Measurements of some of the largest shells are given in Table III.

The genital anatomy (Text-fig. 28) is similar to that of European material (Hubendick, 1951); the length of the penis sheath is between half and one-third that of the preputium, the prostate bears a single internal fold, and the spermathecal duct is very long and thin.

The central teeth of the radula are asymmetrically bicuspid and on either side of them lie 21–25 lateral and marginal teeth (Text-fig. 29). Hubendick's illustration shows the 1st and 2nd lateral teeth as being tri- and bicuspid respectively, but in the Ethiopian material the 3rd–5th teeth were sometimes bicuspid while the 2nd laterals were not always so.



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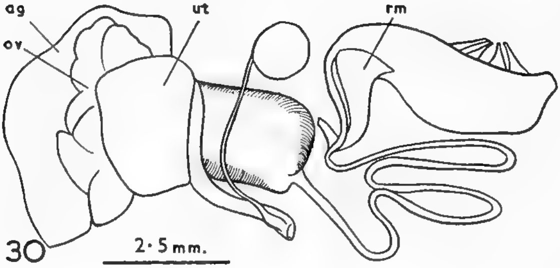

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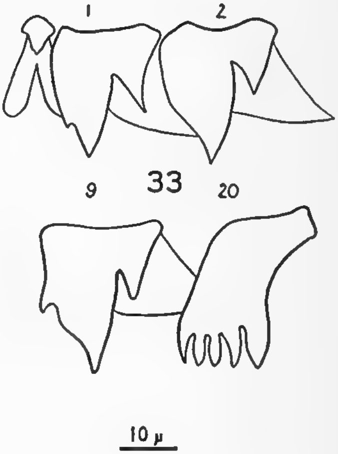

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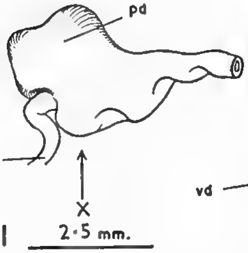

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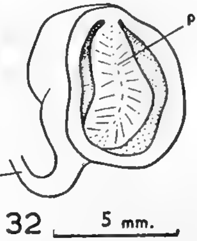

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Fig. 28. *Lymnaea truncatula* (Müller), genital system.
Fig. 29. *L. truncatula*, radula teeth.
Fig. 30. *Lymnaea natalensis* (Krauss), genital system.
Fig. 31. *L. natalensis*, lateral view of prostate.
Fig. 32. *L. natalensis*, transverse section through prostate at position *x* in Fig. 31.
Fig. 33. *L. natalensis*, radula teeth.

Transition between the lateral and marginal teeth usually begins in the 9th longitudinal row with the development of one or two small cusps on the outer edge of the ectocone. Teeth in the 12th row which Hubendick shows as being of tricuspid lateral structure, are of multicuspid marginal form. Hubendick omits the basal part of the 17th tooth which in these specimens bears two or three small cusps on the outer side.

Lymnaea truncatula has been recorded from Ethiopia (Jickeli, 1874) and South Africa (Connolly, 1939) and examination of the present material indicates that it is correct to refer Ethiopian material to this widely distributed European species.

Hubendick (1951) examined material from the eastern side of Mount Elgon, Kenya, at 7,000 ft. and concluded that *L. mweruensis* described by Connolly (1929) from the northern side of Mt. Kenya should be regarded as a synonym of *truncatula*. Mandahl-Barth (1954) found a single specimen in the Eldama River at 8,000 ft. and tentatively recorded it as *L. mweruensis*. The type specimen of *mweruensis* (Pl. 8) has been compared with the Debra Markos material from which it can be readily distinguished by its less swollen whorls, more elongated aperture with a narrowly reflexed inner margin, and its pale colour. It may be that *L. mweruensis* is only a variant of *L. truncatula* and that this species has a widely scattered distribution in the highlands of North-east Africa, but this can only be established by extensive further collecting.

TABLE III.—*Shell Proportions of Large Specimens of* Lymnaea truncatula *from Ethiopia: (Shell Length/Aperture Length and Shell Length/Aperture Width)*

Shell length (mm.)	*l/ml*	*l/mw*
8·7	1·45	2·72
7·7	1·64	2·48
6·5	1·76	2·83
6·3	2·03	2·03
6·3	1·75	2·86
6·2	1·77	2·58
5·9	1·84	2·68
5·7	1·84	3·00
5·6	1·75	2·54
5·5	1·96	2·75
5·2	1·79	2·88
4·9	1·81	2·88
4·4	1·76	2·75
Type specimen of *L. mweruensis* Connolly		
6·1	1·85	3·05

Lymnaea natalensis (Krauss, 1848)

Limnaeus natalensis Krauss. var. *exsertus* v. Martens, 1866.
Limnaea orophila Morelet, Jickeli, 1874.
Limnaea africana Bourguignat, 1883.
Limnaea caillaudi Bourguignat, 1883.

Limnaea gravieri Bourguignat, 1883.
Limnaea acroxa Bourguignat, 1883.
Limnaea exserta v. Martens, 1897.
Radix pereger (Müller). Piersanti, 1940.

LOCALITIES: 2 (8); 4 (6); 5 (8).

There is considerable variation in the shell shape (Pl. 8), although in all the specimens the spire is moderately well developed and the majority resemble *L. natalensis caillaudi* as illustrated by Mandahl-Barth (1954). A few smaller specimens with more exserted spires resemble Mandahl-Barth's figures of *L. exserta* v. Martens, but the prostate, instead of being of the cylindrical shape that he describes as being typical of *exserta*, is widely dilated distally as in *natalensis* (Text-fig. 31). The genital system is shown in Text-fig. 30; a transverse section through the prostate shows a single internal fold (Text-fig. 32). A large number of the lateral radula teeth show a tendency to a reduction of the endocone resulting in a bicuspid condition (Text-fig. 33).

DISCUSSION

The material on which this paper was based was collected from a relatively small area during a period of about six weeks of the rainy season from September to October, 1957. It cannot be claimed, therefore, that it is completely representative of the freshwater gastropod fauna of the Ethiopian highland region, but there is little doubt that the collection contained the majority of the species that occur in the Chokke Hills. Any conclusions which may be drawn from the results of this work must therefore be qualified by this geographical and seasonal restriction, but such conclusions may have wider application and it is to be hoped that this account will provide a basis for further investigations.

In discussing the fauna of any closely defined area it is often as important to account for the absence of species that might reasonably be expected to occur there as it is to consider those species that have been found. Deficiencies are only significant when the collections have been as exhaustive and thorough as they were in the present case. It is probable that the absence of members of the *Bulinus africanus* and *B. forskali* species complexes, also of any prosobranch snails, can be accounted for by climatic conditions mainly due to altitude, for members of these groups occur in similar latitudes at lower levels. Neuville & Anthony (1906) reported *B. africanus* from the Addis Abbaba region at an altitude of about 8,000 ft., and Ayad (l.c.) found large numbers of *B. globosus* in both Lake Tana (6,000 ft.) and the River Abbai at a point 2 miles from its source in the Lake. The type locality of *B. abyssinicus* is in Southern Ethiopia and specimens from Somalia have been studied by Mandahl-Barth (1957*c*). There are no reports in the literature of members of the *B. forskali* group anywhere in the higher regions of Ethiopia, but they have been recorded from all of the surrounding territories. It is well known that the freshwater prosobranchs in Africa are restricted to lower altitudes but the absence of the Ancylidae is surprising for it is a widely distributed family and the descriptions of the habitats investigated appear to be quite suitable for the requirements of its members.

Of the six species described in this paper five are truly African but the sixth, *Lymnaea truncatula*, is a ubiquitous palaearctic species. On the evidence at present available it is impossible to determine whether the Ethiopian populations are relicts of a distribution that was formerly more widespread, or whether they are a recent introduction by man or migratory birds. The occurrences of this species reported from South Africa may not be in any way connected with the Ethiopian foci and are more likely to be a recent human importation. If birds are held responsible for their transport it is surprising that there are not more palaearctic gastropod species present which might also have originated in this manner, but this same argument could equally well be used to discount the idea of relict populations. *Ancylus fluviatilis* Müller is another palaearctic species that is generally believed to occur in northern Ethiopia (Walker, 1914 and Pilsbry & Bequaert, 1927) although no specimens appear to have been collected since those originally described by Blanford and Jickeli. The possibility that *L. mweruensis* may be a local form of *L. truncatula* confined to highland regions further to the south in East Africa cannot be overlooked, for there must be a fairly effective isolation between populations of a species which is confined to highland areas, and such isolation could easily give rise to distinct local forms. There are a number of species of insects that are endemic to particular massifs in Ethiopia (Scott, 1958) and there is every reason to expect the evolution of local races in other groups.

Of the five purely African species present *Bulinus sericinus* presents the most interesting problems. It has been pointed out in the descriptive section of this paper that *B. sericinus* has been considered at various time to have affinities with both *B. truncatus* and *B. tropicus* and that it is now considered to be a subspecies of *B. truncatus* (Mandahl-Barth, 1960). Observations on the morphology of the present material certainly support the idea of a relationship with the *truncatus* group. However, it has been found in the laboratory that the North African and Middle Eastern forms of *truncatus* do not breed easily at temperatures below 25° C., while *sericinus* is able to maintain itself at altitudes at which the maximum temperature does not reach this level, and may fall to freezing point at night. Further, Ayad points out that there is evidence that *B. sericinus* does not act as an intermediate host of *Schistosoma haematobium* in Eritrea which is in contrast to the characteristic host rôle of species of the *truncatus* group.

It is also premature to regard *Biomphalaria rueppelli* as a synonym of *B. pfeifferi*, although they are undoubtedly closely related ; *rueppelli* from the Sudan breeds easily in the laboratory but considerable difficulty has been experienced with the establishment of colonies of *pfeifferi* from several localities. Epidemiological evidence points to *rueppelli* as the intermediate host for *Schistosoma mansoni* in Ethiopia although this parasite is not common in the highland areas.

The three remaining species, *Anisus natalensis*, *Gyraulus costulatus* and *Lymnaea natalensis* have a very wide distribution throughout Africa and their presence in this collection is not remarkable. Their altitude limits appear to be about 9,000 ft. and beyond this level *Lymnaea truncatula* was the only freshwater gastropod collected.

Although *Bulinus sericinus* and *Biomphalaria rueppelli* appear to be abundant in the highlands of Ethiopia and are the potential intermediate hosts of *Schistosoma*, there are relatively few records of *haematobium* or *mansoni* infection and it is probable that the average temperatures are too low for satisfactory development of the larval flukes within the snails. Schwetz (1951) reported the occurrence of *S. mansoni* in *B. pfeifferi* from Lake Bunyoni at 6,000 ft. in Uganda and claimed that this was apparently the highest altitude record for the transmission of the disease. It is possible that the small number of records of schistosomiasis from highland areas is due to the small scale or absence of medical surveys. If in fact the disease is more widespread than is thought, it may depend on being continually introduced by the movements of human hosts from lower altitudes in areas where conditions are suitable for continuous local transmission. Until contrary facts are available it must be assumed that suitable conditions exist in Ethiopia for a great extension of schistosomiasis infection with the impending development of the country and increased population movements.

SUMMARY

1. The internal and external morphology of six species of freshwater gastropod molluscs collected in the vicitinity of Debra Markos (8,100 ft.) by the Cambridge Botanical Expedition to Ethiopia 1957 is described. The species are: *Bulinus sericinus* (Jickeli), *Biomphalaria rueppelli* (Dunker), *Gyraulus costulatus* (Krauss), *Anisus natalensis* (Krauss), *Lymnaea truncatula* (Müller), and *Lymnaea natalensis* Krauss.

2. Evidence is presented to show that *Bulinus shackoi* (Jickeli) represents an extreme form in a continuous range of variation within *Bulinus sericinus* (Jickeli). *B. sericinus* is regarded as being closely related to *B. truncatus* (Audouin), but reasons are given for preserving its distinct status within the *truncatus* group.

3. A small species of planorbid which closely resembles *Anisus abyssinicus* (Jickeli) conchologically has been assigned to *A. natalensis* (Krauss) after study of the internal anatomy of the Ethiopian and South African material. The structure of the penis differs from all previous descriptions of species of *Anisus* and related genera.

4. Differences have been found between the large samples of *Lymnaea truncatula* collected and the type specimen of *L. mweruensis* Connolly, the significance of which can only be assessed when further material from the type locality of the latter species is available.

5. The absence from the collection of species that are widespread in freshwaters over the rest of Africa is discussed.

APPENDIX

Climate

Although there is some rainfall in every month of the year in the Ethiopian Highlands, two distinct wet seasons occur, the "little" rains in the early part of the year and the main rains that last from the beginning of July to September in the vicinity of Debra Markos.

The expedition made daily recordings of rainfall, and maximum and minimum temperatures, and comparable data were obtained from Debra Markos airfield. Midday temperatures at Camp 1 (9,800 ft.) were about 15° C. and the average night minimum 7° C. At Camp 2 (11,700 ft.) the extremes were more marked, at midday the temperature often rose above 21° C. and at night fell to freezing point.

Geographical Positions of Collecting Points

Camp 1. Eight miles south-west of Mt. Talo and 20 miles north of Debra Markos, on the " old Italian road " running across the mountains to Mota. Close to a Wednesday hill-top market. 37° 48′ E., 10° 31′ N. 9,800 ft.

Camp 2. About 28 miles NNE. of Debra Markos. On the ridge known as Arat Makereke just below the easternmost and largest of the peaks, above the village of Arogay Amba. 37° 48′ E., 10° 35′ N. 11,700 ft.

Collecting Stations

1. Ussata Stream near Nug-Oil plant, Debra Markos. 37° 43′ E., 10° 30′ N. 8,100 ft. Stream flowing rapidly through marshy meadowland. Exposed to the sun, with brown muddy water and a few still bays at the edges. *Callitriche* and *Polygonum* present. Dry from February to April inclusive.
2. Abbain stream, 2 miles south of Debra Markos by Addis Ababa road. 8,000 ft. Slow flowing, with muddy water and rushes at the edges. Average width 12 ft., maximum depth 6 ft.
3. Small stream arising from a spring near Abbain stream, 37° 45′ E., 10° 03′ N. 7,800 ft.
4. Stream 4 miles west of 37° 45′ E., 10° 03′ N. 7,800 ft. Slow flowing with muddy water and bottom. 10–20 ft. wide, more than half filled with tall rushes. Dammed to make a bathing pool.
5. Large stream by ford at Ejubi, 15 miles south of Debra Markos. 7,900 ft. Very slow flowing and muddy with wide marshes. Choked with rushes except at ford.
6. Small stream, 1–10 ft. wide, with marshy depressions, 20 miles north of Debra Markos. 37° 48′ E., 10° 31′ N. 9,9000 ft.
7. Temporary marsh with vegetation of wet meadow type with *Ranunculus* and *Carex* dominant, 9 miles north of Debra Markos. 8,600 ft.
8. Similar to 7. 10,000 ft.
9. Marshy seepage area ½ mile from Camp. 2. 12,000 ft.
10. Small fast flowing clear stream, 28 miles NNE. of Debra Markos. 37° 48′ E., 10° 35′ N. 11,700 ft.
11. Temporary marsh beside Ussata stream in Debra Markos (locality 1).

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List of Labels used in Figures

ag—albumen gland
an—anus
ca—carrefour
cvd—cut end of vas deferens
ic—interstitial cusp
imr—intermediate mantle ridge
k—kidney
lpl—left pilaster
lpp—lumen of preputium
mc—mantle collar
mct—cut edge of mantle
med—median rectal ridge
n—cell nucleus
ng—nidamental gland
ot—ovotestis
ov—oviduct
p—penis
pa—papilla
pb—pseudobranch
pc—pericardium
pd—distal part of prostate
pf—prostate fold
pp—preputium
pr—prostate
ps—penis sheath
rm—retractor muscles of preputium
rr—lateral rectal ridge
rpl—right pilaster
s—transverse septum
sp—spermatheca
spd—spermathecal duct
ur—ureter
ut—uterus
vd—vas deferens
vs—vesicula seminalis

PLATE 8

Top row: left—*Lymnaea natalensis* (Krauss), form resembling *L. exserta* (Martens), from locality 1 (×3); right—*L. natalensis*, form resembling *L. natalensis caillaudi* (Bourguignat), from locality 1 (×3).

Middle row: left—*Lymnaea truncatula* (Müller), locality 6 (×6); right—*L. mweruensis* Connolly. Type specimen from Mweru, Mt. Kenya (×6).

Bottom row: *Bulinus sericinus* (Jickeli), left to right—typical form from locality 1 (×4); "*shackoi*" form from locality 1 (×4); ribbed form from locality 3 (×4); inflated form from locality 2 (×4).

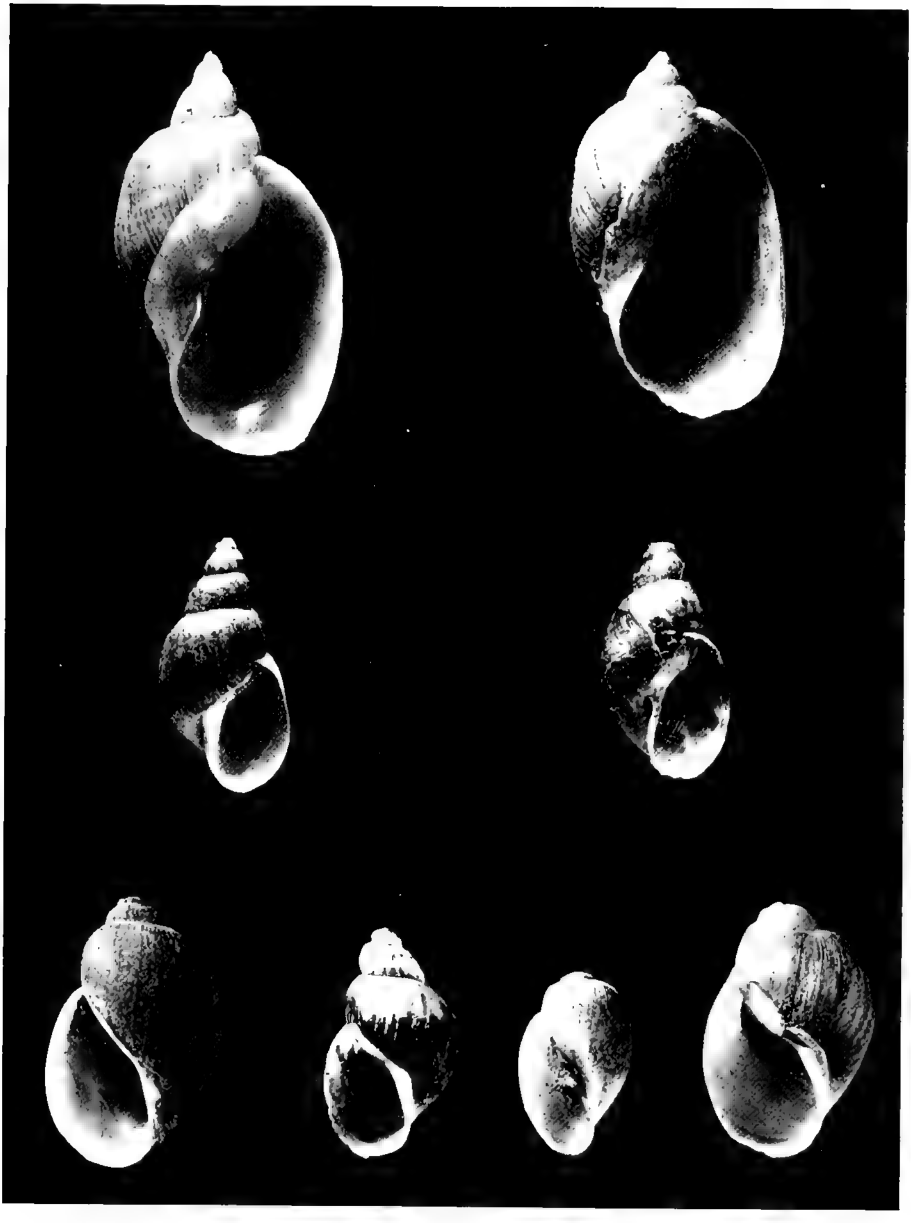
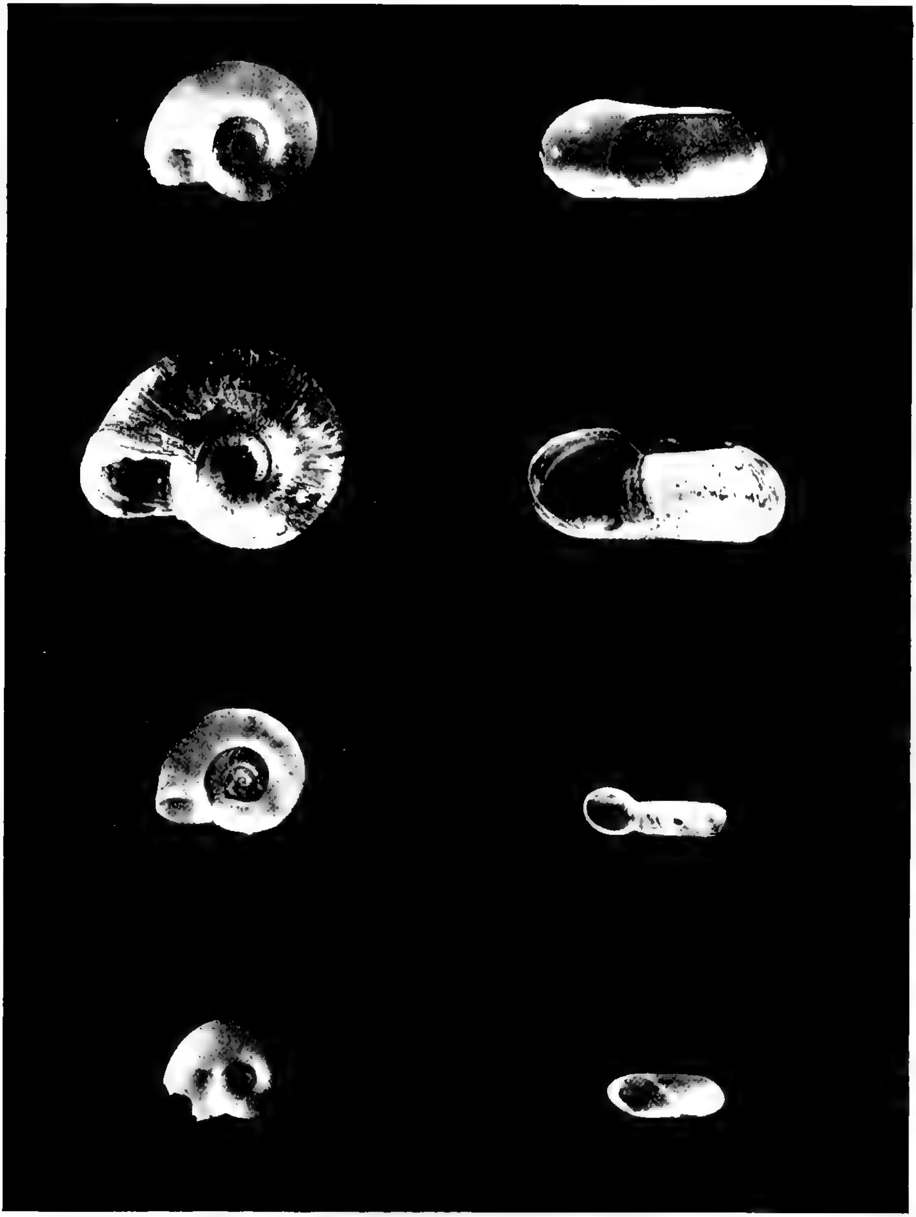


PLATE 9

Top row : *Biomphalaria ruepelli* (Dunker), from locality 3 (×3) (Apertural view ×4).
Second row : *B. rueppelli*, "*adowensis*" form from locality 3 (×4).
Third row : *Anisus natalensis* (Krauss) from locality 4 (×6).
Fourth row : *Gyraulus costulatus* (Krauss) from locality 3 (×6).



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By B. P. HALL & R. E. MOREAU

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INTRODUCTION

THE latest comprehensive list of birds of the Ethiopian Region, that of Sclater (1924–30), gives about 1,700 species of land-birds (most of them polytypic) as resident on the continent of Africa south of the Sahara; and of these about one-fifth are mentioned as known only from the type locality or from a very limited area. Although since 1930 further collecting has shown many of these birds to be more common and/or widespread, and taxonomic study has reduced a number to the status of subspecies (or synonyms), enough apparently rare species remain to provide a striking contrast with, for example, the Palaearctic Region and hence to present in Africa an evolutionary problem that merits discussion. To put this in perspective it is useful to recall that the area of Africa south of the Sahara amounts to about eight million square miles. Moreover, since the Secondary epoch it has not been subjected to any extensive invasion or dissection by the sea and has carried the same climatic belts as the present, particularly the equatorial rainbelt, flanked on each side by a belt of savanna climate (with a long dry season), though not necessarily in exactly the locations they now occupy (Moreau, 1952).

It is necessary at the outset to determine what limits to apply for purposes of discussion; and in the nature of the case they have to be arbitrary. After some trials we have decided to deal with all those species occurring on the African mainland which appear in Sclater's list (together with those subsequently described) as known from a range, whether discontinuous or not, that does not extend more than 250 miles in any direction. This means that the greatest possible area within the scope of this discussion would be 250 miles each way. Even this, though slightly larger than England and Wales, represents less than 1% of the area of the Ethiopian Region; but, as will appear from the discussion below, nearly all the species known to be strictly localized prove on examination to be confined individually to areas of less than 3,000 square miles, about 0·04% of the land surface south of the Sahara (and about the size of Kent and Sussex combined).

If we apply these criteria strictly we find that 333 of Sclater's " species " qualify for primary consideration and about a quarter of these still do so in the light of the latest information, both geographical and taxonomic. We have added 13 that merit special consideration, because they are known from very few specimens indeed, and/or are known from only two localities remote (more than 250 miles) from each other.

The selected 96 species are discussed individually in the following pages, and the remaining species are relegated to the appendix, with reasons there given. For each selected species we discuss whether the recorded range is likely to be extended by further exploration. Where the bird concerned lives exclusively in a certain vegetation type, especially montane evergreen forest,[1] an attempt has been made with the aid of large-scale contoured maps, from published statements, through correspondence and occasionally from personal knowledge, to assess the total area of suitable habitat. From the area occupied some idea can be formed of how many individuals such as restricted species may number at the present time.

While in selecting species for discussion an exact standard can be applied for the geographical limits, no such standard is possible in deciding whether certain populations, isolated from their nearest relatives, qualify as species (and therefore merit discussion) or as subspecies. The taxonomist's judgement of degree of relationship in birds that are not only fully allopatric (namely, those whose ranges do not overlap) but are also geographically isolated, is ultimately subjective, a personal assessment of whether, given the opportunity, the birds would freely interbreed. Moreover, his criteria may not be identical in all groups of birds. At one extreme, two birds can generally be accepted as conspecific when their differences are slight, especially when affecting only a single character. At the other extreme there is no difficulty in accepting as distinct species birds which, though obviously related, show such differences in size, proportions, colour, pattern, voice or behaviour that interbreeding would not be expected in nature whatever the opportunity. Between the two extremes there fall numerous doubtful cases in which check-list convention demands a yes-or-no decision which cannot in fact be respectably scientific. For our purpose we need not be bound by this, and in the case of 16 birds we thankfully take refuge in the means of evasion provided by Mayr (1942 : 165) when he proposed the term " semi-species " for those geographically isolated forms about whose status it is difficult to come to a decision.

We have also found it advantageous to use the concept of the superspecies, as

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[1] As defined and mapped in the *Vegetation Map of Africa*, 1959 (Oxford Univ. Press). " In tropical Africa, evergreen forest above 1300 m. altitude usually differs from its lowland counterpart in floristic composition, in the abundance of epiphytic bryophytes and in the smaller height of the trees. *Olea, Ocotea, Juniperus, Podocarpus, Schefflera* and *Pittosporum* are among the many general characteristic of this type." For the occurrence of typical montane bird communities 1300 m., equivalent to 4,250 ft., is on the low side except on mountains very close to the sea. Inland the altitude of 5,000 ft. is more acceptable as the lower limit (cf. Chapin, **1** : 91).

redefined by Mayr *et al.* (1953 : 29)—" a monophyletic group of very closely related and largely or entirely allopatric species ". Again, the classification is to some extent subjective : " either the species, although completely isolated from each other, are morphologically as different as normally sympatric species, or they are in geographical contact without interbreeding or there is actually a slight distributional overlap ". Our " rare " species have been assigned to superspecies wherever it seemed appropriate to do so. It may be noted that, allopatry being a criterion for acceptance as semispecies, birds so classified are *ipso facto* regarded as members of superspecies.

Under specific headings in the systematic list critical papers are given in full but not listed in the bibliography, while references to the standard regional handbooks are quoted only with the author's name, volume and page number (e.g. Bannerman, **6** : 118) and full titles are listed in the bibliography. For convenience, the order and nomenclature used in our list are based primarily on Sclater, but modified to come more into line with those modern taxonomic conceptions which seem to be generally accepted.

We would emphasize that much of the detail in this study is provisional. Further exploration will increase some of the known ranges and further study modify some of the taxonomic judgements, but we believe that the main impressions will hold good.

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SYSTEMATIC LIST

The number in brackets in each specific heading refers to the number of that species on the accompanying map.

PHASIANIDAE—Pheasants and Francolins

Francolinus harwoodi (64)

Cheesman & Sclater, 1935, *Ibis* (13) **5** : 188. Praed & Grant, **1** : 244.

Known only from the type locality and the two places from which Cheesman obtained specimens, all of which lie within about a hundred miles on the Upper Blue Nile or its tributaries, in mountainous country south-east of Lake Tana (not " south-west " as given by Praed & Grant). If, as seems possible, the habitat of this species is the gorges of the river, its actual range must be very limited, but from Cheesman's remark that it was well known to the local people and prized for the table, its numbers may not be small.

F. harwoodi appears to be a member of the *natalensis/hildebrandti* group, which are birds often found in thick cover in rocky river valleys from Natal to central Kenya. The males of *harwoodi* look most like those of the southern *natalensis*, having a similar distinctive U-shaped pattern on the black-and-white feathers of the breast, differing from the plainer feathers of the East African *hildebrandti*. The females are not known, but when found it will be interesting to see whether, like those of *natalensis*, they resemble the males, or whether they have orange breasts like the female *hildebrandti*. The three species should be considered as members of a superspecies.

Francolinus camerunensis (65)

Bannerman, **1** : 332. Boulton & Rand, 1952, *Fieldiana Zool.* **34** : 39. Chapin, **1** : 710. Schouteden, **1** : 239.

Known from about a dozen specimens from the forest on Mount Cameroon between 5,000 and 7,000 ft., which would give it a range of less than 80 square miles. It is unlikely to occur elsewhere since Serle has not found it in similar habitat on neighbouring mountains where, however, there is no evidence that it is replaced by another species. (Schouteden has shown that the bird described as *Francolinus camerunensis ruandae* Saceghem, 1942, *Bull. Soc. Bot. Zool. Congol. Leopoldville*, **5** (1–2) : 18, is a specimen of *F. nobilis*.)

Chapin suggests that *F. camerunensis* may be allied to *F. nobilis* of the eastern Congo mountains and *F. jacksoni* of Kenya, which occupy the same ecological niche. To these we would add *F. castaneicollis*, *F. erckelii* and *F. ochropectus* of north-eastern Africa and *F. swierstrai* of Angola. While the differences in colour and pattern among these species are considerable each species has sufficient points of similarity with at least one of the others for us to regard them all as forming a superspecies. The male of *camerunensis* is closest to that of *nobilis*, both having red bills and legs and a patch of scarlet skin round the eye : both are plain, relatively unpatterned birds but whereas *camerunensis* is dark brown and grey, *nobilis* is a rich maroon chestnut on the mantle and underparts. Recent collecting by Boulton and by Serle (awaiting publication) has confirmed that there is striking sexual dimorphism in *camerunensis*, the female being heavily patterned in brown, black and white. *F. swierstrai* (see below) also has marked sexual dimorphism and in most other members of the superspecies the females tend to be either duller or more vermiculated on the wings than the males.

Francolinus swierstrai (18)

Chaetopus swierstrai Roberts, 1929, *Ann. Trans. Mus.* **13** : 72—Mombolo, Cuanza Sul, Angola. Synonym *Francolinus cruzi* Themido, 1937, *Ext. Compt. Rend. 12th Congr. Int. Zool. Lisb.* 1935 : 1833—Hanha,[1] Benguela, Angola.

Heinrich, 1958, *J. Orn.* **99** : 322. White, 1945, *Ibis*, **87** : 466. Hall, 1960, *Bull. Brit. Mus. (Nat. Hist.) Zool.* **6** (7) : 407. Traylor, 1960, *Publ. Cult. Co. Diam. Ang. Lisboa*, **51** : 142.

Found in or on the edge of montane forest in the Bailundu highlands and on the Mombolo plateau, and in 1956 by Rudebeck (awaiting publication) in a patch of relict forest on the Chela escarpment 200 miles to the south. Much of the montane forest in Angola has recently been destroyed and suitable habitat is probably now limited to a few square miles on such peaks as Mount Moco and Mount Soque and even smaller patches on the higher parts of the escarpment.

F. swierstrai has a red bill and legs like *camerunensis*, *nobilis*, *jacksoni* and *castaneicollis* but has no red skin round the eye. The male, with its black-and-white underparts, is unlike any other of the montane francolins in the colour of the plumage, but is rather similar to *jacksoni* in pattern and has been noted to have a similar call. The female (on Traylor's description) differs from the male in being marked above with blotches and vermiculations and having a different pattern below. In these respects the sexual dimorphism is similar to that found in *F. camerunensis*, but Traylor (*in litt.*) tells us that the patterning of the two females is not very similar. In spite of the distance separating *swierstrai* from other members of the group we consider it part of the superspecies.

Francolinus jacksoni (46)

Jackson, 1938, **1** : 256. Praed & Grant, **1** : 254. Chapin, **1** : 710.

Found in the Kenya Highlands on both sides of the Rift : in the east on Mount Kenya and the Aberdares from the edges of forest and bamboo between 7,500 and 10,000 ft., in the west from the Mau (*Ibis*, 1915 : 19) at the southern end, and from the Cherenganis at the northern end (Williams *in litt.*). The area in which the species occurs may reach 5,000 sq. miles. Three subspecies have been described but verification with longer series is desirable.

F. jacksoni, with its plain chestnut-and-white feathers of the neck and underparts, reddish tail and red eyelids, is in some ways intermediate between *nobilis* of the East Congo mountains and *castaneicollis* of southern Abyssinia, and is closest to the western race of the latter, *F. c. kaffanus*. *F. nobilis* is a more richly pigmented and less patterned bird with a blackish tail and extensive bare skin round the eye, while

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[1] We take this "Hanha" to be the locality on the escarpment (13° 18′ S., 14° 12′ E.) not the one in the environs of Benguela town, as assumed by Themido, where *F. swierstrai* is most unlikly to occur.

F. castaneicollis is heavily patterned with black, grey, chestnut and white (except in *F. c. atrifrons*), has a brown tail and apparently no red skin round the eye or on the eyelids.

Francolinus ochropectus (63)

Francolinus ochropectus Dorst & Jouanin, 1952, *Oiseau*, **22** : 71—Plateau du Day, Cercle de Tadjoura, French Somaliland.

Dorst & Jouanin, 1954, *Oiseau*, **24** : 161–170.

Known only from one area of forest above 3,500 ft., predominantly *Juniperus procera*, about 9 sq. miles in extent. In southern Abyssinia and in the Gadabursi Hills and the Golis Range of (British) Somaliland the juniper forests are occupied by *F. castaneicollis*, while in northern Abyssinia and Eritrea *F. erckelii* is the montane francolin, so it seems very likely that *ochropectus* is confined to the Plateau du Day.

F. ochropectus is closest to *F. erckelii*, having a similar blackish bill and yellow legs (unlike the other members of the superspecies). It has also similarities in the pattern of the feathers though differing strikingly in colour, being predominantly a grey bird with grey and dull orange markings, instead of a brown bird with rich chestnut markings. Nevertheless the relationship between the two seems closer than that between any other two members of the superspecies and it may be best to regard *ochropectus* as a semi-species.

OTIDIDAE—Bustards

Eupodotis humilis (60)

Archer & Godman, **2** : 350. Peters, **2** : 223.

The smallest of the African bustards, known definitely only from (British) Somaliland, where the extreme localities for specimens are Bulhar, on the west coast, and Bohotleh, 200 miles to the south-east, but there is no obvious ecological reason why it should be so restricted and Archer expected it would be found more widely in the semidesert to the south and east, which has hardly been explored ornithologically.

In appearance *E. humilis* is most like *E. vigorsii* and *E. rüppellii* of south-western Africa, and notwithstanding the difference in size and the distance intervening the three can be regarded as forming a superspecies.

COLUMBIDAE—Pigeons

Columba albinucha (51)

Van Someren, V. G. L. & G. R. C., 1949, *Uganda J.* **13**, spec. suppl. : 25. Goodwin, 1959, *Bull. Brit. Mus.* (*Nat. Hist.*) *Zool.* **6** (5) : 14.

A handsome pigeon known from nine or ten different localities in an area of lowland forest about 200 miles by 50 in the eastern Ituri district of the Congo and in the adjacent Bwamba district of Uganda, where it was common. It may well be found to have a wider range.

It was thought at one time to be a race of the widespread *C. arquatrix*, which it resembles in some respects of colour and pattern. The Van Somerens however found the two birds together at Bwamba, where both fed in the lowland forests by day but *C. arquatrix* returned at night to higher ground. Since *arquatrix* is typically a highland bird it seems possible that the breeding ranges of these two pigeons do not actually overlap, but they must be in close proximity. In the circumstances, while they are evidently closely related, we, like Goodwin, regard the two as distinct species, but in view of the possible overlap not as members of the same superspecies. This view is open to revision if it is proved that the breeding ranges are segregated.

MUSOPHAGIDAE—Turacos

Tauraco ruspolii (58)

Benson, 1945, *Ibis*, **87** : 499. Moreau, 1958, *Ibis*, **100** : 107.

Known with certainty only from the isolated juniper woods above 6,000 ft. at Arero, where Benson found it. The locality at which the type was collected is not known but from the collector's route Moreau has shown that it also could well have come from Arero. The juniper woods at Arero are only about 10 sq. miles in extent, according to Benson (*in litt.*). From personal experience he believes the bird to be absent from the highland forests nearest to Arero to the west, namely at Mega, Yavello and Alghe. The most likely other place for *ruspolii* to be found seems to be a still smaller patch of juniper about 35 miles to the east of Arero, but the possibility cannot be excluded that it may be discovered somewhere to the north-east, if any suitable habitat occurs in the 200 miles of ornithologically unexplored country between Arero and Ginir (see *Ibis*, 1958 : 108).

T. ruspolii seems to be allopatric to *T. leucotis*, the species it most resembles, and the two could possibly be considered conspecific. There are, however, conspicuous differences in the colour of the crest, the pattern of the face and the eye-wattle, so that it is best considered at least a semi-species.

Tauraco bannermani (66)

Serle, 1950, *Ibis*, **92** : 357. Moreau, 1958, *Ibis*, **100** : 104.

Found only in the patchy montane forest of the Bamenda–Banso highlands above 6,000 ft., which probably, we estimate, does not exceed 200 sq. miles in all. It is a bird unlikely to be overlooked, and we think it improbable that it will yet be found elsewhere.

T. bannermani is generally very like *T. erythrolophus* of western Angola, over 1,000 miles away, but differs in shape and colour of the bill and the shape of the nostrils. We regard them as forming a superspecies.

STRIGIDAE—Owls

Phodilus prigoginei (86)

Phodilus prigoginei Schouteden, 1952, *Rev. Zool. Bot. Afr.* **46** : 424—Muusi, 2,430 m., highland north-west of Lake Tanganyika.

The genus *Phodilus* is known in Africa only from the type of *P. prigoginei*, which was collected in an unspecified habitat in a locality where typical montane forest birds such as *Tauraco johnstoni* and *Pseudocalyptomena graueri* have been obtained. It may well occur on other mountains west of the Ruzizi valley, but even if so would have a range of less than 500 sq. miles.

The only other member of the genus, *P. badius*, covers a wide range in forests of Asia and Indonesia : *prigoginei* and *badius* differ surprisingly little, slightly in colour, in shape of bill and in size of the feet and claws. The two would be considered conspecific were it not for the immense distance separating them ; but in the circumstances *prigoginei* is regarded as a species, forming a superspecies with *badius*.

Bubo vosseleri (37)

Praed & Grant, **1** : 661. Peters, **4** : 118.

An eagle-owl known only from the type and another specimen " half-grown and still covered with nestling feathers, but certainly *B. vosseleri* " (Stresemann *in litt.*), also from Amani (3,000 ft.) in the East Usambara Mts. It must surely be a forest bird but, while nothing could be easier to overlook than an owl, Moreau and his African collectors in 18 years at Amani had no definite indication of this bird's existence. It may be added that it cannot now be ascertained where the information given by Praed & Grant on its food etc. came from (Praed *in litt.*), and there may perhaps have been some transposition of data.

On present evidence, *B. vosseleri* might be a bird of lowland forest, reaching its upper limits at Amani or a highland bird occupying one or both of the East and West Usambara massifs. In either case the bird's range would not exceed about 500 sq.miles at the outside.

Peters and Sclater both place *vosseleri* as a race of *B. poensis*, a forest species of West Africa and the northern Congo, the most easterly locality for which is 900 miles from Amani. The two birds differ somewhat in colour and pattern and Stresemann, who has kindly examined the specimens of *vosseleri* for us, considers that it should be kept as a species. It is perhaps best regarded as a semi-species.

CAPRIMULGIDAE—Nightjars

Caprimulgus binotatus (6)

Chapin, **2** : 432.

The type of this dark nightjar was collected at Dabocrom (" forested Gold Coast ", probably inland from Takoradi—see Chapin, **4** : 657) in 1850 but has only been found since by Bates' collectors 900 miles away in the forest of the Cameroons at Efulen, Metet and Bitye, in a triangle of about 400 sq. miles. All the five specimens there were found asleep during the day in tangled creeper. It is a bird that might well be present but undiscovered throughout much of the forest of western Africa, though unlikely to be common. On the other hand the timber-cutting in much of the Ghana forest may have exterminated the species there.

The rectrices of *C. binotatus* do not all lie in the same plane but those forming the two sides meet at an angle. This character has led Chapin and Peters to place the species in a monotypic genus, *Veles*. We agree with Bannerman and Sclater in not accepting this as a generic character.

APODIDAE—Swifts

Apus toulsoni (12)

Lack, 1956, *Ibis*, **98** : 39.

Known only from three specimens taken on the west coast of Africa at Landana and Luanda, 250 miles apart, but may be more common than is supposed since few swifts have been collected in Angola.

Lack, believing only two specimens were known, provisionally placed *toulsoni* as a race of *A. horus*, though suggesting it might be merely a mutation, since it differs only in having the rump the same colour as the back instead of white. A third specimen in New York (Traylor *in litt.*), also from Luanda, reduces the likelihood of *toulsoni* being a mutation. The difference between a white and a dark rump in swifts seems likely to be of more than subspecific importance, but if *toulsoni* is proved to have a breeding range allopatric to that of *horus* it could perhaps be considered an exceptionally well-marked subspecies. On the other hand both *horus* and *toulsoni* have been collected at Landana and if their breeding ranges overlap *toulsoni* must rank as a species. Provisionally we treat it as such.

CAPITONIDAE—Barbets

Lybius rubrifacies (47)

Chapin, **2** : 525.

A black-and-red barbet occupying an area about 100 miles square south and west of Lake Victoria, across the Uganda–Ruanda–Tanganyika borders. Pitman tells us that this is rather open country with euphorbia, acacia and figs, and therefore hardly to be regarded as ecologically peculiar. A hundred miles separate this area from the southern edge of the range of *L. guifsobalito* which inhabits rather richer, more wooded country north of the Kampala–Fort Portal road. The country in between has been little explored ornithologically and is, in Pitman's view, more suited to *rubrifacies*, which may therefore have a more extensive range—up to some 20,000 sq. miles.

The two birds are very alike, but *rubrifacies* has a paler bill and lacks the red throat and white-edged wing-coverts of *guifsobalito*. They may also have different calls, for Pitman has never heard in *rubrifacies* territory any call similar to the distinctive and penetrating call of *guifsobalito*. We think the two should be regarded as forming a superspecies.

Lybius chaplini (24)

Pitman, 1932, *Ibis* (13) **2** : 304. Benson & White, 1957 : 62.

A distinctive brown-and-white barbet with a red face found in an area 150 miles square between the Kafue River, Kalomo and Lusaka in central Northern Rhodesia. Pitman found it in woodlands, thickets and open cultivation. Benson (*in litt.*) tells us that it tends to inhabit more open country, and is perhaps more strictly confined to figs, than the common red-and-black barbet of the area *L. torquatus*, though both may be seen together. Their voices are quite distinct.

The relationship in eastern Africa between the brown-and-white barbets of the *leucocephalus* group and the predominantly black-and-red barbets of the *torquatus* and *guifsobalito/rubrifacies* group is too complex to discuss fully here. It is sufficient to say that since similar distinctive patterns and colours occur in forms of both groups there may have been interbreeding, resulting in hybrid populations that have become stabilized. *L. chaplini* appears to be one such. It is most like the *leucocephalus* group, in particular the Kenya white-bellied race *L. l. senex*, but has some red in the head and yellow edges to the wings and tail, which suggests the influence of *torquatus*. It is, however, separated by 800 miles from the main range of the *leucocephalus* group in the Iringa district of central Tanganyika, and by 900 miles from the isolated *L. leucocephalus leucogaster* at Quilengues in western Angola. A possible inference is that the brown-and-white birds were once more widespread south of the equator but have been invaded and overrun by the black-and-red birds, leaving an isolated brown-and-white population in western Angola, and a hybrid population in Northern Rhodesia which has developed into a full species.

INDICATORIDAE—Honey-guides

Indicator pumilio (87)

Indicator pumilio Chapin, 1958, *Bull. Brit. Orn. Cl.* **78** : 46—Tshibati, 6,400 ft., south-west side of L. Kivu, Congo.

A small honey-guide found in the mountains west of Lakes Edward and Kivu, in the Kivu volcanoes and south to Itombwe north-west of L. Tanganyika (Chapin *in litt.*). All the localities lie within a strip 200 miles by 80, of which not more than about 4,000 sq. miles provides suitable habitat.

It is found alongside *I. e. exilis*, which it resembles most closely in general colour and pattern, but which is larger and heavier, with a disproportionately larger bill. Chapin (1958 and **4** : 633) believes the small bill of *pumilio* may indicate relationship with the paler *meliphilus* of East Africa (which he shows should be regarded as specifically distinct from *exilis*) ; but he thinks the differences in colour are great enough to warrant regarding *pumilio* as a distinct species. These colour differences are, in fact, no greater than those between *I. conirostris* and *I. minor*, which are usually now regarded as conspecific, but whereas the darker coloration of *conirostris* and the paler of *minor* can be correlated with habitat in forest and more open country respectively, this seems not to be true of *pumilio* and *meliphilus*, for *meliphilus* has been recorded from forest, in Northern Rhodesia and Nyasaland, as well as from Brachystegia, in Nyasaland, and acacia, in Kenya (cf. Benson, 1953 : 45 ; Benson & White, 1957 : 65 ; Granvik, 1934 : 51). In the present state of knowledge of the ranges and relationships of *pumilio, exilis* and *meliphilus* it is impossible to designate a superspecies.

PICIDAE—Woodpeckers

Campethera tullbergi (67)

Serle, 1950, *Ibis*, **92** : 349, 366 ; 1954, *Ibis*, **96** : 60 ; 1957, *Ibis*, **99** : 417. Chapin, **2** : 568.

Known from montane forest on the Obudu plateau of Eastern Nigeria, Cameroon Mt., Kupé Mt., Rumpi Hills and the Bamenda–Banso highlands above 5,000 ft. but nowhere common, the total area inhabited probably not exceeding 350 sq. miles. (A dark specimen from Oku in the Banso highlands has been separated as *C. t. wellsi*, but see Serle, 1950.)

Chapin suggests that *C. tullbergi* is allied to *C. taeniolaema* of montane forest in the eastern Congo and East Africa. Indeed, with the upper parts indistinguishable, the two are more similar than are the little woodpeckers *cailliautii* and *permista*, respectively spotted and striped below, which are now known to interbreed (Chapin, 1952, *Ibis* : 535). Below, *taeniolaema* is heavily barred, while *tullbergi* has a spotted abdomen and fine vermiculations on the throat and chest, more pronounced in the female ; and since, unlike *cailliautii* and *permista*, they are separated by over 1,000 miles we regard them as semi-species at least.

EURYLAIMIDAE—Broadbills

Pseudocalyptomena graueri (88)

Lowe, 1931, *Proc. Zool. Soc. Lond.* : 445–461. Schouteden, **6** : 7.

A green broadbill known only from three places in montane forest at about 6,500 ft. west of the Ruzizi valley, north of Lake Tanganyika. Its total area inhabited may well be under 2,500 sq. miles.

Lowe has shown that anatomically *Pseudocalyptomena* has diverged little from the oriental members of the family, to some of which it is more similar in plumage than to the other African genus of broadbills, *Smithornis*.

ALAUDIDAE—Larks

Mirafra williamsi (55)

Mirafra williamsi Macdonald, 1956, *Bull. Brit. Orn. Cl.* **76** : 71—Marsabit, Kenya.

Discovered in " an overgrazed area " with sandy soil, some grass and small bushes near Marsabit and in the Didd Galgalla desert 36 miles to the north on black lava soil. It must be expected more widely in the semi-desert areas of north-eastern Kenya and Somaliland.

Macdonald found *williamsi* to be most like *M. cordofanica* of the southern edge of the Sahara, though it has a stouter bill and is dark brown and not sandy-rufous on the back. Further field observations are needed to establish its affinities.

Mirafra pulpa (54)

Mirafra pulpa Friedmann, 1960 (Apl.), *Occ. Pap. Bost. Soc. Nat. Hist.* **5** : 257—Sagon (= Sagan) R. at long. 37° 30″ E., Shoa, Ethiopia. (Synonym *Mirafra candida* Friedmann, 1930 (July), *Auk*, **47** : 418—Archer's Post, northern Guaso Nyiro R., Kenya.)

Praed & Grant, **2** : 46. White, 1960, *Bull. Brit. Orn. Cl.* **80** : 22. Hall, 1961, *Bull. Brit. Orn. Cl.* **81** : 108.

M. pulpa is provisionally regarded as a species, pending further investigation into the ecology and taxonomy of the larks of northern Kenya. It is known only from one specimen from the type locality, and one adult and two young birds from Archer's Post, 300 miles to the south. Like the preceding species, it may prove to have a wide range.

It has been considered by different authors as conspecific with *M. cantillans marginata* and with *M. williamsi*, both of which occur in the area between the two *pulpa* localities, *williamsi* in the more arid, and *cantillans* in the less arid districts. However Hall has shown there are differences in size and colour which indicate it is distinct from both other species.

Calandrella fringillaris (21)

Gyldenstolpe, 1927, *Arkiv. Zool.* **19** : 23 ; 1934, *Ibis*, (13) **4** : 291. Meinertzhagen, 1951, *Proc. Zool. Soc. Lond.* **121** : 89–100. MacLachlan & Liversidge, 1957 : 254.

Known only from two stations (Leeuw Spruit and Vredefort Road) on the main railway west and north-west of Heilbron, northern Orange Free State, and from 126 miles to the north-east in the Transvaal at Bethal and at Estancia (20 miles east of Bethal), where Prozesky has recently collected three males. He has provided the only field notes available on this lark (notes attributed to *Alauda fringillaris* prior to 1927 refer to *Mirafra passerina*—see Gyldenstolpe) which he found in small flocks of about ten birds on short-grass veld : they appeared dark in the field. Maps 1 and 2 in Acock's " Veld Types of South Africa " (1953, *Union of S. Afr. Dept. of Agric. Bot. Surv. Mem.* 28) suggest that the lark may be associated with the area of Sweet Grassveld in which these localities lie, and which now has a discontinuous distribution in the Transvaal but was formerly more widespread.

Botha's Lark bears a striking resemblance to *Calandrella* (*Spizocorys*) *c. conirostris*, the race of the Pink-billed Lark found in the Orange Free State and Transvaal. The male, female and immature bird (the type of *Botha difficilis*) of *C. fringillaris* in the British Museum, and the three males from Estancia, show that the two species differ chiefly in the legs and feet ; *fringillaris* has comparatively long legs (tarsus ♂ 21, ♀ 20 mm.) and a long hind claw, which is straight and stout for 10–15 mm. in the male and straight for 10 mm. in the female, tapering thereafter to a fine curved tip : the tarsus in *conirostris* is under 18 mm. and the hind claw short and curved. There is also a difference in the wing, that of *fringillaris* being longer (♂ 83–84, ♀ 81 mm.) with a well-developed first (outside) primary extending about 11 mm. beyond the coverts, whereas in *conirostris* the wing is under 80 mm. and there is no visible first primary. *C. fringillaris* is paler on the abdomen than birds of the eastern race of *conirostris* (though western races of *conirostris* are paler throughout) but matches in colour and pattern above, and in the tail. Both species have similar heavy, pink bills and are alike in immature plumage. (The young bird examined of *fringillaris* has a white throat as in the adult, contrary to the statement by McLachlan & Liversidge.) Meinertzhagen has shown that there are not sufficient grounds for recognizing either *Botha* or *Spizocorys* as distinct from *Calandrella* and with this we agree.

The other closely-related South African lark is the paler *Calandrella starkii* with a horn-coloured bill, which is sympatric with *C. conirostris* through much of the range of that species in the west but which does apparently extend eastwards as far as Heilbron or Bethal and may be replaced here by *C. fringillaris.* However since both *starkii* and *fringillaris* seem to be more closely related to *conirostris*, with which they are sympatric, than to each other, they cannot be regarded as forming a superspecies.

Calandrella obbiensis (59)

Meinertzhagen, 1951, *Proc. Zool. Soc. Lond.* **121** : 89–100. White, 1958, *Bull. Brit. Orn. Cl.* **78** : 80.

Known only from three specimens taken at Obbia and Mogadishu, 300 miles apart on the coast of Somalia, but likely to be more widespread and less rare than this would indicate.

It is a puzzling species, for which no field notes are available, and its generic associations are uncertain. Meinertzhagen included it provisionally with *Calandrella,* though noting that it had a longer first primary than others of that genus. No one seems to have discussed its status in relation to *Eremalauda dunni* of the Sahara and Arabian desert (which Meinertzhagen regards as an atypical *Ammomanes*). Though *obbiensis* and *dunni* differ in colour they have similar bills, first primaries and feet, except that *obbiensis* has a slightly longer and straighter hind claw. They may be related, but only further collecting and field data of *obbiensis* can resolve this.

MOTACILLIDAE—Wagtails and Pipits

Anthus sokokensis (38)

Sclater & Moreau, 1932, *Ibis* (13) **2** : 670. Moreau, 1940, *Ibis* (14) **4** : 456. Hall, 1961, *Bull. B.M.* (*Nat. Hist.*) *Zool.* **7** (5) : 281.

Known only from (*a*) the Sokoke forest on the coast north of Mombasa, (*b*) scrubby forest at Moa, 100 miles south along the coast, and (*c*) the Pugu forest (at about 1,000 ft.) west of Dar-es-Salaam, a further 120 miles south. It is not a typical forest bird but is found on the edges or in clearings of these coastal forests, which are of a poor type. Similar habitat occurs sporadically on this stretch of the coastal plain and perhaps may do so further south. It may well not now exceed an area of a few hundred square miles in all, but would have been more continuous in recent historical times before the coastal belt suffered from " development ".

The rich colour, blotchy markings on the throat and breast, and pointed rectrices make *A. sokokensis* look unlike any other pipit. Although it has points of size, structure and pattern in common with *A. caffer* (see Hall), in our view the two birds are too distinct to be treated as a superspecies.

Macronyx sharpei (45)

Jackson, **2** : 831. Praed & Grant, **2** : 78.

Common but very local on open grass and in cultivation between 7,000 and 8,000 ft. on either side of the Rift Valley in Kenya, but not apparently found on the neighbouring mountains of Mt. Elgon and Mt. Kenya. Suitable habitat cannot cover more than half the 2,500 sq. miles which lie between the contours mentioned.

M. sharpei looks very like the widespread yellow-throated longclaw, *M. croceus*, which is typically a bird of lower altitudes. However, *M. sharpei* is more lemon-yellow below, with no continuous black collar on the breast, has different field characters and is smaller, which is the reverse of the rule within those species which show difference of size with altitude. Evidently it must be accepted as a species.

TIMALIIDAE—Babblers etc.

Turdoides hindei (44)

Van Someren, 1932, *Nov. Zool.* **37** : 338.

Apparently limited to an area of less than 2,500 sq. miles of broken savanna country in the eastern foothills of the east Kenya Highlands, approximately Fort Hall–Kitui–south Ukamba (Machakos). On the north and west *T. melanops* is recorded from within 40 miles at Nanyuki and Kikuyu.

The plumage of *hindei* is a mixture of sooty brown, white and rufous with exceptional individual variation, which naturally suggests hybrid origin. It is difficult to suggest, however, how the characters of *hindei* can have been arrived at by interbreeding between any of the other species of East African *Turdoides*, for none are as dark or have as much rufous in the plumage. In pattern and colour certain specimens of *hindei* suggest a close relationship with *T. leucopygia*, which occurs in much of eastern and central Africa but not in Kenya (in fact, not between southern Abyssinia and south-western Tanganyika), but the tail of *hindei* is somewhat longer than the wing, instead of shorter as in *leucopygia*. Of the Kenya species which seem closest, the brown-and-white, almost unpatterned *T. hypoleuca* also has a long tail, and occurs in the same country as *hindei*, while *melanops*, which *hindei* appears to replace, has something of the same scalloped pattern to the plumage but a short tail. There seems no alternative at present to regarding *hindei* as a species.

Lioptilus rufocinctus (89)

Chapin, **3** : 223. Schouteden, **6** : 133. Delacour, 1950, *Oiseau*, **20** : 189. Mayr, 1957, *J. Orn.* **98** : 29.

A montane forest babbler known only from seven localities between 5,500 and 9,000 ft. in the 200 miles from Lake Kivu to Mt. Kabobo, west of L. Tanganyika. The area inhabited is probably under 3,000 sq. miles.

Since *L. chapini* was discovered in 1949 in the Ituri district at about 4,600 ft. it has sometimes been considered conspecific with *rufocinctus*, although the birds differ in shape and colour of beak and *rufocinctus* has a distinctive black cap, without eye stripe. Now that Prigogine (1960, *Rev. Zool. Bot. Afr.* **61** : 16) has discovered a new form of *chapini* at 4,800 ft. in forest at Butokolo (28° 16′ E., 2° 42′ S.), south-west of L. Kivu, there is more reason to consider the two as distinct species, though they are not truly sympatric since they apparently live at different altitudes. We regard them as forming a superspecies with *L. gilberti* (see below).

Lioptilus gilberti (68)

Kupeornis gilberti Serle, 1949, *Bull. Brit. Orn. Cl.* **69** : 50—Kupé Mt. near Essusong, British Cameroons.

Serle, 1954, *Ibis*, **96** : 61 ; 1957, *Ibis*, **99** : 630. Mayr, 1957, *J. Orn.* **97** : 29.

Found between 4,000 and 6,000 ft. on Kupé Mt., the Rumpi Hills and the Obudu plateau over the Nigeria border, usually in primary forest, but occasionally in secondary. Neighbouring mountains with apparently suitable habitat have failed to produce this species, so that the total area it inhabits probably does not exceed 70 sq. miles.

L. gilberti was originally ascribed to a new genus, but the discovery of *Lioptilus* (*Kupeornis*) *chapini* later in the same year provided a link with *rufocinctus* and the three birds are now usually considered congeneric. *L. gilberti* is larger than *chapini* and the two differ in the colour and pattern of the throat and breast, but the shape and colour of bill and the colour and pattern of the crown and mantle are very alike.

Picathartes oreas (7)

Webb, 1949, *Avic. Mag.* **55** : 149. Delacour & Amadon, 1951, *Ibis*, **93** : 60–62. Serle, 1952, *Bull. Brit. Orn. Cl.* **72** : 2–6 ; 1954, *Ibis*, **96** : 72. Good, 1953, **2** : 27. Bannermann, **8** : 464.

Known only from a strip 200 miles long and between 20 and 90 miles from the sea, from Mamfe in the British Cameroons to the northern edge of Spanish Guinea. It builds under rocky overhangs in densest forest and suitable nesting sites must be very limited. It may occur further south and east in former French territory but all known localities are comprised in an area of 7,000 sq. miles.

It has differences in structure, colour and pattern from the only other member of the genus, *P. gymnocephalus*, which inhabits the West African forest, from Togoland to Sierra Leone. These peculiar birds have been considered variously as aberrant crows, starlings and babblers ; Bannerman gave the genus family status : Delacour & Amadon concluded that the Picathartes are aberrant babblers ; Serle, 1952, pointed out their similarities to the Malayan *Eupetes macrocercus* (itself of uncertain affinities) and on the basis of personal knowledge thought that the Picathartes should be kept " in or near the Corvidae ".

PYCNONOTIDAE—Bulbuls

Phyllastrephus orostruthus (28)

Phyllastrephus orostruthus Vincent, 1933, *Bull. Brit. Orn. Cl.* **53** : 133—Namuli Mt., Portuguese E. Africa.

Phyllastrephus orostruthus amani Sclater & Moreau, 1935, *Bull. Brit. Orn. Cl.* **56** : 16—Amani, Tanganyika.

Vincent, 1935, *Ibis* (13) **5** : 365.

The two patches of montane forest in which the only two known specimens of this bulbul have been collected are 700 miles apart. Even in these patches it is probably very uncommon, for it has a distinctive song which would not allow any great numbers to remain unobserved. It might still be found on other mountains with forest patches, but it seems possible that it is a species which has been overrun by the widespread *P. fischeri*, the common *Phyllastrephus* of all types of East African forest. The forest islands in which *orostruthus* has been found total less than 100 sq. miles.

P. orostruthus is a very distinct species with no obvious affinities, the heavy, blotchy streaks on the breast distinguishing it from all other members of the genus.

Phyllastrephus poliocephalus (69)

Chapin, **3** : 173. Serle, 1950, *Ibis*, **92** : 360 ; 1954, *Ibis*, **96** : 63 ; 1957, *Ibis*, **99** : 634. Young, 1946, *Ibis*, **88** : 371.

A bulbul of montane forest apparently common on Mt. Kupé and the Rumpi hills and also found on Cameroon Mt. and the Obudu plateau, eastern Nigeria, but not on Manenguba Mt. or the Bamenda–Banso highlands. The area it inhabits may therefore not exceed 150 sq. miles.

Chapin suggested that *poliocephalus* might be considered conspecific with *flavostriatus* and *alfredi*, which occupy montane forests in southern and eastern Africa. The only outstanding difference in appearance is that *poliocephalus* has uniform bright yellow underparts instead of white with yellow streaks, as in the East African birds. But the song of *poliocephalus* as described by Young is so unlike that of *P. flavostriatus* (see *Ibis*, 1932 : 676) that the current treatment of the two as distinct species may be accepted. They should however be regarded as forming a superspecies.

Phyllastrephus poensis (70)

Serle, 1950, *Ibis*, **92** : 346, 373 ; 1954, *Ibis*, **96** : 63 ; 1957, *Ibis*, **99** : 635.

Found on most of the Cameroon highlands, on the Obudu plateau of Eastern Nigeria and on Fernando Po. Since its habitat is montane forest between 4,500 and 7,000 ft. the actual area it occupies is probably under 500 sq. miles.

P. poensis in the Cameroon highlands and *P. baumanni* of the forest to the west seem to take the place in West Africa of *P. fischeri*, which is widespread in the forests of east and central Africa. The three species look rather alike, though differing in the structure of the bill and the colour of the eye, and together form a superspecies.

Pycnonotus (Arizelocichla) montanus (71)

Serle, 1950, *Ibis*, **92** : 375 ; 1954, *Ibis*, **96** : 65. Chapin, **3** : 118. Peters, **9** : 251.

Only about a dozen specimens are known, from secondary forest and forest clearings above about 5,000 ft. on Cameroon Mt., Manenguba Mt., the Rumpi Hills and the Bamenda–Banso highlands. Serle found it uncommon and the area of suitable habitat probably does not exceed 300 sq. miles though it is possible that the bird may yet be found on the neighbouring Kupé Mt. or the Obudu plateau.

Chapin pointed out that *montanus* may be closely related to *masukuensis*, a bird of forest between about 3,000 and 7,000 ft. in the eastern Congo, Tanganyika and Nyasaland. The resemblance between *montanus* and nominate *P. masukuensis* of Nyasaland is indeed striking, though they differ slightly in the colour of underparts, the darkness of the bill and the stronger development of whiskers in *montanus*. It is perhaps best to consider *montanus* and *masukuensis* as semi-species.

MUSCICAPIDAE, MUSCICAPINAE—Flycatchers

Muscicapa lendu or ***Muscicapa itombwensis*** (90)

Alseonax lendu Chapin, 1932, *Amer. Mus. Nov.* **570** : 11—Djugu, west of L. Albert, Belgian Congo.

Muscicapa lendu itombwensis Prigogine, 1957, *Rev. Zool. Bot. Afr.* **55** : 406—Ibachilo, 28° 28′ E., 3° 45′ S., 5,700 ft., Itombwe, north-west of L. Tanganyika, Belgian Congo.

Chapin, **3** : 627. Schouteden, **7** : 383. Vaurie, 1953, *Bull. Amer. Mus. Nat. Hist.* **100** : 521.

The type of *lendu* was collected at about 5,500 ft. and regarded by Chapin as probably restricted to montane forest. Later collectors in the area have failed to find other specimens. This has led to doubts on the validity of the form, Vaurie believing it to be a hybrid between *M. olivascens* and *M. aquatica*, and Schouteden that it is an aberrant *olivascens*.

At two localities in montane forest 300 miles south of the type locality of *lendu* Prigogine has recently obtained six specimens that he has described as a subspecies of *lendu* although they differ quite strongly in bill structure. It is possible that no further evidence may ever be available on the status of *lendu*, for Prigogine reports that the forests in the Lake Albert area are being heavily reduced. We have not examined the type of *lendu* and have nothing to add to Prigogine's argument, but consider it might be best to regard *itombwensis* as an independent species for the present, rather than to attach it to *lendu*, which is of doubtful status.

Melaenornis ardesiaca (91)

Melaenornis ardesiaca Berlioz, 1936, *Bull. Mus. Hist. Nat. Paris*, **2** (8) : 329—Mbwahi west of L. Kivu, Belgian Congo.

Chapin, **3** : 617. Schouteden, **7** : 375. Prigogine, 1953, *Ann. Mus. Roy. Congo Belge*, **24** : 62. Williams, 1959, *Bull. Brit. Orn. Cl.* **79** : 51.

A flycatcher fairly common locally in woods, thickets or forest on the mountain slopes from west of Lake Edward to L. Tanganyika, and in extreme south-west Uganda at Kigezi. Its range is about 200 miles from north to south but since it is found only between 5,000 and 8,000 ft. the area inhabited may be less than 2,500 sq. miles.

Its plumage is blue-grey, in some ways intermediate between the shiny blue-black of the southern *M. pammelaina* and the dark sooty grey of the northern *M. edolioides*, both of which are birds of lower and more open country. It differs from them also in having a yellow eye (noted by Williams as very conspicuous in the field) not a brown eye, and is smaller but with a heavier bill. In both structure and habits *edolioides* and *pammelaina* seem closer to each other than to *ardesiaca*.

All three species of *Melaenornis* have been collected within 100 miles of each other in the area where Ruanda, Uganda and the Congo meet, but they seem mutually exclusive. We regard them as members of a superspecies.

Platysteira laticincta (72)

Serle, 1950, *Ibis*, **92** : 604.

A wattle-eye confined to montane forest above 5,000 ft. on the Bamenda highlands between Bamenda and Oku. At lower altitudes there, and on neighbouring mountains, its place is taken by *P. cyanea*. Species of both *Platysteira* and of the related genus *Batis* seem usually to be mutually exclusive and it is unlikely therefore that *laticincta* will be found outside this small area 50 × 20 sq. miles in extent, in which the total area it inhabits probably does not exceed 100 sq. miles.

P. laticincta is very like *P. peltata*, which is found in both montane and gallery forest in Angola, and in fringing forest and scrub widely over central and eastern Africa. *P. laticincta* differs only in being slightly smaller, with a disproportionately shorter tail, and shorter, wider bill, and in having a broader breast band in the male. In conjunction with the isolation of *laticincta* these differencs lead us to class it as a semi-species.

(For notes on *Muscicapa gabela* see under Turdinae, and for *Chloropeta gracilirostris* see under Sylviinae.)

MUSCICAPIDAE, TURDINAE—Thrushes

Turdus ludoviciae (62)

Archer & Godman, 1961, **4** : 1137.

Confined to juniper forest on the mountains. It is fairly common in the Golis Range, in an area not exceeding 40 × 10 sq. miles, and also 200 miles to the east above Erigavo, in the juniper belt on the Warsangli Escarpment. Archer thinks it might possibly also be found in the juniper of the Gadabursi Hills behind Jiffa and Buramo, near the Abyssinian border, which are about 80 miles to the west of the known localities. Even if so the total area occupied would probably be well under 1,000 sq. miles.

T. ludovicae is a grey bird with a black-streaked throat. Its combination of dark plumage with vestigial orange in the under wing-coverts suggests it may be a link taxonomically, as to some extent it is geographically, between the African thrushes of the *T. olivaceus* or *T. libonyanus* groups and the Palaearctic and Indian blackbirds, *T. merula* and *T. simillima*.

Turdus helleri (42)

Bednall, 1958, *East Afr. Nat. Hist. Soc. Journ.* **99** : 17.

Collected only in montane forest above 5,000 ft. in the Teita Hills, southern Kenya, but also seen by Bednall on Kilimanjaro, 60 miles to the west, at about 6,500 ft. The avifauna of Kilimanjaro being comparatively well known, it is probable that the *helleri* seen was a straggler, in which case we can regard as its habitat only the forest on the Teita Hills, which according to the District Commissioner, Teita (per Myles North) does not exceed 1,000 acres (less than 2 sq. miles), made up of four patches.

T. helleri has sometimes been regarded as merely a melanistic subspecies of *T. olivaceus* but the blackness of its head, throat and breast, unlike all races of *olivaceus* in both the intensity and distribution of the melanin, suggests that *helleri* has attained specific status. Furthermore North (*in litt.*) has reason to believe that it may have a very different song. If *helleri* is found to breed on Kilimanjaro the case for specific distinction is conclusive, since *T. o. deckeni* is also resident there.

Geokichla oberlaenderi (49)

Chapin, **3** : 577. Schouteden, **6** : 200.

The only published records of *G. oberlaenderi* are from lowland forest near Beni and Arebi in the north-eastern Congo, but it has also been obtained by Prigogine at Kakanda, west of the Ruzizi valley, 300 miles to the south (specimen in Tervuren). It may well be widespread, though rare, in the Congo forest.

G. oberlaenderi looks very like *G. c. crossleyi* of the Cameroon highlands and we would be prepared to treat them as conspecific were it not that the localities of *G. crossleyi pilettei* suggest that it may overlap *oberlaenderi* in the Beni area. Chapin points out that there is a possibility that *oberlaenderi* is the female and *pilettei* the male of the same species, though he considers it unlikely. Provisionally we regard *oberlaenderi* as a species.

Geokichla cameronensis (8)

Serle, 1950, *Ibis*, **92** : 607. Good, 1953, **2** : 60. Chapin, **3** : 576.

A thrush known from only four localities all within 50 miles of the coast, from Ndian in the British Cameroons to Doum and Grand Batanga 200 miles south. It is a bird of thick lowland forest and may possibly range further south and east.

The bird described by Sassi as *G. princei graueri* from the eastern Belgian Congo was transferred by Sclater to *cameronensis* but erroneously (Chapin). The two species *princei* and *cameronensis* have some resemblance in facial pattern but differ in size, proportions and colour and do not seem particularly closely related. We therefore regard *cameronensis* as a good species.

Cossypha isabellae (73)

Serle, 1950, *Ibis*, **92** : 346, 608 ; 1954, *Ibis*, **96** : 68 ; 1957, *Ibis*, **99** : 644.

Fairly common in the montane forest over 4,500 ft. on Mt. Cameroon (*C. i. isabellae*), Manenguba Mt., the Rumpi Hills, Bamenda–Banso highlands, and the Obudu plateau of Eastern Nigeria (*C. i. batesi* with a browner back). On Kupé and Fernando Po its place is taken by *C. bocagei granti* and *C. b. insulana*, so its range is unlikely to prove more extensive and the area the species inhabits must be under 350 sq. miles.

In the eastern Congo mountains *C. archeri* is the ecological parallel of *C. isabellae*, and is in many ways a similar bird, showing parallel subspecific variation. However *archeri* has a disproportionately longer tail and tarsus, and a finer bill with weaker bristles. There are also differences in the extent of the white in the plumage. We are satisfied that *isabellae* and *archeri* can be treated as distinct species, forming a superspecies which might also include *bocagei*.

Cossypha heinrichi (15)

Cossypha heinrichi Rand, 1955, *Fieldiana Zool.* **34** (31) : 327—Duque de Bragança, N. Angola.

Heinrich, 1958, *J. Orn.* **99** : 356.

Known only from the type locality, where it was found in the undergrowth of one strip of gallery forest bordering a small stream in savanna country at about 3,500 ft. Future exploration may be expected to show it has a wider range, most likely along some of the other west-flowing rivers of northern Angola.

C. heinrichi is distinguished from all other cossyphas by its pure white head and neck. Those which are nearest in this respect, *C. albicapilla* and *C. niveicapilla*, have the white confined to the crown and their backs black, not olive-grey as in *heinrichi*. We accept *C. heinrichi* as a species without close relatives.

Sheppardia gabela (14)

Muscicapa gabela Rand, 1957, *Fieldiana Zool.* **39** : 41—15 km. south of Gabela, Angola.

Heinrich, 1958, *J. Orn.* **99** : 128. Hall, 1961, *Bull. Brit. Orn. Cl.* **81** : 45. Da Rosa Pinto, 1960, *Bol. Cult. Mus. Angola*, **2** : 17.

Hall has shown reason to regard this newly discovered species as an akalat and not a flycatcher.

Heinrich and da Rosa Pinto (*in litt.*) found it to be very local in patches of secondary forest within 25 miles of Gabela. This forest forms part of the " coffee-forest " which lines the escarpment, and there are similar patches both to the north and south, though extensive planting is destroying much of the undergrowth, and suitable habitat for this bird may well be limited to a few hundred square miles.

In spite of the lack of orange coloration on the breast, *S. gabela* is very like *S. cyornithopsis* of the lower Cameroons, and might be regarded as a semi-species.

Alethe lowei (30)

Alethe lowei Grant & Praed, 1941, *Bull. Brit. Orn. Cl.* **61** : 61—8 miles south of Njombe (6,600 ft.) southern Tanganyika.

Lynes, 1934, *J. Orn. Sond.* : 82 (under *Sheppardia cyornithopsis*). Zimmer & Mayr, 1943, *Auk*, **60** : 256.

Known only from two specimens, the type, a female just coming into breeding condition, seen in the " forest-jungle ", and a male (in the Coryndon Museum) from the Uwemba forest (about ten miles south of the type locality). This akalat might be expected in any of the forest patches of the Southern Highlands block of Tanganyika, which total something like 1,000 sq. miles (cf. Gillman's *Vegetation Map of Tanganyika*, 1949).

In colour *A. lowei* is very like *Sheppardia sharpei*, differing only in having a more rufous and well-defined eye-stripe ; however, as Grant & Praed pointed out, it has stouter and darker feet, shorter and fewer rictal bristles, and a broader and longer first primary. The tarsi of the specimen we have examined are broken but, as far as can be judged, they are also longer, about 27 mm. against 24 mm. The bill is also narrower than in most specimens of *sharpei*.

Grant & Praed believed *A. lowei* to be closest to *A. montana* of the Usambara Mts., which, though a larger bird with no dull orange on the underparts, matches well above, and has a similar pattern and colour on the head and face. Zimmer & Mayr, without being able to see the type, suggested that *lowei* was conspecific with *Alethe* (*Bessonornis*) *anomala* but this cannot be accepted. Apart from the marked and multiple differences in plumage the two species evidently occur together for, according to his labels, Lynes found both *lowei* and *A. a. grotei* in forest 8 miles south of Njombe (see further discussion under *A. montana* below). We feel obliged to treat both *lowei* and *montana* as distinct species (forming a superspecies) which provide links between *Alethe* and *Sheppardia* but are not typical of either.

Alethe montana (36)

Sclater & Moreau, 1933, *Ibis* (13) **2** : 17.

Known only from dry evergreen forest above 5,500 ft. in the north-west corner of the West Usambara Mts., northern Tanganyika. This forest covers less than 10 sq. miles ; if the species extends throughout the highland forest of the west Usambara massif it might occupy an area of about 100 sq. miles, but from the collecting that has been done without finding the bird this is not likely.

Sclater placed *montana* as a race of *Alethe* (*Bessonornis*) *anomala*. Though strikingly different in colour and pattern from the races of southern Tanganyika and northern Nyasaland (*A. a. mbuluensis*, *grotei* and *macclounii*), *montana* has some resemblance to more southern races (*anomala* and *gurue*) in size and in the general colour above, but differs in the pattern of the face and the lack of orange tone on the underparts. As noted above, we find the facial pattern suggests a closer relationship with *A. lowei*.

Alethe choloensis (27)

A. c. choloensis Sclater, 1927—Cholo Mt., S. Nyasaland.

Alethe choloensis namuli Vincent, 1933, *Bull. Brit. Orn. Cl.* **53** : 138—Namuli Mt., Portuguese East Africa.

A. c. choloensis is found in rain-forest on the mountains south of Lake Nyasa, *A. c. namuli* on Chiperone Mt. just inside the Portuguese border, and the isolated Namuli Mt. 60 miles to the east. The whole range of the species lies within a circle of 60 miles radius, and the total area of the forest the bird inhabits cannot exceed 50 sq. miles. It probably will not be found outside its present known range, since in the mountains of northern Nyasaland its place is taken by *A. fülleborni*, and south of the Zambesi a good deal of collecting has failed to discover it in the montane forest.

Although allopatric to *A. fülleborni* and found in similar habitat, *choloensis* differs in colour, pattern and size and must be accepted as a distinct species. The two form a superspecies.

Pogonocichla swynnertoni (22)

Swynnerton, 1907, *Ibis* (9) **1** : 61–67.

Smithers *et al.*, 1957 : 112. Da Rosa Pinto, 1959, *Ostrich suppl.* 3 : 113.

Known only from highland forest areas in a strip about 100 miles long on the eastern border of Southern Rhodesia, and 80 miles to the east on the isolated Mt. Gorongoza. In Rhodesia Swynnerton's Robin is common only on Mt. Selinda between 2,800 and 5,000 ft., but is found also in the Melsetter and Umtali areas. The available habitat within this range cannot exceed 100 sq. miles. Stuart Irwin (*in litt.*) informs us that there is much suitable forest northwards in Inyanga, though the levels below 3,000 ft. there have been well explored without finding it. *P. swynnertoni* is sympatric throughout its range with the only other member of the genus, *P. stellata*, which occupies forest over a greater altitudinal range and a vastly greater geographical range, namely from Cape Province to Mt. Elgon. The two birds have marked similarities in colour and general pattern but differ in some important points, both in adult and juvenile plumage and in the shape of the bill. Swynnerton found both species common and both to be mainly insectivorous ground-feeders, though the differences in bills argues some ecological segregation. *P. swynnertoni* lays a clutch of two, *P. stellata* of three, but it is not known whether the duration of the breeding seasons and the number of broods raised differ. This is an interesting case in which populations of an original stock must have diverged to specific level in isolation, one species subsequently invading the range of the other, and, in at least some localities, both so adjusting themselves ecologically that both remain common.

Namibornis herero (19)

Bradornis herero de Schauensee, 1931, *Proc. Acad. Sci. Philad.* **83** : 449—Usakos, South West Africa.

Vaurie, 1953, *Bull. Amer. Mus. Nat. Hist.* **100** : 477. Hoesch & Niethammer, 1940, *J. Orn. Sond.* : 249. Macdonald, 1957 : 130. McLachlan & Liversidge, 1957 : 354.

Apparently confined to a strip of western Damaraland about 80 miles wide and 200 miles long from the Erongo plateau to the Naukluft Mts. It lives in thick bushes in hilly and rocky areas, extending during the rainy season into the edge of the Namib desert. Since it is easily overlooked and its habitat does not seem particularly specialized, it may well range further north towards the Angola border, where little collecting has been done.

N. herero combines something of the build of a large *Bradornis* with much of the plumage of an *Erythropygia* though it lacks the distinctive tail-pattern. Hoesch & Niethammer transferred it from the Flycatchers to the Thrushes, partly on field characters. They quote Steinbacher (unpubl.) as agreeing, after anatomical examination of a specimen, but give no indication of the characters used. They were followed by Macdonald who had further field data and also a young bird which showed remnants of a speckled juvenile plumage unlike the streaked plumage of young *Bradornis*. On the other hand Vaurie in his generic revision of the Flycatchers (written before Macdonald's work was published) reaffirms that *herero* is a *Bradornis*. This we cannot accept, on both the juvenile characters and personal field experience

(B. P. H.). We regard *N. herero* as having no close relatives, and probably with more affinities to the Thrushes than to the Flycatchers.

MUSCICAPIDAE, SYLVIINAE—Warblers

Seicercus herberti (74)

Serle, 1950, *Ibis*, **92** : 346, 610 ; 1954, *Ibis*, **96** : 69 ; 1957, *Ibis*, **99** : 647.

Fairly common in parts of the forest between 3,000 and 7,000 ft. on Fernando Po, the Obudu plateau of Eastern Nigeria, and most of the mountains of the Cameroons, though apparently absent from the Bamenda–Banso highlands. The total area inhabited must be under 300 sq. miles.

In Angola and the eastern Congo the montane forest is occupied by *S. laurae* and *S. laetus* respectively : both these birds differ in many respects from *herberti*, most notably in the lack of the black cap and broad white eye-stripe, and *herberti* must be regarded as a distinct species, and all three as members of the same superspecies.

Bradypterus grandis (10)

Bannerman, **5** : 73. Chapin, **3** : 434, 436. Rand *et al.*, 1959, *Fieldiana Zool.* **41** : 343.

The type of *B. grandis* was collected in high *Pennisetum* grass at Bitye, in the former French Cameroons, and was for long the only known specimen. However Beatty has recently collected three more at M'Bigou and Mimongo in Gaboon, 300 miles to the south, in dense low growth of recently abandoned plantations. Since he reports that the birds were rarely seen, only attracting attention by their song, it is likely that they have been overlooked in other suitable localities in the Cameroons and Gaboon.

Chapin and Rand have discussed the relationship between *grandis*, *carpalis*, a bird of lowland papyrus swamps in the north-eastern Congo and Uganda, and *graueri* of swamps in the eastern Congo mountains. All three have small differences in pattern and colour, and in the edgings of the wing coverts, which are described as white in *carpalis* (not seen by us). The tail feathers vary in width and apparently in number, *grandis* having ten broad feathers, *graueri* twelve rather narrower, and *carpalis* is recorded variously as having ten or twelve broad. The smallest species is *graueri* and the largest *carpalis*, which has a disproportionately long hind claw and short tail. Especially as all appear to be ecologically different, we agree with Rand and Chapin and regard all three as distinct, though related, species, forming a superspecies.

Bradypterus graueri (92)

Chapin, **3** : 434. Schouteden, **7** : 325. Rand *et al.*, 1959, *Fieldiana Zool.* **41** : 344.

B. graueri, accepted above as a full species, has been recorded only from the Rugege forest, east of Lake Kivu, and from swamps on the west Kivu volcanoes and west of Lake Edward above 7,000 ft. Further specimens in Tervuren recently collected by Prigogine are from Nyawarongo, " west of Lake Kivu, on the mountains above Kalehe 2° S., 28° 49′ E." (Schouteden *in litt.*). All these localities are within 60 miles of Lake Kivu but *graueri* might well occur in other high-altitude swamps in the Congo mountains. The total area of suitable highland swamp cannot exceed a few square miles and it is difficult to imagine how it can ever have done so.

Apalis sharpei (4)

Bannerman, **5** : 92.

Known only from (*a*) an unsexed specimen from an unspecified locality in Ghana ; (*b*) a male from thick bush country with large forest trees near streams " at Bandama", Ivory Coast ; (*c*) a male from tree-ferns lining a ravine on the Birwa plateau, Sierra Leone. Thus the bird probably occurs sporadically through the West African forests at least from Ghana to Sierra Leone, but is either very rare or very elusive.

The female is not known but it seems to us likely that the tail-less female, described as *A. hardyi* and now usually accepted as *A. goslingi hardyi*, may be in reality a female *sharpei*, for it was collected at Bandama on the same day as the male *sharpei* and bears a consecutive collector's number. The two differ chiefly in the colour of the throat, which is black in the male and pale rufous in the female. (A similar sexual dimorphism is found in nominate *A. rufogularis* though in other races both sexes have pale throats.) The small differences in bill size and wing length between *A. sharpei* and the type of *A. hardyi* are consistent with sexual differences.

A. sharpei forms part of a complex group, all of which are predominantly grey birds with grey tails tipped with white. Other members are (a) *bamendae* of forest in the Bamenda highlands, and *goslingi* of lowland forest in the northern and central Congo south to Angola, both of which have short tails, as in *sharpei*, and rufous throats, pale in *goslingi* ; (b) the longer-tailed eastern montane forms *porphyrolaema*, *affinis*, *vulcanorum*, *chapini*, *strausae*, *bensoni* and *kaboboensis*, all rufous-throated except for *kaboboensis*, both sexes of which have a black throat. The striking resemblance in all but tail-length between the black-throated males of *sharpei* of West Africa and *kaboboensis* from the west side of Lake Tanganyika, and between the rufous-throated *bamendae* and the *porphyrolaema* group 1,000 miles away gives some reason to regard the whole group as a single species. Alternatively two species comprising the long-tailed and short-tailed forms respectively might be recognized. However, we agree with Chapin that it is best provisionally to keep the lowland *goslingi* distinct from the montane *bamendae*, and we also think *sharpei* should tentatively be kept distinct until more is known about all these birds. We therefore class *sharpei*, *bamendae* and *goslingi* as semi-species forming a superspecies with the *porphyrolaema* group.

Apalis bamendae (75)

Serle, 1950, *Ibis*, **92** : 612.

The four known specimens of *A. bamendae* (discussed under the preceding species) were collected in forest patches above 4,000 ft. in the neighbourhood of Bamenda. Serle found it high up in the foliage and it is probably therefore a bird that easily escapes attention. It is likely to range throughout the Bamenda–Banso highlands, where we estimate there may be 200 sq. miles of forest, and it may yet be found on other mountains.

Apalis kaboboensis (93)

Apalis kaboboensis Prigogine, 1955, *Rev. Zool. Bot. Afr.* **51** : 240—Mt. Kabobo, west of L. Tanganyika.

Mayr, 1957, *J. Orn.* **98** : 30. Prigogine, 1960, *Ann. Mus. Roy. Cong. Belg.* **85** : 81.

Known only from forest on Mt. Kabobo between 5,000 and 6,000 ft. Since *A. porphyrolaema vulcanorum*, which has a rufous and not a black throat, occurs on the neighbouring massif north-west of the lake, *kaboboensis* is possibly restricted to Mt. Kabobo and therefore to an area of forest under 2,000 sq. miles. Although Mayr regarded *kaboboensis* as conspecific with *porphyrolaema*, we feel that it may have diverged more than this would indicate, and to be consistent with our treatment of *sharpei* (above) we treat *kaboboensis* as a semi-species.

Apalis karamojae (53)

Euprinoides karamojae Van Someren, 1921 (Feb.), *J. E. Afr. Ug. Nat. Hist. Soc.* **16** : 25 (not Van Someren, 1921 (May), *Bull. Brit. Orn. Cl.* **41** : 120, as given by Sclater and Praed & Grant)—Mt. Kamalinga, Karamoja, NE. Uganda.

A bird that is most imperfectly documented. Since its discovery it was known for 40 years only from a small part of eastern Uganda, but while this paper was in preparation Stronach collected a specimen (of a darker population) some 450 miles to the south, on the other side of Lake Victoria in north-central Tanganyika. The Uganda records rest on the type, a specimen in the British Museum from about 30 miles away at the base of Mt. Debasian (Kadam), and a third in the Coryndon Museum from Mt. Moroto, 50 miles to the north. These localities are all in an area of less than 1,000 sq. miles. No first-hand information is available about the habitat, but these Uganda birds do not seem to be montane. The Debasien bird came from the base of the mountain and Williams (*in litt.*) tells us that the Moroto specimen was collected with other birds which were likely to have come from the lower slopes of the mountain, where the vegetation is " thick and high bush and small trees, especially along the seasonal watercourses ". By contrast, for the Tanganyika specimen we have precise details : Stronach (*in litt.*) collected it in a belt of *Acacia drepanolobium*, with some *A. kirkii*, at Itumba, close to the swampy Wembere depression, 75 miles ESE. of Nzega. Thus the species as a whole is evidently non-montane but the vegetation type it inhabits seems to vary a good deal. The present wide separation of the Uganda and Tanganyika populations may be largely due to the very extensive clearing and cultivation in recent times round the shores of Lake Victoria. The bird's range is more likely originally to have extended round the eastern side of the lake than the western, where the higher rainfall produces quite a different kind of vegetation, with much evergreen forest.

A. karamojae does not appear to have any close relatives. In the white patch on its wing it is unlike any other *Apalis*. In other respects it might be thought to resemble a bleached *A. thoracica* but it has very much weaker legs and feet.

Apalis (? Orthotomus) moreaui (29)

Apalis moreaui Sclater, 1931, *Bull. Brit. Orn. Cl.* **51** : 109—Amani, East Usambara Mts., Tanganyika.

Apalis moreaui sousae Benson, 1945, *Bull. Brit. Orn. Cl.* **66** : 19—Njesi plateau, Portuguese East Africa (east side of L. Nyasa).

White, 1960, *Bull. Brit. Orn. Cl.* **80** : 152.

The type localities of the two subspecies lie 650 miles apart and the species has not been found on any of the intervening mountains, although if it were present its characteristic call would draw attention to it. In each locality less than ten specimens have been collected in montane forest, which in the East Usambara Mts. is barely 100 sq. miles in extent, and on the Njesi plateau probably not more than 10 sq. miles.

The long bill of *moreaui* distinguishes it from all forms of *Apalis.* White has suggested that it should be considered congeneric with *Artisornis metopias.* This also is a montane forest species with, like *moreaui,* the extreme localities in Usambara and Portuguese East Africa, but *metopias* has been collected on several of the intervening mountains. With White's suggestion we would agree subject to the nest of *moreaui,* at present unknown, proving to be a stitched structure like that of *metopias.* At the same time we have re-examined specimens of *Artisornis metopias* and compared them with tailor birds from Asia, and find no reason why *Artisornis* should not be submerged in the genus *Orthotomus* (cf. Friedmann, 1928, *Ibis* : 476). *A. metopias* shows no significant morphological differences and in colour is remarkably like *O. sepium.*

Scepomycter winifredae (33)

Artisornis winifredae Moreau, 1938, *Bull. Brit. Orn. Cl.* **58** : 139—Uluguru Mts., Tanganyika.

Grant & Praed, 1941, *Bull. Brit. Orn. Cl.* **62** : 30. Moreau, 1946, *Bull. Brit. Orn. Cl.* **66** : 44. Williams, 1951, *Ibis,* **93** : 469.

A distinctive chestnut-headed warbler known only from the Uluguru Mts. between 5,500 and 7,000 ft., in both wet and dry types of evergreen forest, which cover less than 100 sq. miles. It shows a preference for areas with heavy undergrowth and dense secondary growth, and is difficult to locate except by its call, a soft whistle. It might yet be found in one or more of the patches of montane forest on the mountains to the west but the total area it inhabited would still be very small.

Although the type, a young bird, was originally referred very tentatively to *Artisornis, winifredae* was later placed in a monotypic genus on the structure of the nostrils. The discovery of fully adult specimens shows it to be a bird of heavier build than any of the tailor-birds, and with a broader heavier bill. It seems to have no close relatives and the best course at present is to keep it in its monotypic genus.

Urolais epichlora (76)

Serle, 1950, *Ibis,* **92** : 612 ; 1954, *Ibis,* **96** : 69 ; 1957, *Ibis,* **99** : 648.

Found throughout the British Cameroons, on the Obudu plateau of Eastern Nigeria and on Fernando Po. Usually a bird of montane forest, it has been collected in savanna at 3,000 ft. between Mt. Kupé and Mt. Manenguba, so might possibly be found more widely. The area inhabited may perhaps be taken as 600 sq. miles.

The only difference from *Prinia* observable in the skin is the green colour of much of the plumage, which is probably due to nothing more than a general infusion of lipochrome. Only the absence of sufficient information on the field characters, especially of nests and eggs, makes us refrain from transferring the species to *Prinia.*

Poliolais (? Orthotomus) lopesi (77)

Serle, 1949, *Bull. Brit. Orn. Cl.* **69** : 74 ; 1950, *Ibis,* **92** : 613 ; 1954, *Ibis,* **96** : 69 ; 1957, *Ibis,* **99** : 649. Boulton & Rand, 1952, *Fieldiana Zool.* **34** : 53.

A bird of the undergrowth and thickets in primary and secondary montane forest of Fernando Po (*P. l. lopesi*), Cameroon Mt. (*P. l. alexanderi*), Manenguba, Kupé Mt. and the Rumpi Hills (*P. l. manengubae*), which has also been seen on the Obudu plateau of Eastern Nigeria. Its habitat is probably therefore limited to under 350 sq. miles. It is usually found singly, or in small family parties, but nothing is yet known of its nesting habits. This is unfortunate, for there is a marked resemblance between *Poliolais* and the tailor-bird *Orthotomus* (formerly *Artisornis*—see p. 341) *metopias*, and knowledge of the nests would help to determine their relationship. The similarity to *metopias* is most striking in the females of *P. l. manengubae.* Both birds have rufous heads, slightly brighter in *metopias,* and olive-brown backs with the same ragged texture to the plumage due to the barbs being widely separated : both have ten rather narrow, debilitated rectrices, slightly graduated, but whereas in *metopias* all are grey-brown, in *lopesi* the outer three pairs are white. Both have olive-brown wings with exceptionally broad primaries, similar wing formulae, similar white under wing-coverts flecked with rufous, and with a white edging to the angle of the wing. Below, both have a mixture of rufous, white and grey, though in *metopias* the rufous is more pronounced on the throat and the abdomen is whiter : both have olive-brown thighs. The bills and legs are alike, and the species are close in size, as the following table shows, though *lopesi* is slightly larger, with a relatively shorter tail.

The male of *lopesi* differs in being all grey except for the outer pairs of white rectrices, white under wing-coverts, some white in the abdomen and olive-brown flanks and thighs. The young bird of *lopesi* is similar to the female except that the rufous in the head is greatly reduced and the whole underparts are green. In young *metopias* the underparts are probably yellower (" olive-yellow "), and the head more rufous than the adult (see *Ibis,* 1933 : 27).

Poliolais lopesi and *Orthotomus metopias*

	Wing		Bill		Tail		Tarsus	
	♂	♀	♂	♀	♂	♀	♂	♀
O. metopias, 9 ♂, 7 ♀	47–52	45–49	16–17	16–17	36–39	34–37	21–23	21–23
	(49·7)	(47·2)	(16·6)	(16·5)	(38·1)	(35)	(22)	(22)
P. l. manengubae, 7 ♂, 6 ♀	53–57	47–53	16–17	16–17	34–38	24–28	23–25	21–23
	(54·8)	(50·5)	(16·4)	(16·4)	(35·2)	(26)	(23·9)	(22)
P. l. alexanderi, 1 ♂, 1 ♀	53	50	16	15	31	25	23	22
P. l. lopesi, 4 ♂, 3 ♀	54	50–51	16–17	15–16	30–34	25	23	21–22

Although there is no tailor-bird known with marked sexual dimorphism or white rectrices, these characters do not preclude the two species being congeneric (similar differences are found in *Apalis*), and in other respects the similarities are so striking that we recommend the transfer of *lopesi* to *Orthotomus* if it is found to stitch its nest. Meanwhile we retain the monotypic genus.

Prinia leontica (2)

Prinia leontica Bates, 1930, *Bull. Brit. Orn. Cl.* **51** : 51—Birwa Peak, Kono district, Sierra Leone.

Bannerman, **5** : 225. White, 1960, *Bull. Brit. Orn. Cl.* **80** : 150.

Known only from four highland localities within an area of 50 miles by 50 on either side of the Sierra Leone–Guinea border. It lives in thickets bordering streams at altitudes from 1,600 to 4,500 ft., but was found to be commonest in the mountain ravines. If, as seems likely, it is confined to mountains it will not be found outside this small area, except perhaps on Bintumane Peak, 30 miles to the north-west.

White considers that *leontica* is " no more than a well marked subspecies of *leucopogon* ", the white-chinned Prinia, which reaches its western limit in the British Cameroons about 1,500 miles away. The two birds are alike in many respects but *leontica* is slightly smaller and has the throat grey like the breast, the eye creamy white instead of red-brown and a strong suffusion of buff on the abdomen and thighs—in this respect more like the eastern *P. l. reichenowi* than the western *P. l. leucopogon*. We consider that *leontica* has diverged sufficiently to be regarded as a semi-species.

Prinia robertsi (23)

Prinia robertsi Benson, 1946, *Bull. Brit. Orn. Cl.* **66** : 52—Vumba, near Umtali, S. Rhodesia.

Benson, 1946, *Ostrich,* **17** : 291. Smithers *et al.* 1956 : 126.

Found in the highlands above 4,500 ft. on the eastern edge of Southern Rhodesia in a strip about 170 miles from north to south. Stuart Irwin *in litt.* informs us that it is a bird of " bracken-briar ", tree heath and forest edge rather than a forest species and that this type of habitat covers only about 5% of the total land area within the bird's range—probably therefore under 500 sq. miles. *P. robertsi* is apparently common where found but has not yet been recorded from neighbouring Portuguese territory, where it might perhaps occur in a small area.

Although little distinguished in colour from other dull prinias, *P. robertsi* is well characterized as a species by its exceptionally long, narrow, steeply graduated and rather ragged tail. Though not so exaggerated, this is slightly reminiscent of the Asiatic prinias of the subgenus *Suya*, but there is no other feature to suggest close relationship.

Graueria vittata (94)

Chapin, **3** : 243. Schouteden, **7** : 232. Prigogine, 1953, *Ann. Mus. Roy. Cong. Belg.* **24** : 55.

Known from five localities at 5,000–7,000 ft. scattered over 250 miles between Lakes Edward and Tanganyika. It is a bird of montane forest, which in this area may cover about 5,000 sq. miles. Prigogine believes it is not particularly rare but very inconspicuous.

It appears to have no close relatives and even its family is uncertain. Its short, stout legs, and strong, slightly hooked bill are not very warbler-like, but Chapin thinks it is best kept with the Sylviidae rather than with the bulbuls or babblers. He also discusses some affinities between *Graueria* and *Macrosphenus*, but they are not close.

Macrosphenus pulitzeri (17)

Macrosphenus pulitzeri Boulton, 1931, *Ann. Carn. Mus.* **21** (1) : 50—Chingoroi, western Angola.

Delacour, 1946, *Oiseau*, **16** : 12. Chapin, **3** : 245. Hall, 1960, *Ibis*, **102** : 435.

This long-bill is known only from two specimens from the neighbourhood of Chingoroi, taken in " dry, evergreen forest " (Boulton) and " secondary forest " (da Rosa Pinto *in litt.*) and from one taken at Vila Nova do Seles, also in secondary forest on the escarpment, about 110 miles north of Chingoroi (da Rosa Pinto). The bird may well occur in other relict patches of forest on or under the escarpment but these are unlikely to cover a total of more than a few hundred square miles.

The species was described on a single specimen, said to differ from all other members of the genus in the shape of the bill, the length of the tarsus, and in the wing/tail ratio, having the tail longer in relation to the wing than *M. concolor*, *M. kempi*, or *M. flavicans*, and shorter than in *M.* (*Suaheliornis*) *kretschmeri*. No direct comparison was made in colour between the species. Chapin believed *pulitzeri* to be the geographical representative of *concolor* which ranges fron West Africa to Uganda, reaching its southern limits in north-eastern Angola.

We have examined the specimen from Novo do Seles (unfortunately tail-less, as is the second Chingoroi specimen) which closely resembles the type in size and shape, but is slightly darker above and below (Parkes *in litt.*). We do not find the bill of *pulitzeri* distinct, since it can be matched by those of some specimens among the large series of *concolor* available to us, which vary considerably. On the other hand we find that *pulitzeri* differs in colour from the other three green species, *concolor*, *flavicans* and *kretschmeri*, in having more melanin throughout ; it is dark, more olive-brown, above, darker olive below, and has black lores with a black spot in front of the eye, some black in the ear-coverts, and black, rather than grey, bases to all the body feathers. These colour differences alone do not necessarily indicate more than subspecific variation, but considered in conjunction with the anatomical differences of the wing/tail ratio and, in particular, the length of the tarsus, we regard *M. pulitzeri* as a full species, forming a superspecies with *concolor*.

Sclater allocated the genus *Macrosphenus* to the babblers, and Praed & Grant to the bulbuls, but we follow Chapin in including it in with the warblers although no detailed reasons for doing so appear to have been published (see Delacour).

Chloropeta gracilirostris (26)

C. g. gracilirostris Ogilvie-Grant, 1906 : Mokia, south-east of Ruwenzori.

Chloropeta gracilirostris bensoni Amadon, 1954, *Ostrich,* **25** : 141—mouth of Luapula River, Lake Mweru, N. Rhodesia (synonym *C. g. brédoi* Schouteden, 1955).

Grant & Praed, 1940, *Bull. Brit. Orn. Cl.* **60** : 91. Chapin, **3** : 450. Schouteden, **7** : 329.

The swamp representative of the aberrant broad-billed flycatcher-warblers, it is known from two areas 700 miles apart ; in the north there are several records around Lakes Edward, George, Bunyoni and Mutanda, where suitable swamps are unlikely to total 100 sq. miles : in the south the species has been found only at the mouth of the Luapula on Lake Mweru, being apparently absent from both the Bangweola marshes and " Mweru Marsh " (Benson *in litt.*).

Sclater and others include *gracilirostris* in the genus *Chloropeta* along with two other species, *natalensis* and *similis*. *C. natalensis* ranges from Angola and Abyssinia to Natal at altitudes up to about 7,000 ft., usually in open areas with plenty of low bushes or bracken. *C. similis* lives from 6,000 ft. upwards, associated with the edge of forest and bamboo thickets on mountains throughout East Africa, so that on some it occupies the higher slopes and *natalensis* the lower. Because *gracilirostris* has a longer bill and much larger feet than the other two species Grant & Praed separated it as a monotypic genus but the differences can be regarded as merely adaptations to its life in aquatic vegetation ; and we, like Chapin and Amadon, retain *gracilirostris* in the genus *Chloropeta*. Although their habitat preferences are well-defined, geographically the three species are not so clearly allopatric that they come within the definition of a superspecies.

HIRUNDINIDAE—Swallows

Hirundo megaensis (56)

Hirundo megaensis Benson, 1942, *Bull. Brit. Orn. Cl.* **63** : 10—Mega, S. Abyssinia.

Benson, 1946, *Ibis* : 287. Mayr, 1957, *J. Orn.* **98** : 28.

A swallow known only from an area of about 3,000 sq. miles from north of Yavello to south-east of Mega. There it is common in the short-grassed country with small thorn-bushes between 4,000 and 4,500 ft., which does not seem to form an ecological island. Its southern limit is an escarpment dropping to 3,000 ft. (which one would not have thought a feature of great importance to a swallow), but no sort of natural boundary can be suggested for its limits in other directions, where Benson failed to find it in apparently suitable country.

H. megaensis is most like *H. leucosoma* of West Africa but lacks the white patch in the wing and has differences in tail-pattern and colour, as well as rather different field characters. It seems to us sufficiently distinct to be considered a full species. Mayr associates *dimidiata* of southern Africa with these two to form a superspecies.

Psalidoprocne fuliginosa (78)

Bannerman, **5** : 297. Young, 1946, *Ibis,* **88** : 381. Serle, 1950, *Ibis,* **92** : 618. White, 1961, *Bull. Brit. Orn. Cl.* **81** : 32.

Since the bird described as *P. f. sammetina* from the Bamenda highlands does not belong to this species but to *P. petiti* (see Bannerman), *P. fuliginosa* is known only from Fernando Po (from 1,000 ft. upwards) and from Cameroon Mt., where it is common from 2,500 ft. to 9,000 ft. over clearings in the forest, and above the timber line. If its habitat is regarded as the unforested areas in these mountains, then the area it inhabits must be under 100 sq. miles, for its place is taken on other mountains of the Cameroons by *P. petiti*, and in the lowlands by *P. nitens*.

P. fuliginosa is the only member of its genus which is uniform brown with the metallic sheen virtually absent: it is perhaps closest to *P. antinorii* of Abyssinian montane forest which has a faint purple-brown sheen, white under wing-coverts (brown in juveniles) and a more deeply forked tail. The two might be considered members of a superspecies (cf. White).

PRIONOPIDAE—Helmet-shrikes

Prionops gabela (13)

Prionops gabela Rand, 1957, *Fieldiana Zool.* **39**: 43—15 km. south of Gabela, western Angola.

Hall, 1960, *Bull. Brit. Mus.* (*Nat. Hist.*) *Zool.* **6** (7): 437; 1960, *Ibis*, **102**: 435. Da Rosa Pinto, 1961, *Bol. Cult. Mus. Angola*, **2**: 17.

This helmet-shrike is now known from six specimens, taken within 25 miles of Gabela. Most were found in secondary forest or clearings on the escarpment but one was collected in a tangled thicket on the coastal plain. It can be expected in any similar cover on or below the Angola escarpment, and suitable habitat may cover several hundred square miles.

Rand has shown this helmet-shrike to be intermediate in some respects between the widespread *P. retzii*, which it much resembles in colour, and *P. plumata* (*poliocephala*), which has a similar forward growth of the frontal feathers. It has not yet been established whether *P. gabela* is indeed allopatric to either of these species, which have been collected above the escarpment. Provisionally it might be considered as forming a superspecies with *P. retzii*.

LANIIDAE—Shrikes

Laniarius atroflavus (79)

Serle, 1950, *Ibis*, **92**: 619; 1957, *Ibis*, **99**: 660. Good, 1953, **2**: 116.

Common in the forest of most mountains of the British Cameroons and extending over the borders to Babadjou on the eastern extension of the Bamenda highlands in former French territory and to the Obudu plateau, Eastern Nigeria. The total area it inhabits probably does not exceed 500 sq. miles.

The bright yellow underparts distinguish *atroflavus* from other boubous and it has apparently no close relatives.

Telophorus (Chlorophoneus) kupeensis (80)

Chlorophoneus kupeensis Serle, 1951, *Bull. Brit. Orn. Cl.* **71**: 41—Kupé Mt., Kumba Division, British Cameroons.

Peters, **9** : 337.

Known only from four specimens taken in the forest on Kupé Mt. It is either very rare or hard to find, for after the original pair had been obtained it was only rediscovered after several attempts. If indeed it occurs nowhere else it has a range of less than 8 sq. miles.

It is a very distinct species, larger than other members of the genus, showing an approach to *Malaconotus* and, though like *T. multicolor* in the colour and pattern of the back, it has a distinctive white throat, grey chest and yellow-green abdomen and under tail-coverts.

Malaconotus gladiator (81)

Stresemann, 1924, *J. Orn.* : 85. Chapin, **4** : 45. Serle, 1950, *Ibis*, **92** : 622 ; 1954, *Ibis*, **96** : 72.

A green-breasted bush-shrike known from five specimens from Camaroon Mt., the Rumpi Hills, near Lake Bambulue in the Bamenda highlands, and the Obudu plateau, Eastern Nigeria (F. C. Sibley *in litt.*). Serle and Sibley both found it in forest or forest strips between 5,000 and 6,500 ft. but the fact that Sibley found the stomach of his specimen to be full of large locusts suggests that it had foraged in the surrounding grasslands. It may occur on all the Camaroon mountains but the total area inhabited is unlikely to exceed 300 sq. miles.

Having only the type-specimens to consider, Stresemann believed *gladiator* to be a green mutation of the widespread savanna species *M. poliocephalus* (now *M. hypopyrrhus*), but its rediscovery by Serle and Sibley establishes it as a good species with a different habitat from *hypopyrrhus*. In addition to the different colour of the breast, *gladiator* differs from *hypopyrrhus* in having the yellow tips to the wing and tail feathers reduced to a minimum, or absent, a variable amount of grey on the chin, and no white in front of the eye. It has also a grey, not yellow, eye. The two birds may be regarded as forming a superspecies. The extension of green in the plumage of *gladiator*, i.e. the extension of melanin, is consistent with adaptation to evergreen habitat.

Malaconotus alius (34)

Known only from the forest on the Uluguru Mts. of Tanganyika Territory between 5,000 and 6,000 ft. The area it inhabits is probably under 100 sq. miles, but it might occur in the small forest patches on the mountains to the west.

It differs from all other members of the genus in having a shiny black, instead of a grey head, and a brown eye. In the lack of yellow tips to the tail and wing feathers it is similar to *M. gladiator*, and also shows an approach to this species in having a suffusion of green on the underparts, especially the flanks and thighs, but it is a smaller bird. The resemblances are as likely to be due to convergence as to closeness of relationship and in view of the distances separating them we do not regard them as forming a superspecies.

CORVIDAE—Crows

Zavattariornis stresemanni (57)

Zavattariornis stresemanni Moltoni, 1938, *Orn. Monatsb.* **46** : 80—Yavello, S. Abyssinia.

Benson, 1946, *Ibis*, **88** : 448. Lowe, 1949, *Ibis*, **91** : 102. Ripley, 1955, *Ibis*, **97** : 143.

The Abyssinian " Bush-crow " has a very restricted range, in park-like *Acacia* country that occupies parts of an area of about 1500 sq. miles round Yavello, Mega and Arero. Neither Benson nor von Rosen (*in litt.*) on personal experience can account for its absence to the east or west, where the country appears similar, but to the south the country becomes more open, and to the north higher, which may limit the distribution in these directions.

The taxonomic relationships of *Zavattariornis* are equally puzzling. In life *Zavattariornis* in several respects reminded Benson of a starling, but, while Lowe doubted on anatomical grounds that it is either a starling or a corvid, the original describer and subsequently Amadon and also Ripley (after anatomical examination) have all classified it as a corvid, probably closest to the choughs.

STURNIDAE—Starlings

Cinnyricinclus (Pholia) femoralis (43)

Van Someren, 1922, *Nov. Zool.* **29** : 129 ; 1939, *Journ. E. Afr. Nat. Hist. Soc.* **14** : 112. Wigram, 1948, *Nature in E. Afr.* **5** : 3. Amadon; 1956, *Amer. Mus. Nov.* **1803** : 4.

Published information on the distribution of this montane forest starling is scarce but has been supplemented for us by Williams (*in litt.*). It inhabits Kilimanjaro, apparently to the exclusion of its closest relative, *C. sharpii* (which is more widespread, from Abyssinia to Nyasaland) and also occurs in Kenya where it breeds alongside *C. sharpii* at Limuru, 20 miles north-west of Nairobi. In the forest of the southern end of the Chyulu Hills van Someren found both *femoralis* and *sharpii* in flocks, *femoralis* feeding on fruits of *Cornus volkensii* and *sharpii* on fruits of a species of *Sapium*. There are also sight records of *femoralis* on Mt. Kenya and at Molo, on the west side of the Rift Valley, " where it appears to be a spasmodic visitor or perhaps just overlooked " (Williams). Williams thinks that *femoralis* is much the shyer of the two species, keeping more to the tree-tops, especially of *Juniperus procera*, while *sharpii* at times feeds very near the ground. While the northern and southern limits of the range of *femoralis*, namely Mt. Kenya and Kilimanjaro, are 200 miles apart, the scanty data available suggest that the area actually occupied is probably less than 5,000 sq. miles, but more if *femoralis* fully occupies the forests west of the Rift Valley.

In Kenya, while it is still uncertain whether *femoralis* and *sharpii* actually breed in the same forests, they are at least partly sympatric. The two species seem closely related, differing chiefly in the colour and pattern of the underparts, which in *femoralis* are contrasting blue-black and white, and in *sharpii* wholly light buff. There are also small differences in structure, and in the plumage of the young. The third member of the genus, *C. leucogaster*, is more distinct and is not confined to forest.

NECTARINIIDAE—Sunbirds

Cinnyris rockefelleri (95)

Cinnyris rockefelleri Chapin, 1932, *Amer. Mus. Nov.* **570** : 16—9,000 ft. on Mt. Kandashomwa, west of Ruzizi valley, Belgian Congo.

Chapin, **4** : 236. Schouteden, **8** : 198. Williams, 1950, *Ibis*, **92** : 645 ; 1951, *Ibis*, **93** : 469. Hendrickx & Massart-Lis, 1952, *Ibis*, **94** : 531.

Found only at a few localities between 8,500 and 10,000 ft. in the chain of extinct volcanoes 100 miles long west of the Ruzizi valley from west of Lake Kivu to Lake Tanganyika. It is evidently a bird of the bamboo and heath zones, which, in this area, cannot cover more than 100 sq. miles.

The relationships between the montane double-collared sunbirds, *rockefelleri*, *regius* (subspp.), *moreaui*, *loveridgei* and *mediocris* (subspp.), are difficult to understand. The male of *C. rockefelleri* looks most like that of *C. regius*, and the female (by description) like those of *C. moreaui* and *C. loveridgei*. However *rockefelleri* is larger than *regius* and furthermore both are found on the same mountains at the same altitudes so cannot be considered conspecific. Apart from these two, the general similarities of plumage and otherwise allopatric distribution of the sunbirds concerned suggest that all could be treated as conspecific. However Williams has shown that at least *loveridgei* and *moreaui* have diverged in several respects from the rest of the group, and, to a less degree, from each other and may have achieved specific status. Since *rockefelleri* is in some characters a link between these two and *regius* we accept it also provisionally as at least a semi-species.

Cinnyris moreaui (31)

Cinnyris mediocris moreaui Sclater, 1933, *Ibis* (13) **3** : 214—Maskati, 6,000 ft., Nguru Mts., east central Tanganyika.

Praed & Grant, **2** : 785. Williams, 1950, *Ibis*, **92** : 645.

This sunbird (discussed under the preceding species) has been found in forest patches at three mountain localities within 100 miles in central Tanganyika, namely, on the discontinuous line of highlands formed by the Nguru and Ukaguru Mts. and Uvidunda 70 miles south of Kilosa. These forest patches probably cover less than 100 sq. miles. The bird may possibly occur on other forested mountains of Tanganyika, though there are few on which the closely allied sunbirds *loveridgei*, *mediocris* or *regius* have not already been found.

Provisionally we regard *moreaui* and *loveridgei* as semi-species (cf. Williams) until more is known of their breeding habits and immature plumages, though the differences between them are not great.

Cinnyris loveridgei (32)

Williams, 1951, *Ibis*, **93** : 469.

C. loveridgei (discussed under the two preceding species) seems typically to be a bird of montane forest but has adapted itself also to clearings from 2,500 to 7,500 ft. in the Uluguru Mts. Since neighbouring mountains are all occupied by allied species, its range is probably limited to the Ulugurus and the area inhabited to under 500 sq. miles.

Chalcomitra ursulae (82)

Grote, 1948, *Ibis*, **90** : 339. Serle, 1950, *Ibis*, **92** : 627 ; 1954, *Ibis*, **96** : 75.

A small dull-coloured sunbird known from six specimens collected on Fernando Po, Cameroon and Kupé Mts., and from a good series from the Rumpi Hills (also in British Cameroons). It ranges from 3,200 to 6,500 ft. and has been collected in primary and secondary forest and, on Fernando Po, in low bushes on the mountain side. The area it inhabits probably does not exceed 300 sq. miles. It has a general resemblance to the partly sympatric *Cyanomitra olivacea* but is far smaller, has a darker throat, a more pronounced metallic blue forehead, and orange instead of red pectoral tufts.

Cyanomitra oritis (83)

Serle, 1950, *Ibis*, **92** : 627 ; 1954, *Ibis*, **96** : 76.

Common in the montane forest on Fernando Po and in the British Cameroons, its place being taken below 5,000 ft. by the green-headed *C. verticalis*. The area it inhabits is under 600 sq. miles.

Males of *C. oritis* differ from *verticalis* in having the head blue, not green, and the underparts olive-yellow instead of green. Moreover the female of *C. oritis* has metallic plumage on the throat and breast like the male. In this latter respect, and in the blue tone of the metallic plumage, *oritis* is similar to *C. alinae* of the montane forest of the eastern Congo, but the two species differ in the colour of the back and the colour of the abdomen. The lowland species *verticalis* and the two montane species, *oritis* and *alinae*, may be regarded as forming a superspecies.

Anthreptes pallidigaster (39)

Anthreptes pallidigaster Sclater & Moreau, 1935, *Bull. Brit. Orn. Cl.* **56**—Sigi valley, 4 miles east of Amani, Tanganyika.

Praed & Grant, **2** : 816. Moreau & Moreau, 1937, *Ibis* (14) **1** : 337.

A white-bellied sunbird found in evergreen forest up to 3,000 ft. in the East Usambara Mts. and, commonly, in tall *Brachystegia* in the Sokoke Forest on the Kenya coast 200 miles to the north (Williams *in litt.*). It might also be expected in other relict forest patches on or near the East African coast but, on present knowledge, the area it inhabits is less than 250 sq. miles.

It has no close relatives.

Anthreptes rubritorques (35)

Praed & Grant, **2** : 811. Chapin, **4** : 193. Moreau & Moreau, 1937, *Ibis* (14) **1** : 335.

A mountain sunbird, found on forest edge between 3,000 and 5,000 ft. on both the East and West Usambara Mts. and in the Nguru Mts. 100 miles to the south-west. It probably occupies less than 2,000 sq. miles.

It is very like *A. rectirostris* and *tephrolaema* of West and Equatorial Africa, east to Mt. Elgon, and all are considered conspecific by some authors. The males of the three forms differ in the colour and pattern of the throat and breast. No specimens sexed as females are known from the Usambara Mts. but there are two unsexed specimens in Berlin believed by Stresemann to be females, and one " breeding " female in the British Museum from the Nguru Mts., presumed to be the same form though there is no male for comparison. These suggest that the females of *rubritorques* may differ from those of *rectirostris* and *tephrolaema* in having a considerable amount of metallic plumage above : the Nguru female furthermore has a trace of a metallic band at the sides of the breast. If these differences are substantiated we consider that *rubritorques* has diverged sufficiently to be regarded as a semi-species.

Anthreptes pujoli (3)

Anthreptes pujoli Berlioz, 1958, *Bull. Mus. Hist. Nat. Paris* (2) **30** : 494—Sérédou area, 45 km. south of Macenta, (French) Guinea.

A species founded on a single male (which we have not seen) believed from its black bill to be fully adult. It was collected in country between 2,000 and 4,000 ft. described as mostly forested (and probably not ecologically peculiar).

A. pujoli is described as generally similar in size and colour to a female of *A. tephrolaema*, but having distinctive light markings on the wings. The West African representative of *tephrolaema*, *A. rectirostris*, is found in the same area, for a young male with metallic plumage coming in on the head and mantle was collected by Bates 35 miles south-east of Macenta. Unless the type of *pujoli* is an aberrant specimen it must represent a distinct species, and we provisionally accept it as such, as has been done also by Rand (*in litt.*) for the *Check List of the Birds of the World*.

PLOCEIDAE—Weavers

Ploceus bannermani (84)

Serle, 1950, *Ibis*, **92** : 631. Moreau, 1960, *Ibis*, **102** : 469.

Known only from about half a dozen specimens from the edges of, and openings in, evergreen forest at 5,000 ft. and upwards on Manenguba Mt. and the Bamenda highlands of the Cameroons. The area it occupies is therefore probably less than 200 sq. miles. It may possibly occur on one or more of the neighbouring mountains, where however Serle has collected without finding it.

It is a member of the *Ploceus baglafecht* species-group, but cannot be regarded as forming a superspecies with it since it is sympatric with *P. b. neumanni* : its closest relative may be *P. nigrimentum* which has been found 600 miles to the south-east (see below).

Ploceus batesi (9)

Good, 1953, **2** : 157.

A forest weaver known only from a few specimens from a line of localities, Lolodorf, Sangmelima, and R. Ja, about 100 miles long in the former French Cameroons.

The species might well range into the neighbouring parts of Gaboon on the south and Moyen Congo on the east, which are imperfectly known ornithologically.

It is another of the *P. baglafecht* species-group, but with a distinctive chestnut crown in the males. There is no reason why both this and the next species should not be regarded as forming a superspecies with *baglafecht*.

Ploceus nigrimentum (11)

Chapin, **4** : 313. Moreau, 1960, *Ibis*, **102** : 316. Rand *et al.*, 1959, *Fieldiana Zool.* **41** : 382.

Known only from savanna at Dhambala on the Bateke plateau (2,400 ft.) in the Moyen Congo, and from above 5,000 ft. at Mombolo and Galanga, 650 miles to the south in the Bailundu highlands of Angola, where there is montane forest, woodland and grassland. Nothing definite can therefore be said of its habitat, but this weaver must be expected elsewhere.

P. nigrimentum is most like *P. bannermani*, but with a black, not green, back and marked sexual dimorphism, is distinctive enough always to have been regarded as a separate species.

Ploceus aureonucha (50)

Chapin, **4** : 372.

A forest weaver of exceptionally beautiful and varied coloration known only from about half a dozen specimens from a triangle of forest with sides of about 100 miles (i.e. an area of about 5,000 sq. miles) in the north-eastern Congo near Beni. It may well occur more widely. It seems to have no near relative.

Ploceus golandi (40)

Williams & Clancey, 1959, *Ibis*, **101** : 247.

The type of this black-headed weaver, described in 1913 from the Sokoke forest on the Kenya coast, remained unique until the species was rediscovered there in 1955. It may perhaps be found in other relict patches on the East African coast but the area it inhabits, as known at present, is less than 150 sq. miles.

Its closest relative appears to be *P. weynsi* of the Congo forest, from which it differs in having the back black and green instead of all black, and the underparts plain yellow instead of patterned. We regard them as members of a superspecies.

Ploceus castaneiceps (41)

Moreau, 1959, *Bull. Brit. Orn. Cl.* **79** : 159–161.

A weaver that forms colonies in a few swamps in a narrow strip on both sides of the Kenya–Tanganyika border, the extreme points of its known range being Arusha, Mkomasi, and the neighbourhood of Mombasa. Fuggles-Couchman, who has paid special attention to this bird, has failed to find it west of Arusha (personal communication). These points enclose about 8,000 sq. miles, much of which is arid, and within it swamps probably account for less than 50 sq. miles.

It is apparently a good species sympatric with the very similar *P. bojeri* and *P. aureoflavus*, both of which have wider ranges and are not confined to swamps.

Ploceus spekeoides (52)

Ploceus spekeoides Grant & Praed, 1947, *Bull. Brit. Orn. Cl.* **68** : 7—Nariam, Teso, central Uganda.

Moreau, 1960, *Ibis*, **102** : 309.

Known only from an area about 100 miles by 150 in Teso and Lango districts Uganda, where it breeds over water in open country and is not uncommon. Pitman (*in litt.*) tells us that, on the basis of his local knowledge, there is no apparent reason why it should not occur more extensively.

It is extremely like *P. spekei* in plumage and both forms have the first primary more reduced than in any other *Ploceus* species. It is, moreover, allopatric, though not contiguous, to *spekei* of north-eastern Africa, their ranges being separated by about 100 miles. However since *spekeoides* is much smaller than *spekei*, differs in female plumage and seems to differ in habits, it is for the present regarded as at least a semi-species.

Ploceus flavipes (48)

Chapin, **4** : 388. Moreau, 1960, *Ibis*, **102** : 306. Prigogine, 1960, *Rev. Zool. Bot. Afr.* **61** : 364.

An all-black weaver known from about half a dozen specimens collected in a narrow triangle of forested country covering about 3,000 sq. miles east of Avakubi in the eastern Congo, and including part of the area from which *P. aureonucha* is known. It may well occur more extensively in the Congo forests.

Owing to its peculiar large nostrils, *flavipes* has been treated by some authors as a separate, monotypic, genus, while others have regarded it as a *Malimbus*. There are no biological data to help in judging its closest affinities.

Malimbus ibadanensis (5)

Malimbus ibadanensis Elgood, 1958, *Ibis*, **100** : 622—Ibadan, Nigeria.

Elgood (*in litt.*) tells us that this weaver appears to be confined to an area of " forest fringe " about 45 by 10 miles between the Ogun and Oshun rivers, near Ibadan. Since this does not seem to be an ecological island the bird is likely to be more widely distributed.

Three other species of *Malimbus*—*M. rubricollis*, *M. nitens* and *M. scutatus*—also occur in the area, and the possibility of *ibadanensis* being a hybrid was very carefully considered, only to be discarded, before it was described as a species. Specimens subsequently obtained have supported this view, for no intermediates have been found (Elgood).

ESTRILDIDAE—Waxbills, etc.

Cryptospiza shelleyi (96)

Chapin, **4** : 448. Schouteden, **9** : 403.

One of the four known species of crimson-wing, all of which are found in the montane forests of Ruwenzori and the eastern Congo. It is the rarest and the most restricted in range, being confined to the mountains from Ruwenzori south to the

Ruzizi valley, on both sides of L. Kivu. It has not been found below 6,200 ft. and the area it inhabits is probably less than 1,500 sq. miles.

It is larger than the other three species and also has a bill which is disproportionately heavier, suggesting that it may take different food.

Estrilda nigriloris (25)

Chapin, **4** : 550. Schouteden, **9** : 414.

Found only on the banks of the Lualaba River near Lake Upemba (in the Katanga), and in swampy plains to east and west of the lake. The total area it inhabits may not exceed 1,000 sq. miles.

E. nigriloris has sometimes been treated as a subspecies of *E. astrild* or as merely a colour phase, in which the red patch on the lores and round the eye has been replaced by black. However *nigriloris* has a bill appreciably smaller and the facial patch more restricted than in any race of *astrild*. Also, its whole plumage is more suffused with pink than in the local, Katanga, race *E. a. cavendishi* though similar in this respect to *E. a. angolensis*. Although *E. astrild* is widespread over most of Africa, no specimens have been collected within the area of *nigriloris*, the nearest being from Masombwe, 70 miles east of Lake Upemba. The two forms must provisionally be regarded as allopatric, but the differences between them seem to us more than subspecific and provisionally we regard *nigriloris* as a species, as did Chapin when he described the bird. We regard *nigriloris* as forming a superspecies with *astrild*.

Estrilda cinderella or ***thomensis*** (16)

Shelley, 1905, *Birds of Africa*, **4** : 220. Chapin, **4** : 527. Da Rosa Pinto, 1960, *Bol. Cult. Mus. Angola*, **2** : 15.

The type of *cinderella* was collected in 1905 at " Deep Sloot ", Angola (about 13° S., 13° 50′ E.), near Chingoroi, in the escarpment country above the coastal plain. Two other specimens have now been reported by da Rosa Pinto, which are believed to have come from the escarpment near Dondo, about 250 miles north of Chingoroi.

On description the unique type of *E. thomensis* (said to be in Coimbra) could well be identical, but it has not been possible to compare specimens. This type is alleged to have come from São Tomé Island, and Shelley quotes a second specimen from there, but no others are known and recent collectors on São Tomé have failed to find the species. The most striking character of *cinderella* is the bright red on the flanks and lower abdomen. In the opinion of Traylor (*in litt.*), who has examined the type of *cinderella* in New York, it seems in other respects to belong to the *caerulescens-perreini-incana* group, but must be regarded as a species.

Lagonosticta vinacea (1)

Bannerman, **7** : 333.

The type came from the Casamance River, between Gambia and Portuguese Guinea, where the only definite localities appear to be Gunnal (12° 15′ N., 15° 45′ W.) and Bissao, both near the coast. In Gambia it has been collected near the coast and has also been seen by Cawkell and Moreau in drier country up river, but it seems to be one of the scarcest of the Estrildidae found in the territory. We have been unable to find a record of it north of Gambia, or further inland. On present information the range is only about 150 miles each way, where the ecology is not peculiar.

L. vinacea, in our opinion, forms a superspecies with *L. nigricollis,* which ranges from the interior of Ghana to Darfur and Uganda, and *L. larvata* of the eastern Sudan and Abyssinia. The males of all have black masks but whereas *larvata* has a dull pink wash on the head and breast and *nigricollis,* the geographically intermediate form, is wholly grey except for its tail, *vinacea* has a grey crown, a pink wash on the back and wings, and a beautiful vinaceous pink below. The female of *vinacea* is also distinctive, being washed with salmon pink above and below, unlike the dull buffish-brown of the other two species, of which *nigricollis* is the paler and greyer.

Nesocharis shelleyi (85)

Chapin, **4** : 517. Serle, 1950, *Ibis,* **92** : 637.

The nominate race of this olive-backed waxbill occurs on Fernando Po and Cameroon Mt., and the slightly larger *N. s. bansoensis* on Manenguba Mt. and the Bamenda–Banso highlands, where Serle found it common between 5,000 and 6,000 ft. in the montane forest. The area the species inhabits is probably under 500 miles as it is now unlikely to be found on other highlands in the Cameroons.

It is a matter of opinion whether or not *N. ansorgei* from the eastern Congo mountains and western Uganda should be considered conspecific with *shelleyi.* It is slightly longer in the wing, with a disproportionately longer tail and heavier bill, and has a narrow band of white dividing the black of the head from the olive-yellow of the breast. We regard them as semi-species.

FRINGILLIDAE—Finches

Poliospiza leucoptera (20)

Winterbottom, 1960, *Ibis,* **102** : 390. Skead, 1960, *The Canaries, Seed-eaters and Buntings of Southern Africa* : 84–86.

A dark seed-eater, confined to an area about 130 miles × 100 in the mountains of south-western Cape Province, north to the Cedarberg and east to the Klein Zwartberge near Ladismith, but not the Cape Peninsula. It is closely associated with thick *Protea* growth (which has, however, a much more extensive range).

Although *leucoptera* has no green edges to the wings and only a trace of green on the edges of the tail, in other respects it looks like a small *P. burtoni,* which is a bird of montane bush and forest in the tropics, with its nearest representative 1,400 miles away in Angola. Provisionally, however, we accept them as separate species, possibly forming a superspecies.

Carduelis (Warsanglia) johannis (61)

Williams, 1956, *Ibis,* **98** : 531 ; 1957, *Bull. Brit. Orn. Cl.* **77** : 157.

Found in juniper and euphorbia in the highlands of the Erigavo district, eastern British Somaliland (Warsangli country). Its known range is limited to 1,000 sq. miles (of which much may not be suitable habitat), and there is no reason to expect that it is much more extensive.

Now that the female and juvenile plumages are known there seems no justification for retaining *johannis* in a monotypic genus, for both indicate closer relationship to the Yemen linnet " *Pseudacanthis* " *yemenensis* than is apparent in the males. In Meinertzhagen's opinion (*Birds of Arabia* : 94) *Pseudacanthis*, hitherto also regarded as a monotypic genus, does not merit distinction from the other linnets, and it is more realistic now to refer both the Yemen and the Somali birds to *Carduelis*, and to combine them in a superspecies.

CLASSIFIED SUMMARY OF THE RARE SPECIES

Taxonomic Categories

1. Members of superspecies, 52.

(a) Semi-species, 17 : *Francolinus ochropectus, Tauraco ruspolii, Bubo vosseleri, Campethera tullbergi, Pycnonotus montanus, Platysteira laticincta, Turdus helleri* (see text), *Sheppardia gabela, Apalis sharpei, Apalis bamendae, Apalis kaboboensis, Prinia leontica, Cinnyris moreaui, Cinnyris loveridgei, Anthreptes rubritorques, Ploceus spekeoides, Nesocharis shelleyi.*

(b) Other members of superspecies, 35 : *Francolinus harwoodi, Francolinus camerunensis, Francolinus swierstrai, Francolinus jacksoni, Eupodotis humilis, Tauraco bannermani, Phodilus prigogenei, Lybius rubrifacies, Lioptilus rufocinctus, Lioptilus gilberti, Picathartes oreas, Phyllastrephus poliocephalus, Phyllastrephus poensis, Melaenornis ardesiaca, Cossypha isabellae, Alethe lowei, Alethe montana, Alethe choloensis, Seicercus herberti, Bradypterus grandis, Bradypterus graueri, Macrosphenus pulitzeri, Hirundo megaensis, Psalidoprocne fuliginosa, Prionops gabela* (see text), *Malaconotus gladiator, Cinnyris rockefelleri, Cyanomitra oritis, Ploceus batesi, Ploceus nigrimentum, Ploceus golandi, Estrilda nigriloris, Lagonosticta vinacea, Poliospiza leucoptera, Carduelis johannis.*

2. Species not members of superspecies, 41.

(a) Species broadly sympatric with what appear to be very close relatives, 10 : *Columba albinucha, Indicator pumilio, Calandrella fringillaris, Pogonocichla swynnertoni, Cinnyricinclus femoralis, Chalcomitra ursulae, Ploceus bannermani, Ploceus castaneiceps, Malimbus ibadanensis, Cryptospiza shelleyi.*

(b) Species believed to be of hybrid origin, 2 : *Lybius chaplini, Turdoides hindei.*

(c) Other species of which close relatives are detectable but which for various reasons are not assigned to superspecies, 10 : *Apus toulsoni, Mirafra williamsi, Anthus sokokensis, Macronyx sharpei, Muscicapa itombwensis* (*lendu*), *Chloropeta gracilirostris, Turdus ludoviciae, Geokichla cameronensis, Malaconotus alius, Estrilda cinderella.*

(d) Very distinct species, without obvious relatives within the genus, 12 : *Caprimulgus binotatus, Calandrella obbiensis* (see text), *Phyllastrephus orostruthus, Cossypha heinrichi, Apalis karamojae, Apalis moreaui, Prinia robertsi, Laniarius atroflavus, Telephorus kupeensis, Anthreptes pallidigaster, Ploceus aureonucha, Ploceus flavipes.*

(e) Species forming monotypic genera, 7 : *Pseudocalyptomena graueri, Namibornis herero, Sceptomycter winifredae, Urolais epichlora* (see text), *Poliolais lopesi* (see text), *Graueria vittata, Zavattariornis stresemanni.*

3. Species of uncertain status, 3 : *Mirafra pulpa, Geokichla oberlaenderi, Anthreptes pujoli.*

Classification by Area and Ecological Association

In classifying the " rare " species by area it is convenient to divide them into three groups as follows : (A) Species of such well-defined habitat that some estimate can be made of the maximum area occupied. (B) Those for which no estimate can be made of the area occupied but for which instead the known geographical range can be quoted. (C) Others for which no estimate can be made of range or area inhabited.

GROUP A. Species classified by area occupied. " M " is appended for montane birds, " MF " for those associated with montane forest, " F " for lowland forest, and " S " for swamp. A species that is known only from widely separated localities is denoted by " (W) ".

Species which do not occupy an area of more than 100 sq. miles ; *Francolinus camerunensis* MF, *Francolinus swierstrai* MF, *Francolinus ochropectus* MF, *Tauraco ruspolii* MF, *Lioptilus gilberti* MF, *Platysteira laticincta* MF, *Turdus helleri* MF, *Alethe montana* MF, *Alethe choloensis* MF, *Pogonocichla swynnertoni* MF, *Bradypterus grandis* S, *Apalis moreaui* MF (W), *Sceptomycter winifredae* MF, *Psalidoprocne fuliginosa* M, *Malaconotus alius* MF, *Telephorus kupeensis* MF, *Cinnyris rockefelleri* M, *Cinnyris moreaui* MF, *Ploceus castaneiceps* S.

Area occupied 100–500 sq. miles : *Tauraco bannermani* MF, *Phyllastrephus orostruthus* MF (W), *Phyllastrephus poliocephalus* MF, *Phyllastrephus poensis* MF, *Pycnonotus montanus* MF, *Chloropeta gracilirostris* S (W), *Cossypha isabellae* MF, *Sheppardia gabela* F, *Seicercus herberti* MF, *Apalis bamendae* MF, *Apalis kaboboensis* MF, *Urolais epichlora* MF, *Poliolais lopesi* MF, *Prinia robertsi* M, *Macrosphenus pulitzeri* F, *Laniarius atroflavus* MF, *Malaconotus gladiator* MF, *Cinnyris loveridgei* MF, *Chalcomitra ursulae* MF, *Cyanomitra oritis* MF, *Anthreptes pallidigaster* F, *Anthreptes rubritorques* MF, *Ploceus bannermani* MF, *Ploceus golandi* F, *Nesocharis shelleyi* MF.

Area occupied exceeds 2,500 sq. miles : *Indicator pumilio* MF (up to 4,000 sq. miles), *Lioptilus rufocinctus* MF (3,000), *Graueria vittata* MF (5,000), *Cinnyricinclus femoralis* MF (5,000).

GROUP B. Species classified by known geographical range. Those marked " * " may be expected to have a wider range.

Species known only from the area of the type locality : *Phodilus prigoginei, Mirafra williamsi, Cossypha heinrichi, Anthreptes pujoli.*

Species with range under 5,000 sq. miles : *Turdoides hindei* (2,500), *Hirundo megaensis* (3,000), *Prionops gabela* (600)*, *Zavattariornis stresemanni* (1,500), *Malimbus ibadanensis* (450)*.

Range 5,000–62,500 sq. miles : *Eupodotis humilis* (20,000)*, *Columba albinucha* (10,000)*, *Lybius rubrifacies* (10,000)*, *Lybius chaplini* (22,500), *Picathartes oreas*

(14,000)*, *Geokichla cameronensis* (10,000)*, *Namibornis herero* (16,000)*, *Ploceus aureonucha* (5,000)*, *Ploceus spekeoides* (15,000)*, *Ploceus flavipes* (3,000)*, *Lagonosticta vinacea* (22,500)*, *Poliospiza leucoptera* (13,000).

Group C. Species for which no estimate can be made of range or area inhabited. *Caprimulgus binotatus* (2 areas 900 miles apart), *Apus toulsoni* (2 localities 250 miles apart), *Mirafra pulpa* (2 loc. 300 miles apart), *Calandrella fringillaris* (2 areas 126 miles apart), *Calandrella obbiensis* (2 loc. 300 miles apart), *Muscicapa lendu/itombwensis* (see text), *Geokichla oberlaenderi* (2 areas 300 miles apart), *Bradypterus grandis* (2 areas 300 miles apart), *Apalis sharpei* (3 loc. in 600 miles), *Apalis karamojae* (2 areas 450 miles apart), *Ploceus batesi* (100 × ? sq. miles), *Ploceus nigrimentum* (2 areas 650 miles apart), *Estrilda cinderella* (see text).

Geographical Distribution

So far as possible, this is shown on the map, the key to which is appended. The rare species are so closely packed in the two areas comprised in respectively the highlands of the Cameroons and those of the eastern Congo that their distribution is shown in separate detail.

DISCUSSION

Background

Discussion is hampered by lack of information about the history of African birds in general and also about the palaeoclimatology of Africa. Bird fossils are almost wholly lacking on the continent and nothing definite is known about the age of existing species. All that can be said is that, on the most recent generalization for birds as a whole, most existing genera had been developed by the Pliocene (Storer, 1960).

Some geographical details of the Ethiopian Region are important, especially those concerned with the mountains. Briefly, lowland evergreen forest fills much of the Congo Basin and extends westwards across West Africa. Vestiges persist on the East African coast. The remainder of the Ethiopian Region is filled with deciduous " savanna ", changing to dry thornbush and semi-desert towards Somaliland and South West Africa. Orographically most of Africa south of the Zambesi is occupied by a great plateau, but in those parts which are high enough to be ecologically montane they are mostly too dry or are deforested. Vestiges of montane forest remain in south-western Angola. Northwards a chain of great highlands runs along the eastern border of the Congo Basin nearly to the boundary of the Sudan. Abyssinia and Kenya each contain a large compact highland block and in addition there are in eastern Africa, mainly in Tanganyika and Nyasaland, a number of mountains capped with forest and stringently isolated from each other by low dry country. West Africa (west of the Cameroons) shows nothing comparable. At the head of the Gulf of Guinea, and separated by over 1,200 miles of lowland from any of the mountains just mentioned, stands Mt. Cameroon and the compact archipelago of neighbouring mountains ; but in the great extent of the continent to the west of the Cameroons hardly any land reaches the requisite height and no typical montane biome seems to be produced.

Although the Ethiopian Region has not been subjected to any important dissection by the sea in relevant geological time, it has undergone repeated and considerable fluctuations in climate, even in the vicinity of the Equator, especially during the Pleistocene. Geological evidence has been provided for the expansion and contraction of East African lakes and glaciers, for example, and of the Kalahari Sands, especially towards the lower Congo ; but the size of the area affected by each of the changes thus documented and the degree to which they were contemporaneous are still matters for discussion. Moreover, some of the major features of the African landscape, its mountains and lakes, took on their present size and form only late in the Pliocene or in the Pleistocene—that is, to a great extent in the course of the last one million years or so. Apart from such geological evidence, the present distribution of plants and birds in tropical Africa leads to several postulates about conditions in the geologically recent past (summarized by Moreau, in press). In particular, there can be little doubt that at some period (or periods) the montane evergreen forest had a wider distribution, linking the present isolated patches in eastern Africa, the Cameroons and Angola, though probably not those of Abyssinia. For this to occur the climate must have been much cooler and wetter than it is at present over vast areas, though not necessarily over all of them at once. It seems also that lowland forest must for a time have extended from the Congo Basin to the East African coast, which would require in the intervening country a wetter, more equable and in part warmer climate than rules there at present ; that the gap dividing the Upper and Lower Guinea forests must have been in Nigeria rather than where it is now ; and perhaps that at least a corridor of dry conditions joined the semi-arid country north of the Equator with that to the south. These postulates imply a succession of climatic changes that, while less catastrophic than those involved in the Pleistocene glacial vicissitudes of the Holarctic, must have contributed greatly to the evolution of African plants and animals.

It may be added that the distributional picture, with which ornithologists have up to now been dealing in tropical Africa, is on the whole believed not to have been affected, directly or indirectly, by human activity so seriously that any appreciable number of species have become extinct. But many species, and especially nearly all those confined to montane forests, have had their areas reduced since the emergence of agricultural man. Prior to his advent nearly all the rare species for which an area of occupation is estimated in the preceding section would have had a larger one, though still judging from the orography, far within the spatial limitations of this study.

Finally, before embarking on detailed discussion, it is worth emphasizing that the examples on which it is based are extremes, and that a large number of birds of limited or peculiar distribution fail in varying degrees to come within the arbitrary limits we set (see especially those listed in the Appendix).

The Ecological and Geographical Distribution of the Rare Birds

As shown earlier in this paper, over half the rare species belong to montane islands, especially to montane forest. This, of all habitats, is the one least likely to be disturbed in geographical position, whatever the climatic changes of the area as a whole. A shift in the location of the equatorial rainbelt, and consequently of the belts of savanna climate, or a period of reduced rainfall, can cause a wholesale replacement of habitat and consequently of avifauna over a wide area of country—as, for example, when the Kalahari sands advanced north to the lower Congo River. But the effect on an area of montane forest will be merely to raise or lower its boundaries, with consequent change in the area of the ecological island it represents, but not its elimination except where the montane area is of critically low altitude.

As will be seen from the map, the rare species are for the most part concentrated into two groups:

(1) The forests on the mountains at the head of the Gulf of Guinea. Of these Mt. Cameroon and Manenguba are volcanoes, the former recently active, while the other mountains are of granite, gneiss and syenite; but the avifaunas of the mountains do not show any general differences correlated with their geology (see especially data in Serle, *Ibis*, 1950 : 346–347 and Serle, *Ibis*, 1954 : 48).

(2) The forested mountains along the Rift Valley from Lake Albert to Lake Tanganyika. Again, the great geological differences between the active Kivu volcanoes and the ancient crystalline mountains, especially Ruwenzori, are not clearly reflected in the avifaunas. It may be mentioned that to the " rare " species mapped for this central chain of forests could be added some other species that fail to qualify only because, with outlying populations as far north as Lake Edward and as far south as Mt. Kabobo, overlooking the north-west of Lake Tanganyika, their north-to-south extension exceeds our 250-mile limit. Among such species are *Tauraco* (*Ruwenzorornis*) *johnstoni*, *Hemitesia neumanni*, *Coracina graueri* and *Prionops alberti*.

In East Africa there are several rare forest species on relatively small non-volcanic mountains in Tanganyika and just over the Kenya border, but none confined to the greatest of African mountains, the volcanic Kilimanjaro, only one on the numerous (non-volcanic) island mountains of Nyasaland and the contiguous part of Portuguese East Africa, and only two associated with the forest of the Kenya Highlands (one of those also on Kilimanjaro). This situation to some extent finds a parallel in the vegetation, for the forests on some of the small crystalline mountains of Tanganyika are particularly rich in endemic plants.

Apart from the montane forest birds, concentrations of rarities are found, though on a smaller scale, in western Angola and in the relict East African coastal forests. In Angola it has been postulated (Hall, 1960*b*) that the zone along and below the western escarpment has, owing to its proximity to the sea, been less affected by climatic changes than the interior of the country and consequently has served as a refuge for communities intolerant of drought. This is essentially the same argument as that advanced above to account for persistence of individual mountain forests, and to some extent it probably applies to the East African coastal area also.

The group of three rare species in southern Abyssinia is of particular interest because two of them, *Zavattariornis* and *Hirundo megaensis*, are confined to an area of open country that does not seem to be an ecological island. The Abyssinian plateau as a whole, which is mostly much higher than the area in question, certainly possesses some characteristic species, which caused Chapin (**1** : 90) to designate the Abyssinian Highland as a faunal district. Its area is however too great for the characteristic species to qualify as " rare " for the present purpose, and the point about the three under discussion is that they are, for no apparent reason, confined to one and the same small part in the south of the Abyssinian Highland district. Three other species are associated with juniper forest in Somalia, two of which, *Turdus ludoviciae* and *Carduelis johannis* have some affinities with Palaearctic species.

There are two very large areas on the map with exceptional sparsity of rare species, West Africa (west of the Cameroons) and South Africa (south of the Zambesi). The West African paucity is relieved only by *Anthreptes pujoli*, of which nothing is known except the type, *Lagonosticta vinacea*, which is associated with an apparently unspecialized deciduous woodland at the western extremity of the continent, and *Prinia leontica*, which seems to be dependent on submontane conditions in one of the only two areas where these occur in the vast extent of Africa west of the Cameroons. This whole area is indeed peculiarly devoid of barriers that isolate populations, except that the lowland forest is interrupted by the dry belt between Nigeria and Ghana. However, although the isolated " Upper Guinea " forest extending from Ghana to Sierra Leone, and with outliers as far west as Portuguese Guinea, has several endemic species, none is so restricted within it as to qualify as " rare " for the present purpose.

The rare species in southern Africa (south of the Zambesi) are few and ecologically heterogeneous, although two, *Prinia robertsi* and *Pogonocichla swynnertoni*, are confined to the elevated eastern edge of the Southern Rhodesian plateau. Others might have been expected in the mountains further to the south and in the relict forests of Zululand, Natal and the coastal belt of the Cape Province. In fact, several species have a somewhat limited range within the winter-rainfall area of the Cape Province, where endemism in the peculiarly rich flora is very high indeed, but only one bird, *Poliospiza leucoptera* (associated with proteas, not with forest), has its range sufficiently restricted for it to be classed here as rare. There are also species other than *Namibornis herero* endemic to the drier parts of South West Africa that have a range outside our limits.

Finally, it may be noted that although the map shows a group of rare species in the lowland forest of the north-eastern Congo, they are birds that we think might well have a more extensive range.

The Evolutionary Status of the Rare Birds

Of the 96 rare birds seven are so peculiar that they are accepted as monotypic genera. They represent the other extreme on the evolutionary scale from the 17 semi-species which on average are presumably the youngest of all the groups under consideration. Of the 89 species not assigned to monotypic genera, 52 are members of superspecies and the proportion is even higher, 43 out of 60, if the 29 birds of uncertain range (group C and part of group B in the " Classification by area ") are omitted. Ten more species may comparatively recently (on the geological time-scale) have passed through the stage of being members of superspecies; their nearest relatives are obvious but they are broadly sympatric with them (see further discussion below). In these cases presumably after acquiring reproductive isolation one species has invaded the territory of its relative.

The extent to which species that are or have been members of superspecies bulk in the list of rare species is significant. In conjunction with the prevalence of montane birds among the rarities, it emphasizes the importance the numerous isolated montane areas scattered over tropical Africa have had in the evolution of species. Perhaps the most remarkable example is in the francolins, where a montane forest superspecies has " rare " representatives in the Cameroons, Angola, French Somaliland and Kenya. Such birds are indicators of past extension of the parent stock on a vast scale, but unless after they evolved to specific status they occupied larger areas than they do now they are not in the technical sense relicts.

The problem of how far each of the rare species should be regarded as relict or emergent is in fact relative. There would be a strong case for regarding a species as emergent if it appeared to be adapted to some peculiarity of the area to which it is limited, but of such birds there seem, in our present state of knowledge, to be no cogent examples. Failing this, the species with the best claim to be regarded as emergent are those believed to be of hybrid origin, namely, the barbet *Lybius chaplini*, with putative parents *L. torquatus* and *L. leucocephalus*, and the babbler *Turdoides hindei*, with putative parents *T. hypoleuca* and *T. leucopygia* or *melanops*. Although only the first-named of their putative parents are now present in the areas of *L. chaplini* and *T. hindei*, this does not invalidate the hypothesis of their origin. On the contrary, since natural selection and competition normally militate against the successful development of a hybrid species it can be argued that it is most likely to succeed where one parent species overwhelms a small population of the other, which has perhaps been separated from the main body of its species in the course of ecological fluctuations. The numerical inferiority of such a small population, with the resultant limited choice of mates, could lead to interbreeding with the hybrid offspring and the eventual elimination of one parent species in its pure form within the area concerned. At the same time the hybrids would need to be sufficiently well adapted to compete successfully with the other, surviving, parent population. This may have occurred with the two species under discussion ; and whereas *Turdoides hindei* shows the instability of colour and pattern associated with hybrid swarms, *Lybius chaplini* does not, and hence is presumably the older of the two.

Several birds might be cited as probably owing their present restricted range to interspecific competition. Perhaps the clearest case is that of the wattled-eyed flycatcher *Platysteira laticincta*. It is confined to a few square miles of forest in the highest part of the Bamenda–Banso highlands, while forest below 5,000 ft. there (and on neighbouring mountains up to 6,500 ft.) is occupied by *Platysteira cyanea*. It seems impossible that the Bamenda–Banso highlands, which form a continuous block, should ever have provided the degree of isolation necessary for *Platysteira* stock to differentiate there to specific level and the probability is that *laticincta* is making its last stand on the tops against invading *cyanea*. The long-claw *Macronyx sharpei* on the upper grasslands of the Kenya Highlands may be in a closely similar position, islanded among the low-level and geographically more widespread *M. croceus*. A less clear case is that of the bank-swallow *Psalidoprocne fuliginosa*, which is known only from Fernando Po and Cameroon Mt., its place on neighbouring mountains being taken (as high as 9,000 ft.) by *P. petiti*. This is otherwise a lowland bird, and hence not a typical member of the montane avifauna. It seems possible that *fuliginosa* occupied all the mountains of the geographically compact group in the Cameroons but has been progressively eliminated on the mainland by a rising tide of adaptable *P. petiti* except on Mt. Cameroon itself. The greater height of this might give *fuliginosa* a stronghold in the upper levels, with the backing of which its population can withstand *petiti*.

Such cases as *Phyllastrephus orostruthus*, known only from two montane forests 700 miles apart (and rare in both), are almost certainly due to the elimination of intermediate stations ; and the state of at least some of the species, such as *Malaconotus alius*, confined to a single station, is likely to be due to exaggeration of the same process. As an illustration of an earlier stage *Apalis chariessa* may be cited. It is flourishing in a number of forests round the south end of Lake Nyasa ; it is known from one locality nearly 600 miles to the north, at the foot of the Uluguru Mts. of central Tanganyika ; and it was first discovered over 80 years ago 300 miles further north still, on the Tana River, in Kenya, in which country it has not been reported since.

A special situation arises in the case of those rare species which in most or all of their very limited ranges are found co-existing with what appear to be their nearest relatives, especially the bush-robin *Pogonocichla swynnertoni* in Southern Rhodesia with *P. stellata*, the starling *Cinnyricinclus femoralis* in Kenya with *C. sharpii*, the sunbird *Cinnyris rockefelleri* with *C. regius* in the mountains of the south-eastern Congo Basin, the weaver *Ploceus castaneiceps* with *P. aureoflavus* and the estrildine weaver *Cryptospiza shelleyi* with the other three species of the genus on Ruwenzori. Clearly, in each of these cases the species concerned must have evolved in isolation from common stock and at the penultimate stage of their history they formed a superspecies. Then, having attained inherent reproductive isolation, one or more forms invaded the range of another. Such situations must produce a threat to the continued existence of the invaded species if the two are in direct competition, unless local segregation can take place as in the case of the *Platysteira* spp. cited above. On the other hand if the species concerned adapt themselves to sufficiently different ecological requirements they could co-exist indefinitely. Too little is known of the habits of any of the birds quoted as examples of this situation to assess their field relationships, but in fact it is probable that the co-existence of the *Pogonocichla* species has been prolonged. The widespread *stellata* has differentiated subspecifically both to the north and to the south of the *swynnertoni* station and for geographical reasons it is not likely to have accomplished this without having occupied the *swynnertoni* station in the process of its expansion.

A much older relict status is probable for those rare birds which have no close relatives in Africa, whether a bird with no obvious relative in its genus, or a bird forming a monotypic genus, or a bird forming a superspecies with one in another zoological region. It is the last two categories for which the longest period of relict status may be postulated. Examples are *Phodilus prigoginei* and *Pseudocalyptomena graueri*, both birds of montane forest on the eastern edge of the Congo Basin (and presumably very sedentary), which have their nearest relatives in Asia. (Other cases are *Hemitesia neumanni*, from the same mountains, but with a narrow range exceeding from north to south our limitation of 250 miles, and probably also "*Apalis*" *moreaui*, "*Artisornis*" *metopias* and *Poliolais lopesi*—see discussion in Systematic List above.) Unless the connection of these species with evergreen forest has developed only late in their history, which is unlikely, they must have been sundered from their Asiatic relatives ever since southern Arabia ceased to carry forest ; and this can hardly be more recent than the early Pliocene (Moreau, 1952 : 905).

Another group of rare species, the relict status of which is probably ancient, are those accepted as monotypic genera. Two of these are even difficult to place in a family or subfamily. *Graueria* has been ascribed to the bulbuls and the warblers, while the babblers have also been considered ; *Namibornis* to the flycatchers and the thrushes. Other rare species have been the subject of similar uncertainty—*Alethe lowei*, *Alethe montana*, *Sheppardia gabela*, *Macrosphenus pulitzeri*, *Chloropeta gracilirostris* and *Picathartes oreas* (the last three along with their congeners). It seems probable that these birds, as well as the rare monotypic genera, date from a comparatively early stage in the evolution of the passerines.

The processes that have reduced the rare species to their present straits have no doubt been various, with competition and ecological fluctuation the most important. They are particularly difficult to envisage for *Zavattariornis* and *Hirundo megaensis*, which occupy much the same area of open country in southern Abyssinia, and one without obvious ecological distinction. In Angola several species seem to have suffered more than usual from recent human activity in combination with ecological fluctuation (Hall, 1960*b*).

The Systematic Distribution of the Rare Birds

The birds qualifying as rare by our criteria are very unevenly distributed from the systematic point of view, only seven out of over 600 species of non-passerine land-birds, compared with 80 out of less than 1,000 passerines—about 3% against 8%. The disproportion is even more marked when allowance is made for the fact that five of the 17 non-passerines are francolins, four of them in one superspecies.

To some extent the difference between the percentages may be accounted for by the fact that on the whole the non-passerine birds are much bigger and with bigger individual ranges, so that a numerically small population of some species in general occupies a relatively large area. (The francolins are exceptional since they appear to be unusually sedentary.) Moreover, more than half the rare species are associated with montane ecological islands, and especially with montane forest, a habitat in which most of the passerine families are represented and most of the non-passerine are not.

Within the passerines themselves, the proportions of rare species vary much between the families and subfamilies that are best represented, as follows : Muscicapinae 5% (four out of about 87 species), Turdinae 14% (12/86), Sylviinae 13% (16/127), Nectariniidae 12% (8/64), Ploceidae 11% (9/81) and Estrildidae 6% (5/78). But if we omit the species listed in the classified summary as likely to have a more extensive range than at present known, the highest proportion is in the Sylviinae and the Nectariniidae, with about 10% each, while all the others are reduced to 4 or 5%. The difference could mean that the warblers and the sunbirds show an exceptional tendency to differentiate when in isolation ; and in fact the rare species of warblers, though not notably those of sunbirds, include an exceptionally high proportion that are members of superspecies.

Estimates of Surviving Populations

Given approximate areas inhabited, some idea can be obtained of the number of individual birds existing in some of the rare species. Areas are more precise for montane forest birds than for others, but no censuses on tropical mountains exist. However, in temperate forests of various types the density of all species combined only very exceptionally reaches 10 adult birds to the acre (equivalent to about 6,000 to the sq. mile) and in North America does not exceed six (Lack, 1937 ; Mayfield, 1960). In montane forest in the tropics the number of species may be about 40 (examples in Chapin, **1** : 252 ; Moreau, 1935, *J. Linn. Soc. London*, **39** : 285–293 ; Serle, 1950, *Ibis* : 346). If the density of birds in the African montane forests is not strikingly different from that in the temperate forests (and a little personal experience gives no reason to suppose that it is) density of each tropical montane species would on the average be about 150 adults to the square mile. On that basis there are several African species, *Francolinus ochropectus*, *Tauraco ruspolii*, *Turdus helleri* and *Telephorus kupeensis*, the total populations of which are likely to be less than 2,000. More than a dozen others confined to not more than 100 sq. miles might be expected to have total populations below 20,000. In fact, these estimates are very likely too generous, on the analogy of Kirtland's Warbler *Dendroica kirtlandii* in the U.S.A., a species comparable to the rarest African birds but one to which much attention has been directed. Its breeding range lies in an area of 85 miles by 100 which contains much of its exclusive breeding habitat (*Pinus banksiana*). However the bird cannot be found at all in much of the apparently suitable country and after careful census work it is doubtful whether the population reaches 1,000 adult birds (Mayfield, 1960)—i.e. an average of less than one bird to 8 sq. miles of its geographical range. This case is also interesting because the limitation of numbers seems not to be a consequence of human activities, but nest parasitization (by cowbirds) may be critical.

In sum it may be said that there are nearly a score of African species which are likely to consist of at most a few thousand individuals and some that may count no more than a few hundred.

Comparison with Other Zoological Regions

We have seen that in the Ethiopian Region nearly 100 species of birds qualify as " rare " ; and of these perhaps as many as 70 may not lose that status as a result of further collecting. It is unfortunate that we are not in a position to make comparisons with the other two tropical zoological regions, the Oriental and the South American—these areas would need the same kind of investigation as we have undertaken in the present paper for Africa, and for that we do not possess the necessary local knowledge; but direct comparisons with the Palaearctic, the Nearctic and the Australian Regions are possible.

The Palaearctic Region is nearly twice the size of the Ethiopian, but with only two-thirds as many species, about 1,100. On the latest lists (see especially Vaurie, 1959) less than 20 species have ranges restricted within our limits. A point in which they resemble the Africa rarities is that none of them seem to be long-distance migrants. It is remarkable that of the 20 species the western Palaearctic seems able to claim only a single one, *Serinus syriacus* of the mountains in Syria and the Lebanon. Other western species, Moussier's Redstart *Diploötocus* and the Olivetree Warbler *Sylvia olivetorum*, which we are accustomed to think of as uncommonly restricted in range, considerably exceed the 250-mile limit to which we have been working, and so does the Caucasian endemic *Lyrurus mlokosiewiczi*. The remaining " rare " species of the Palaearctic are nearly all Far Eastern and most of them from the semi-deserts and mountains around the borders of China and Tibet. (Of some of these the ranges may well be extended by further exploration.) In the other great focus of endemics, along the Himalayas, hardly any fail greatly to exceed 250 miles in their east-to-west extension. Mention should however be made of one species, *Acrocephalus orinus*, from the upper Sutlej, near Simla, which seems to be unique among Palaearctic passerine species in being known only from the type specimen.

The contrast in respect of rare species between the Palaearctic and Ethiopian Regions is certainly very striking, but so also is that between the Western Palaearctic and the Eastern. We should be inclined to suggest that this may be the result of the different history of the two areas in the Pleistocene. During the glaciations Europe and Asia Minor underwent a much greater change compared with the interglacials and the present than the Eastern Palaearctic, because the latter did not suffer from an immense extension of the ice-cap. Disturbance of the life-zones would have been far less and so consequently the opportunities for widespread alterations in range and for extinction.

The Nearctic is about the size of the Ethiopian Region, with barely half as many species of birds (750). In Canada and the United States there are, it appears, only about nine species that have ranges restricted within our limits, restricted that is in range and/or in numbers without recent human intervention being mainly responsible. As Traylor has remarked (*in litt.*), nearly all of them appear to be " representative species ", i.e. members of superspecies, but in other respects they are very diverse. Three of them belong to the subtropical promontories, Lower California and Florida, obvious refuges. Three of them, Ross's Goose and two limicolines, are birds of the arctic north-west (a group for which there is no parallel in the Palaearctic). Two of these, together with Kirtland's Warbler, are long-distance migrants, a type of bird not represented in the other zoological regions. (For a discussion of " Migratory birds of relict distribution " see Amadon, 1953.)

Finally, thanks to Keast (*in litt.*) it is possible to discuss also Australia, a continent less than half the size of the Ethiopian Region, and with barely one-third as many species of birds (520). With its post-Pleistocene crisis of drought (Keast, 1959) Australia has had a climatic history almost as catastrophic as the Palaearctic and the

Nearctic during the Pleistocene and far more so than the Ethiopian Region as a whole. Keast tells us that a dozen Australian birds, all passerines, would qualify as " rare " by the standards used here. Five of the species, all of different genera and indeed three of them monotypic, are confined to parts of the Cairns–Atherton rain-forests of Central Queensland, which have a total area of perhaps 2,500 sq. miles. These birds presumably are relicts, like the lyrebird *Menura alberti*, confined to the Macpherson Range of southern Queensland. By contrast, the two semi-species of *Petrophassa* pigeons of the " broken rocky gullies and precipices of the northern Kimberleys ", in north-western Australia, seem to Keast, like the rock warbler *Origma rubecula* of the Sydney sandstone, to have evolved in relation to the peculiar environments where they are found. Finally there are four apparently closely related species of the wide-ranging genus *Amytornis*, each confined to the narrow ecological island of a single valley surrounded by country of a type nowhere occupied by birds of this genus. Three of the species, living in the north in broken rocky country and spinifex, are isolated by " unsuitable savanna grassland " consequent on climatic amelioration ; but the fourth, further south, is surrounded by bare stony desert, the result of deterioration. This illustrates well circumstances in which a superspecies has evolved.

Thus all the four zoological regions examined differ in the nature of their rare species. On present knowledge rare species form a much larger proportion of the Ethiopian avifauna than of the others—6% of species, compared with some 2% in the Palaearctic, 1% in the Nearctic and 2% in the Australian. The percentage will certainly be reduced to a greater degree by further exploration in Africa than in the other continents, but even so there is almost certainly a real difference. This is probably attributable in part to the geography of Africa, with its abundance of well-isolated montane areas, and in part to its climatic history, in which there have been less drastic climatic changes but frequent fluctuations contributing to the formation of ecological islands in which species could develop.

Conclusion

On critical examination there still remain nearly 100 African birds, of status ranging from semi-species to monotypic genus, that are known only from extremely few specimens and/or extremely limited ranges. While some of these rarities will certainly be found by further exploration to be less limited than present knowledge indicates, the ranges of many of them are believed to be definitely known. A large proportion of the latter are confined to ecological islands, montane or swamp. Again and again we have cases in which the European equivalent would be the confinement of an entire species to the Pennines or Exmoor in Britain or the Massif Central in France. Nearly a score of the African rarities are probably represented by no more than a few thousand individuals and some by a few hundreds only. For the most part the extreme rarities seem not to be in immediate danger of extinction, but their existence depends absolutely on the survival of forests, in some cases already little better than vestigial, especially in Angola. Even where such forests are protected by legislation, their future cannot be regarded with equanimity.

Notwithstanding these circumstances, it is not easy to designate many of the rare birds as relicts or the opposite. Some two-thirds of them, often widely sundered from their nearest relatives, are members of superspecies. In such cases, in relation to the postulated former wide extension of the parent stock, each existing population is a relict ; but in its present form of a distinct species (or semi-species) it is a relict only if, since acquiring this identity, its range has decreased. It is probable that as a rule this has not happened, and if not, then the various semi-species may be regarded as typically emergent, and this applies most cogently also to the two species believed to be of hybrid origin. On the other hand, those species which lack evident relatives in Africa must have a long history of what must undoubtedly be classed as relict status.

Compared to other areas for which data are available, the Ethiopian avifauna is remarkable for its prevalence of rare species ; and the explanation of this is in the main not difficult. The African topography provides a wealth of ecological islands that are as conducive to speciation as an extensive marine archipelago. The climatic fluctuations in tropical Africa, though considerable, have been less severe than those of the Nearctic and the Palaearctic, with their vast and obliterative glaciations, and probably than those of Australia, with its widespread crisis of drought. Most of the montane refuges of Africa are likely to have persisted as such ever since they first built up to the necessary height and were colonized by the appropriate vegetation. The antiquity of some of the rare birds that have survived in such surroundings is indicated by the difficulty in placing them in the families and subfamilies that are currently recognized.

SUMMARY

1. The " rare " birds are defined as those species which do not have a range of more than 250 miles in any direction, plus 13 others that merit special consideration since they are known from very few specimens and/or two localities remote from each other.

2. Each of the 96 selected species is discussed separately with respect to its range, ecology and status.

3. The species are summarized in (*a*) taxonomic categories, (*b*) by area and ecological association.

4. It is found that more than half the rare species belong to montane islands, especially montane forest and that there are concentrations of rarities in western Angola and coastal Kenya and Tanganyika, three in both southern Abyssinia and Somalia, but relatively few in West and southern Africa.

5. The selected species contain examples of species in many differing stages of the evolutionary scale, some being apparently relict species, some which co-exist with their nearest relatives, some members of superspecies and some of possibly hybrid origin.

6. Of the 96 rare birds only 17 are non-passerine, including five francolins. Among the passerines the warblers and the sunbirds provide the highest percentage of rare species.

7. About 15–20 of the rare species may consist of less than a few thousand individuals and some of no more than a few hundred.

8. A greater percentage of species rank as "rare" in the Ethiopian Region than in the Nearctic, Palaearctic and Australian.

APPENDIX

This gives all those birds ranked as species with a limited range in the *Systema Avium Aethiopicarum* (or by subsequent describers), which for various reasons we regard as ineligible for our main list. In a few cases it is necessary to explain our reasons, but most of the birds fall into two groups: (1) those (denoted by us as "extra-limital"), whose ranges have, since Sclater wrote, been shown to be more extensive than the arbitrary limits we set for our present purpose; (2) those which have, with what seems to us to be good reason, been rejected as full species by other workers. For both groups we have as a rule thought it sufficient to cite the relevant regional work. Convenience is, we think, served by listing each bird under the generic name used in the reference cited, irrespective of subsequent taxonomic "revision".

Melanophoyx vinaceigularis = *M. ardesiaca* (Roberts : 24).
Lampribis splendida = *L. o. olivaceus* (Peters, **1** : 134).
Falco fasciinucha, extra-limital (Ostrich, 1958 : 57, *Ibis*, 1956 : 139, 1960 : 132).
Falco pyrrhogaster = *F. vespertinus* (Grote, 1923, *Orn. Mon.* : 38).
Accipiter hilgerti = *A. ovampensis* (Peters, **1** : 225).
Afropavo congensis Chapin, 1936, extra-limital (Prigogine, 1956, *Service des eaux et forêts, Leopoldville* : 1–4).
Agelastes meleagrides, extra-limital (Bannerman, 1953, **1** : 339).
Numida mulondensis Monard, 1934 = *N. mitrata papillosa* (White, 1945, *Ibis* : 467).
Numida zechi = *N. meleagris galeata* (Bannerman, **1** : 347).
Francolinus finschi, extra-limital (Chapin, **4** : 626).
Francolinus ugandensis = *F. icterorhynchus emini* (Praed & Grant, 1935, *Ibis* : 194).
Francolinus nigrosquamatus = *F. clappertoni nigrosquamatus* (Praed & Grant, **1** : 248).
Francolinus tetraoninus = *F. squamatus schuetti* (Praed & Grant, **1** : 280).
Francolinus bourquii Monard, 1934 = *F. coqui subsp.* (White, 1945, *Ibis* : 467).
Francolinus atrifrons Conover, 1930 = *F. castaneicollis atrifrons* (Benson, 1945, *Ibis* : 392).
Francolinus cruzi Themido, 1930 = *F. swierstrai* (White, 1945, *Ibis* : 467).
Pternistes cooperi Roberts, 1947 = *P. swainsoni* × *P. afer* (Hall, in preparation).
Himantornis whitesidei = *H. haematopus whitesidei* (Chapin, **2** : 27).
Coturnicops ayresi, extra-limital (Praed & Grant, **1** : 294).
Coturnicops macmillani = *Sarothrura ayresi* (Praed & Grant, **1** : 304).
Sarothura lugens, extra-limital (Praed & Grant, **1** : 296).
Sarothura antonii = *S. lineata antonii* (Praed & Grant, **1** : 293).
Sarothura modesta Monard, 1949 = *S. lugens* (Mayr, 1957 : 24).
Choriotis adolf-friederici = *Ardeotis kori struthiunculus* (Praed & Grant, **1** : 327).

Neotis burchelli = *N. d. denhami* (*ibid.*).

Neotis heuglinii, extra-limital (Praed & Grant, **1** : 318).

Lophotis savilei = *L. ruficrista savilei* (Praed & Grant, **1** : 324).

Streptopelia hypopyrrhus = *S. lugens hypopyrrhus* (Chapin, **2** : 157).

Streptopelia fulvopectoralis = *S. decipiens fulvopectoralis* (Praed & Grant, **1** : 490).

Pachycoccyx brazzae = *P. audeberti validus* (Chapin, **2** : 185).

Clamator caroli = *C. cafer* (Grant & Praed, 1936, *Bull. Brit. Orn. Cl.* **56** : 124–126).

Centropus epimodis = *C. senegalensis* (Elgood, 1955, *Ibis* : 586).

Centropus fischeri = *C. monachus fischeri* (Praed & Grant, **1** : 515).

Ruwenzorornis johnstoni, extra-limital (Moreau, 1958, *Ibis* : 73).

Agapornis nigrigenis = *A. lilianae nigrigenis* (Moreau, 1948, *Ibis* : 235).

Protockus bradfieldi Roberts, 1930, extra-limital (Roberts : 175).

Lophoceros williaminae de Schauensee, 1931 = *Protockus bradfieldi williaminae* (Roberts : 175).

Scoptelus cavei Macdonald, 1946 = probably *S. aterrimus*. We have examined the type, a juvenile, and confirm that it shows the distinctions from young *aterrimus* that were noted in the original description. We feel, however, that more specimens, especially adults, are required before *cavei* can be accepted as other than a variant.

Tyto cabrae = *Tyto c. capensis* (Peters, **4** : 84).

Otus icterorhynchus, extra-limital (Chapin, **2** : 372).

Otus holerythrus = *Otus icterorhynchus holerythrus* (*ibid.*).

Scotopelia salvago-raggii = *S. peli* (Praed & Grant, **1** : 662).

Scotopelia ussheri, extra-limital (Bannerman, **8** : 266 ; Rand, 1951, *Fieldiana Zool.* **32** : 597).

Caprimulgus keniensis = *C. pectoralis fraenatus* (Praed & Grant, **1** : 684).

Caprimulgus houyi = *Macrodipteryx longipennis* (Bannerman, **3** : 169).

Caprimulgus koesteri Neumann, 1931 = *C. poliocephalus koesteri* (Hall, 1960*a* : 411).

Micropus niansae, extra-limital, on either of the taxonomic interpretations in Lack, 1956, *Ibis* : 48–54.

Micropus myoptilus, extra-limital (Lack, 1956, *Ibis* : 43).

Micropus achimodzi = *Apus myoptilus* (*ibid.*).

Apus batesi, extra-limital (Chapin, **2** : 254).

Apus schoutedeni Prigogine, 1960 = *A. myoptilus schoutedeni*. We have compared a specimen of *A. schoutedeni* with others of *A. m. myoptilus*, *A. m. chapini* and *A. m. poensis* and note its darker coloration and slight differences in wing formula and tail pattern. Prigogine (*in litt.*) tells us that *chapini* and *schoutedeni* have actually been obtained in the same locality, Butokolo, but there is so far no evidence that their breeding ranges overlap. The situation is complicated by the fact that at least *chapini* has definite seasonal movements and probably has two breeding seasons in the year. For the present we hesitate to admit *schoutedeni* as a distinct species.

Telecanthura melanopygia, extra-limital (Chapin, **2** : 445 ; Good, 1952 : 163).

Lybius leucogaster = *L. leucocephalus leucogaster* (see text, p. 325).

Lybius tsanae = *L. u. undatus* (Praed & Grant, **1** : 737).

Tricholaema flavibuccale = *T. melanocephalum flavibuccale* (Praed & Grant, **1** : 713).

Gymnobucco sladeni, extra-limital (Chapin, **2** : 514).

Viridibucco coryphaea, extra-limital (Chapin, **2** : 493)'

Pogonolius schoanus = *P. chrysoconus xanthostictus* (Praed & Grant, **1** : 737).

Indicator meliphilus, extra-limital (Friedmann, 1955, *U.S. Nat. Mus. Bull.* **208** : 224), though not conspecific with *I. exilis* (Chapin, **4** : 633).

Indicator appelator Vincent, 1933 = *I. exilis meliphilus* (Praed & Grant, **1** : 748).

Indicator propinquus Friedmann, 1943 = *I. e. exilis* (Friedmann, 1954, *Ann. Mus. Cong. Zool.* **1** : 23).

Melignomon zenkeri, extra-limital (Chapin, **2** : 538).

Prodotiscus whitei Horniman, 1956 = *Prodotiscus regulus* (White *in litt.*).

Campethera batesi = *C. punctuligera batesi* (Chapin, **2** : 564).

Mesopicus johnstoni = *M. elliotii johnstoni* (Serle, 1952, *Bull. Brit. Orn. Cl.* **72** : 104).

Mirafra malbranti Chapin, 1946 = *M. africana malbranti* (Chapin, **3** : 47).

Mirafra damarensis = *M. apiata damarensis* (Macdonald, 1952, *Ibis* : 624–635).

Mirafra candida Friedmann, 1930 = *M. pulpa* (Hall, 1961, *Bull. Brit. Orn. Cl.* **81** : 108).

Heteromirafra ruddi, extra-limital (Praed & Grant, **2** : 22).

Heteromirafra archeri = *H. ruddi archeri* (*ibid.*).

Heterocorys breviunguis = *Mirafra chuana* (Roberts, 1938, *Ann. Trans. Mus.* **18** : 320), extra-limital (McLachlan & Liversidge, 1957 : 252).

Ammomanes grayi, extra-limital (Niethammer, 1955, *Bonner Zool. Beit.* : 185).

Pseudammomanes ferruginea = *Ammomanes burra* Bangs, 1930—extra-limital (McLachlan & Liversidge, 1957 : 256 & Macdonald, 1957 : 105).

Pseudammomanes erythroclamys = *Certhilauda albescens erythroclamys* (Macdonald, 1953, *Bull. Brit. Mus.* (*Nat. Hist.*) *Zool.* **1** : 345).

Calandrella athensis = *C. rufescens athensis* (Praed & Grant, **2** : 41).

Aethocorys personata, extra-limital (Praed & Grant, **2** : 45).

Anthus leggei = *A. brachyurus leggei* (Praed & Grant, **2** : 72).

Anthus melindae, extra-limital (Jackson, **2** : 822).

Anthus latistriatus = *A. novaeseelandiae cinnamomeus* (White, 1957, *Bull. Brit. Orn. Cl.* **77** : 32).

Anthus hoeschi Stresemann, 1938 = *A. novaeseelandiae bocagei* (*ibid.* : 33) or perhaps *A. n. hoeschi.*

Anthus bannermani Bates, 1930 = *A. similis bannermani* (*ibid* : 31).

Macronyx grimwoodi Benson, 1955, extra-limital (Hall, 1960*a* : 421 ; Ripley, 1960, *Postilla*, **47** : 6).

Turdoides hypoleuca, extra-limital (Praed & Grant, **2** : 92).

Illadopsis stictigula, extra-limital (Praed & Grant, **2** : 301).

Kupeornis chapini Schouteden, 1949, extra-limital (Prigogine, 1960, *Rev. Zool. Bot. Afr.* **61** : 16).

Picathartes gymnocephalus, extra-limital (Glanville, 1954, *Ibis* : 481).

Suaheliornis albigula = *Phyllastrephus debilis albigula* (Praed & Grant, **2** : 127).

Bleda multicolor = *B. syndactyla multicolor* (Chapin, **3** : 179).

Phyllastrephus rabai = *P. debilis rabai* (Praed & Grant, **2** : 128).

Phyllastrephus olivaceo-griseus = *P. flavostriatus olivaceo-griseus* (Chapin, **3** : 175).
Phyllastrephus lorenzi, extra-limital (Schouteden, **6** : 96).
Phyllastrephus baumanni, extra-limital (Bannerman, **4** : 175).
Arizelocichla chlorigula = *A. nigricans chlorigula* (Praed & Grant, **2** : 138).
Eurillas concolor = *E. montanus* (Bannerman, **4** : 184).
Bradornis bafirawari = *B. pallidus bafirawari*. We have examined the type (Brit. Mus.) and two others of the type series (Amer. Mus. Nat. Hist.) from Wajir, and a specimen from Garissa, Tana River (Chic. Nat. Hist. Mus.) which are the only specimens ascribed to *bafirawari* that we have been able to locate. One of the three from Wajir (♂ A.M.N.H. 265307, wing 75, bill 15, tail 56 mm.) has a streaky head and is in fact a specimen of *B. microrhynchus*, being indistinguishable from others collected in the Northern Frontier District of Kenya; the others are closer to *B. pallidus*, having plain heads, longer finer bills (2 ♂ 17–17·5, 1 ♀ 17 mm.), longer tails (♂ 63–72, ♀ 60 mm.). They are slightly greyer than *pallidus* and have whiter under wing-coverts, and possibly more white in the lores and above the eye, though this is variable. *B. pallidus* is a species sympatric with *microrhynchus* through much of its range but which has not been recorded from the Wajir/Garissa area of north-eastern Kenya, so it seems that *bafirawari* is its geographical representative there and we believe may be considered as a race. Admittedly the wing of *bafirawari* is very short (and the tail disproportionately long) in comparison with that of *B. p. griseus*, the race of central and western Kenya (♂ 78, ♀ 74 against ♂ 94–103, ♀ 93–102) but is not so different from the coastal birds of *B. p. subalaris* (♂ 78–85, ♀ 76–84). *B. p. pallidus* of the Sudan is also a short-winged bird (♂ 77–89, ♀ 75–84) so that the length of the wing in *B. pallidus* seems very variable, and the difference shown by *bafirawari*, combined with the slight colour differences, does not seem sufficient to regard as specific.

We use *B. microrhynchus* in the same sense as did Jackson (1938 : 899) and Friedmann (1937, *Bull. U.S. Nat. Mus.* 153 : 223) since we do not find Grant & Praed (1940, *Ibis* : 518–522) justified in separating the smaller birds ascribed to *microrhynchus* into a distinct and supposedly sympatric species *B. pumilus*.

Dioptrornis semicinctus = *D. fischeri semicinctus* (Chapin, **3** : 608).
Dioptrornis nyikensis = *D. fischeri nyikensis* (*ibid.*).
Dioptrornis toruensis = *D. fischeri toruensis* (*ibid.*).
Myopornis sharpei = *Myopornis böhmi* (Chapin, **3** : 625).
Hyliota slatini = *H. australis slatini* (Chapin, **3** : 599).
Hyliota affinis = *H. v. violacea* (Chapin, **3** : 600).
Hyliota nehrkorni = *H. violacea nehrkorni* (Chapin, **3** : 600).
Batis margaritae Boulton, 1934, extra-limital (Chapin, **3** : 670).
Batis kathleeni White, 1941 = *B. margaritae kathleeni* (Hall, 1960*a* : 424).
Batis reichenowi = *Batis capensis reichenowi* (Praed & Grant, **2** : 201).
Batis ituriensis = probably *B. minima ituriensis* (Rand *et al.*, 1959, *Fieldiana Zool.* **41** : 352).
Batis mystica = *B. m. molitor* (Praed & Grant, **2** : 226).
Batis fratrum, extra-limital (Praed & Grant, **2** : 208).

Batis diops, extra-limital (Schouteden, **6** : 407).
Dyaphorophyia chalybea = *D. blissetti chalybea* (Chapin, **3** : 676).
Tchitrea bedfordi = *T. rufiventer bedfordi* (Chapin, 1948, *Evolution*, **2** : 114).
Turdus nigrilorum = *T. olivaceus nigrilorum* (Chapin, **3** : 584).
Geokichla crossleyi, extra-limital (Chapin, **3** : 578).
Oenanthe albicans = *O. tractrac albicans* (Macdonald, 1957 : 123).
Oenanthe tractrac, extra-limital (*ibid.*).
Oenanthe schalowi = *O. lugubris schalowi* (Praed & Grant, **2** : 268).
Cercomela dubia, extra-limital (Praed & Grant, **2** : 276).
Thamnolea argentata = *T. cinnamomeiventris subrufipennis* (Praed & Grant, **2** : 332).
Bessonornis albigularis = *Dessonornis anomala grotei* (Grant & Praed, 1937, *Bull. Brit. Orn. Cl.* **57** : 79–80 ; Praed & Grant, **2** : 333).
Sheppardia sokokensis = *Sheppardia gunningi sokokensis* (Macdonald, 1940, *Ibis* : 663–671).
Sheppardia bensoni Kinnear 1938=*S. gunningi bensoni* (*ibid.*).
Alethe poliophrys = *Malacocincla r. rufipennis* (Chapin, **3** : 215).
Alethe macclounii = *Dessonornis anomala macclounii* (Praed & Grant, **2** : 303).
Alethe sharpei = *Sheppardia sharpei*, extra-limital (Macdonald, 1940, *Ibis* : 668).
Erythropygia hamertoni = *Agrobates galactotes hamertoni* (Praed & Grant, **2** : 358).
Pogonocichla intensa = *P. stellata* subsp. (Chapin, **3** : 511).
Xenocopsychus ansorgei, extra-limital (Chapin, 1948, *Auk*, **65** : 292).
Seicercus laurae Boulton, 1931, extra-limital (Chapin, **3** : 475).
Seicercus laetus, extra-limital (*ibid.*).
Bradypterus altumi = *Sathrocercus m. mariae* (Grant & Praed, 1941, *Ibis* : 453).
Bradypterus usambarae = *Sathrocercus mariae usambarae* (*ibid.* : 454).
Bradypterus roehli = *Sathrocerus mariae usambarae* (*ibid.*).
Bradypterus msiri = *B. baboecala msiri* (*ibid.* : 446).
Bradypterus castaneus = *Sathrocercus cinnamomeus castaneus* (*ibid.* : 452).
Bradypterus barakae = *Sathrocercus lopezi barakae* (*ibid.* : 455).
Bradypterus victorini, extra-limital (McLachlan & Liversidge, 1957 : 324).
Bradypterus sylvaticus, extra-limital (*ibid.* : 323).
Bradypterus bedfordi = *B. baboecala msiri* (Chapin, **3** : 434).
Bradypterus carpalis, extra-limital (Chapin, **3** : 435).
Bradypterus yokanae = *B. carpalis* (*ibid.*).
Bradypterus camerunensis = *B. mariae camerunensis* (White, 1960, *Bull. Brit. Orn. Cl.* **80** : 19).
Calamornis chadensis = *Calamoecetor rufescens chadensis* (Bannerman, 1937, *Ibis* : 296).
Calamornis ansorgei = *Calamoecetor rufescens ansorgei* (*ibid.* : 297).
Calamornis foxi = *Calamoecetor rufescens foxi* (*ibid.*).
Calamornis neglecta = *Calamoecetor leptorhyncha neglecta* (*ibid.* : 300).
Calamornis jacksoni = *Calamoecetor leptorhyncha jacksoni* (*ibid.* : 299).
Calamornis palustris = *Calamoecetor l. leptorhyncha* (*ibid.*).
Calamornis nuerensis = *Calamocichla gracilirostris nuerensis* (Chapin. **3** : 444).
Calamornis cunenensis = *Calamocichla gracilirostris cunenensis* (Chapin, **3** : 442).

Calamonastes cinereus = *C simplex cinereus* (Grant & Praed, 1942, *Bull. Brit. Orn. Cl.* **62** : 59).

Calamonastes katangae = *C. simplex katangae* (*ibid.* : 60).

Apalis flavigularis, extra-limital (Praed & Grant, **2** : 398).

Apalis argentea Moreau, 1941 = *A. rufogularis argentea.*
Apalis eidos Peters & Loveridge, 1942 = *A. rufogularis eidos*

We consider the two montane forms *eidos*, from Idjwi Islands, Lake Kivu, and *argentea* from Mt. Kungwe, on the eastern side of Lake Tanganyika, to be races of *A. rufogularis.* The one specimen examined of *eidos* can hardly be distinguished from an immature specimen of *A. r. brauni* from Angola, and it seems that in *eidos* the green back and greenish flanks, that are characteristic of young birds in other races, have been retained in adult plumage. In *argentea* the underparts are wholly white in both sexes. Emphasis has been given to the silvery edge to the primaries in this form, but traces of edging are found also in *A. r. angolensis* and *eidos.* The lack of rufous throat in the females of both *eidos* and *argentea* does not seem sufficient reason to consider them specifically distinct from *rufogularis* in view of the variation in throat colour in the males of this polytypic species.

Apalis hardyi = *A. goslingi hardyi* or *A. sharpei* (see text, p. 339).

Apalis schoutedeni Chapin, 1937 = *A. g. goslingi* (probably).

The unique type of *schoutedeni* is a young bird " close to *A. g. goslingi* " (Chapin, **3** : 285). Since *goslingi* is now known from Dundo, north-eastern Angola (Ripley, 1960, *Postilla,* **47** : 7), the type locality of *schoutedeni* lies well within the range of *goslingi* and the likelihood of *schoutedeni* proving a distinct species is remote.

Apalis ruddi, extra-limital (McLachlan & Liversidge, 1957 : 332).

Apalis chariessa, extra-limital (Praed & Grant, **2** : 413).

Apalis chapini = *A. porphyrolaema chapini* (see text, p. 339).

Apalis chirindensis = *A. melanocephala chirindensis* (Smithers *et al.*, 1956 : 119).

Apalis lynesi Vincent, 1933 = *A. flavigularis lynesi* (Praed & Grant, **2** : 399).

Apalis macphersoni Vincent, 1934 = *A. c. chariessa* (Praed & Grant, **2** : 519).

Apalis melanurus, extra-limital (Ripley, 1960, *Postilla,* **47** : 7).

Apalis ruficeps = *Artisornis metopias* (Praed & Grant, **2** : 518).

Eminia cerviniventris, extra-limital (Bannerman, **5** : 101).

Sylvietta chapini Schouteden, 1947 = *S. leucophrys chapini* (Mayr, 1957 : 30).

Sylvietta philippae Williams, 1955, extra-limital (Mayr, *ibid.*).

The specimen referred to by Mayr was collected in the Ain valley, south-east of Burao, British Somaliland.

Eremomela salvadorii, extra-limital (Chapin, **3** : 267).

Hemitesia neumanni, extra-limital (Schouteden, **7** : 235 ; Prigogine, 1960, *Ann. Mus. Roy. Cong. Belg.* **85** : 31).

Cisticola nigriloris, extra-limital (Lynes, 1930, *Ibis* suppl. : 329).

Cisticola pipiens, extra-limital (Chapin, **3** : 359).

Cisticola dambo, extra-limital (Chapin, **3** : 393).

Cisticola carruthersi, extra-limital (Chapin, **3** : 360).

Prinia ansorgei = *P. flavicans ansorgei* (Irwin, 1959, *Bull. Brit. Orn. Cl.* **79** : 127).

Prinia metopias = *Artisornis metopias* or *Orthotomus metopias* (see text, p. 341), extra-limital (Praed & Grant, **2** : 420).

Petrochelidon rufigula, extra-limital (Chapin, **3** : 773).

Petrochelidon fuliginosa, extra-limital (Malbrant & Maclatchy, 1949 : 356).

Phedina brazzae, extra-limital (Chapin, **3** : 742).

Psalidoprocne kösteri Neumann, 1930 = *P. orientalis reichenowi* (Chapin, **3** : 780).

Coracina graueri extra-limital (Schouteden, **6** : 109).

Prionops martensi = *Prionops plumata* subsp. (Chapin, **4** : 96).

Prionops alberti Schouteden, 1933, extra-limital (Schouteden, **8** : 75).

Laniarius alboplagatus = *L. funebris* (Praed & Grant, **2** : 642).

Laniarius erlangeri = *L. aethiopicus erlangeri* (Hall, 1954, *Ibis* : 346).

Laniarius nigerrimus = *L. aethiopicus sublacteus* (*ibid.* and Stresemann, 1947, *Ibis* : 518).

Laniarius fülleborni, extra-limital (Praed & Grant, **2** : 610).

Laniarius niassae Boulton, 1931 = *L. fülleborni* (Meise, 1938 : 175).

Dryoscopus pringlii, extra-limital (Praed & Grant, **2** : 620).

Chlorophoneus nigrithorax = *C. m. multicolor* (Bannerman, **5** : 427).

Chlorophoneus andaryae = *C. sulfureopectus similis* (Praed & Grant, **2** : 643).

Chlorophoneus nigrescens = *C. n. nigrifrons* (Sclater & Moreau, 1933, *Ibis* : 200).

Parus fasciiventer, extra-limital (Chapin, **4** : 99).

Anthoscopus pygmaea Horniman, 1956 = *A. caroli winterbottomi* (Praed & Grant, MS., Birds of the Southern Third of Africa).

Onychognathus gracilirostris = *O. m. morio* (*ibid.*).

Zosterops vaalensis = *Z. pallida vaalensis* (Moreau, 1957, *Bull. B.M. Nat. Hist.* **4** (7) : 383).

Zosterops silvanus Peters & Loveridge, 1935 = *Z. senegalensis silvana* (*ibid.* : 314, 365).

Nectarinia bocagei, extra-limital (Schouteden, 1959, *Rev. Zool. Bot. Afr.* **59** : 326).

Nectarinia purpureiventris, extra-limital (Chapin, **4** : 273).

Nectarinia congensis, extra-limital (Chapin, **4** : 268).

Nectarinia sororia Ripley, 1960, extra-limital—possibly the female of *Nectarinia* (*verticalis*) *bannermani* (Rand & Ripley *in litt.*).

Cinnyris oustaleti, extra-limital (Chapin, **4** : 230).

Cinnyris pembae = *C. chalcomelas pembae.*

Praed & Grant (**2** : 771) give the range as Pemba Island and Lamu. The extension on the mainland at Lamu, within the range of *C. chalcomelas*, is apparently based on two specimens in the British Museum from the Shelley collection. These have no original labels, but the Shelley Museum labels have " Lamu—Kirk " on them. Kirk's " Lamu " collections were made by Africans (*vide History of the Collections in the Natural History Museum*, **2** : 407), and it may be doubted that all the birds actually came from there. If these did not we can regard *pembae* as conspecific with *chalcomelas*, which has an extra-limital range.

Cyanomitra batesi, extra-limital (Chapin, **4** : 206).

Anthreptes yokanae = *A. reichenowi yokanae* (Praed & Grant, **2** : 817).

Gunningia reichenowi = *Anthreptes r. reichenowi*, extra-limital (*ibid.*).
Plocepasser donaldsoni, extra-limital (Praed & Grant, **2** : 866).
Plocepasser rufoscapulatus, extra-limital (Chapin, **4** : 289).
Ploceus duboisi = *P. melanocephalus duboisi* (Chapin, **4** : 340).
Ploceus subpersonatus, extra-limital (Chapin, **4** : 316).
Ploceus olivaceiceps, extra-limital (Praed & Grant, **2** : 920).
Ploceus flavissimus = *P. galbula* (Praed & Grant, **2** : 1052).
Ploceus nicolli Sclater, 1931 = *P. olivaceiceps nicolli* (Moreau, 1960, *Ibis* : 310).
Euplectes zavattarii Moltoni, 1943 = *E. orix pusillus* (Grant & Praed, 1947, *Bull. Brit. Orn. Cl.* **68** : 60).
Notiospiza angolensis, extra-limital (Chapin, **4** : 389).
Anaplectes jubaensis = *A. melanotis jubaensis* (Praed & Grant, **2** : 944).
Drepanoplectes jacksoni, extra-limital (Praed & Grant, **2** : 972).
Parmoptila rubrifrons, extra-limital.

Chapin (**4** : 462) suggests that the forms *rubrifrons* from the Gold Coast and *jamesoni* from the Congo forest may prove to be conspecific with *woodhousei*, which is found in the intervening forests of Nigeria and the Cameroons, and further south ; but that in the absence of specimens showing intermediate characters the differences seem great enough to keep them distinct at present. With this we agree in respect to *woodhousei*, but we believe that in spite of the discontinuous distribution *rubrifrons* and *jamesoni* should be considered conspecific. The types show no differences except that *rubrifrons* is smaller (wing 51 against 56 mm.) and has pale tips to the chestnut feathers of the wing-coverts, nape and sides of the head, which appear speckled.

Cryptospiza jacksoni, extra-limital (Chapin, **4** : 487).
Pirenestes vincenti Benson, 1955 = *P. minor vincenti* (Mayr, 1957 : 33).
Paludipasser uelensis = *Ortygospiza locustella uelensis* (Chapin, **4** : 504).
Paludipasser irisae = *Ortygospiza l. locustella* (Chapin, **4** : 503).
Hypargos margaritatus, extra-limital (McLachlan & Liversidge, 1957 : 448).
Estrilda xanthophrys = *E. troglodytes* (Praed & Grant, **2** : 1053).
Nesocharis ansorgei, extra-limital (Schouteden, **9** : 375).
Hypochaera aenea = *Vidua c. chalybeata* (Friedmann, 1960, *U.S. Nat. Mus. Bull.* **233** : 60).
Hypochaera codringtoni = *Vidua chalybeata codringtoni* (*ibid.* : 61).
Vidua haagneri, probably a hybrid (Smithers *et al.* 1957 : 158).
Serinus citrinipectus Clancey, 1960.

We have examined three males of *citrinipectus* from Panda, Inhambane district, southern Portuguese East Africa, and a number of the aberrant canaries discussed by Stuart Irwin (*Ibis*, 1960 : 503–506) and are in no doubt that they must be considered together, thus giving the " species " an extra-limital range. Irwin believed his highly variable series to be the product of hybridization. Though the three Panda specimens examined show considerable individual variation (not indicated in the original description), the series suggests that at least in that locality the hybrid form has become more stable than in the area from which Irwin's birds came.

Poliospiza flavigula, extra-limital (Praed & Grant, **2** : 1076).
Poliospiza dimidiata = *P. flavigula* (Praed & Grant, **2** : 1086).
Poliospiza collaris = *P. flavigula* (Praed & Grant, **2** : 1086).
Poliospiza pachyrhyncha = *Serinus donaldsoni* (Praed & Grant, **2** : 1086).
Poliospiza whytii = *Serinus striolatus whytii* (Praed & Grant, **2** : 1077).
Linurgus olivaceus, extra-limital (Chapin, **4** : 585).
Linurgus kilimensis = *L. olivaceus kilimensis* (*ibid.*).
Spinus totta, extra-limital (McLachlan & Liversidge, 1957 : 460).
Spinus symonsi = *S. totta symonsi* (*ibid.*).

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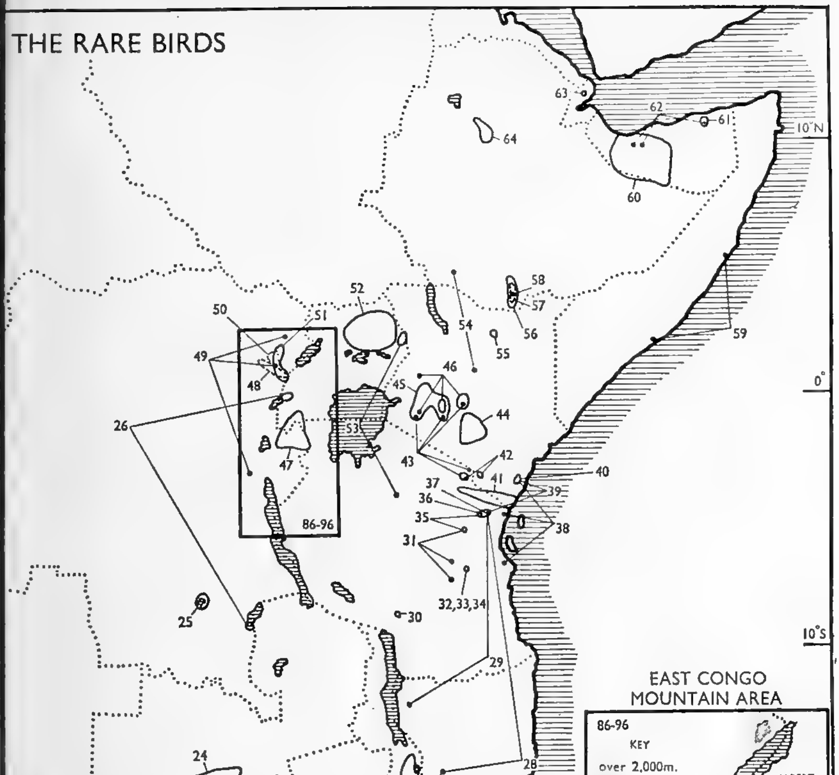
Postscript.

Francolinus (Pternistis) rufopictus

Since this paper was completed further research has shown that the occurrence of *Francolinus rufopictus* in Ruanda cannot be substantiated. The known range of the species is therefore not more than 200 × 150 sq. miles, and *F. rufopictus* qualifies as a " Rare Bird " (see Hall, " The Francolins—a study in speciation ", in preparation).

Lagonosticta vinacea (see page 354).

We have also found a record of *L. vinacea* from Niokolo-Koba Park, Senegal, about 13° N., 13° W. (Dekeyser, 1956, Mem. Inst. Franc. Afr. Noire 48 : 135). This gives the bird a known range of at least 250 miles from west to east and makes it doubtful if its actual range falls within our limits.



THE RARE BIRDS

Key to Species plotted on the Map

1. *Lagonosticta vinacea*
2. *Prinia leontica*
3. *Anthreptes* [illegible]
4. *Apalis sharpei*
5. *Malimbus ibadanensis*
6. [illegible]
7. [illegible]
8. *Geokichla camerunensis*
9. *Ploceus batesi*
10. [illegible] *terus grandis*
11. [illegible] *nigrimentum*
12. *Apus toulsoni*
13. *Prionops gabela*
14. [illegible] *gabela*
15. [illegible]

Francolinus swierstrai
Namibornis herero
[illegible] *piza leucoptera*
[illegible] *rdella fringillaris*
[illegible] *monchla swynnertoni*
Prinia robertsi
Lybius chaplini
[illegible] *lla nigrilores*
Chloropeta gracilirostris
Alethe choloensis
Phyllastrephus orostruthus
Apalis moreaui
Alethe lowei
Cinnyris moreaui
Cinnyris loveridgei
Scepomycter winifredae

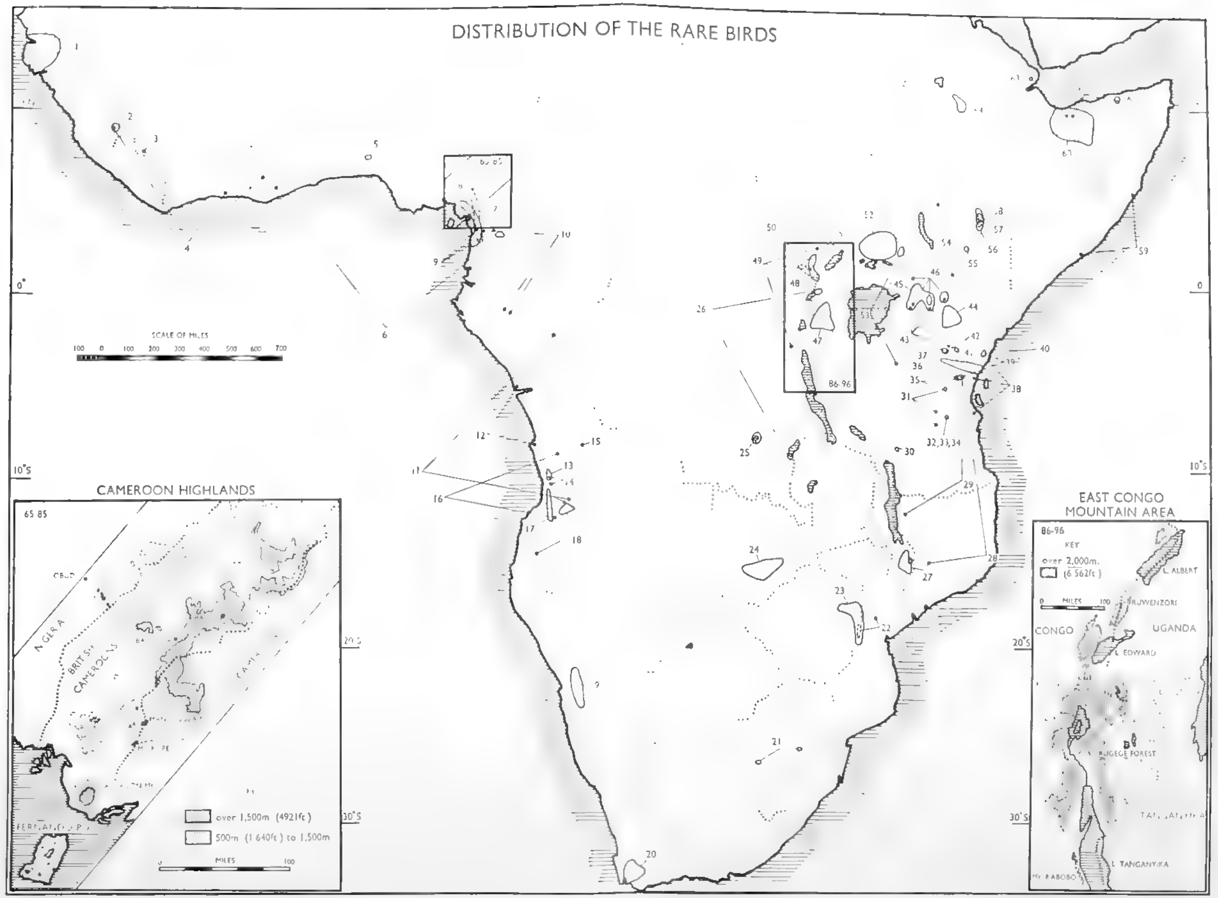
31. *Malaconotus alius*
32. *Anthreptes rubritorques*
36. *Alethe montana*
37. *Bubo vosseleri*
38. *Anthus sokokensis*
39. *Anthreptes pallidigaster*
40. *Ploceus golandi*
41. *Ploceus castaneiceps*
42. *Turdus helleri*
43. *Cinnyricinclus femoralis*
44. *Turdoides hindei*
45. *Macronyx sharpei*
46. *Francolinus jacksoni*
47. *Lybius rubrifacies*
48. *Ploceus flavipes*
49. *Geokichla oberlaenderi*
50. *Ploceus aureonucha*
51. *Columba albinucha*
52. *Ploceus spekeoides*
53 *Apalis karamojae*
54 *Mirafra pulpa*
55 *Mirafra williamsi*
56. *Hirundo megaensis*
57. *Zavattariornis stresemanni*
58. *Tauraco ruspolii*
59 *Calandrella obbiensis*
60. *Eupodotis humilis*
59 *Calandrella obbiensis*
60 *Eupodotis humilis*
61. *Carduelis johannis.*
62. *Turdus ludoviciae*
63. *Francolinus ochropectus*
64 *Francolinus harwoodi.*

Species of Cameroon Highland Area

	Fernando Po	Cameroon Mountain	Rumpi Hills	Kupé Mountain	Manenguba Mountains	Bamenda/Banso Highlands	Obudu Plateau
Francolinus . . .		×					
[illegible]		×	×	×		×	×
[illegible]			×	×			×
[illegible]		×	×	×			×
[illegible]	×	×	×	×	×	×	×
[illegible]		×	×		×	×	
[illegible]						×	
[illegible]		×	×		×	×	×
[illegible]	×	×	×	×	×		×
[illegible]	×	×	×	×	×	×	×
[illegible]	×	×	×	×	×		×
[illegible]	×	×					
[illegible]		×			×	×	×
[illegible]				×			
[illegible]		×	×			×	×
[illegible]	×	×	×	×			
[illegible]	×	×		×	×	×	
[illegible]					×	×	
[illegible]		×			×	×	

Species of East Congo Mountain Area

	West of Lake Albert	Ruwenzori	West of Lake Edward	Kivu volcanoes and north-east of L. Kivu	N.W. & west of L. Kivu	East of L. Kivu and the Ruzizi valley	West of Ruzizi valley & N.W. of L. Tanganyika	Mt. Kabobo
[illegible] *Phodilus* [illegible]								
[illegible]				×	×		×	
[illegible] *mena graueri*								
89. *Lioptilus rufocinctus* .					×		×	×
90. *Muscicapa lendu*	×							
M. itombwensis							×	
91. *Melaenornis ardesiaca* .			×	×	×		×	
92. *Bradypterus graueri* .			×	×	×	×		
93. *Apalis* [illegible] . .								×
94. *Graueria vittata* .			×			×	×	
95. *Cinnyris rockefelleri* . .					×		×	
96. *Cryptospiza shelleyi* .		×	×		×	×		



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HYDROIDS OF THE FAMILY CYTAEIDAE L. AGASSIZ, 1862

By WILLIAM J. REES

CONTENTS

SYNOPSIS

Hydroids of the family Cytaeidae are brought together for the first time in this paper. All medusa-bearing species are placed in the genus *Cytaeis* Eschscholtz, while species with fixed gonophores are placed in *Perarella* Stechow. The problematic genus *Stylactella* Haeckel, 1889, is restricted to the type species *Stylactis vermicola* Allman and retained in the Cytaeidae.

The type specimens of *Stylactis vermicola* Allman, *Stylactella spongicola* Haeckel, *Stylactella abyssicola* Haeckel, *Stylactella niotha* Pennycuik, *Hydractina clavata* Jäderholm, *Stylactis indica* Stechow and *Podocoryne nassa* Millard have been examined, and, where possible, re-described. The hydroid *Cytaeis japonica* Komai has been found to be distinct from the medusa *C. japonica* Uchida, 1927 (which is *C. tetrastyla*) and is here re-named *Cytaeis uchidae*. A new species, *Cytaeis nuda*, is described from Japan; this lives in intimate association with a sponge.

To the genus *Perarella* are referred: *Hydractinia clavata* Jäderholm, *Stylactella spongicola*, *S. abyssicola* and provisionally *Stylactis affinis* Jäderholm; the type species of *Perarella* is *Perigonimus schneideri* Motz-Kossowska.

The hydroids *Cytaeis nassa* and *C. niotha* are distinct despite close resemblances, while *C. uchidae* and *C. nuda* differ from them in having almost mature medusae at liberation. *Cytaeis nuda* lives in a sponge and is noticeably different from *C. uchidae*. *Cytaeis indica* Stechow is an immature colony whose status is uncertain.

1. INTRODUCTION

THE family Cytaeidae was created by Louis Agassiz (1862 : 341) for medusae of the genus *Cytaeis* Eschscholtz. No hydroids belonging to it could be recognized until Komai (1931) found a hydroid and young medusa which he thought belonged to the medusa *Cytaeis japonica*. This discovery was not followed up, except briefly by Rees (1956 : 344), and in this review as many as possible of the type specimens of the species concerned have been re-examined.

Earlier, however, cytaeid hydroids had been described under various genera : *Stylactis*, *Stylactella*, *Hydractinia*, *Perigonimus* and *Perarella*—the genera, other than *Perigonimus*, being usually grouped with the Hydractiniidae. Haeckel (1889) however, recognized the distinctive nature of the *Stylactella* group of hydroids suggesting a family grouping Stylactidae—a suggestion which was never adopted and which cannot now be considered in view of the prior claims of Agassiz's Cytaeidae.

In this paper, the genera *Cytaeis* Eschscholtz, *Perarella* Stechow and *Stylactella* Haeckel are revised and many of the species are re-described either from the type material or from material from the type locality. *Cytaeis* is employed both for cytaeid hydroids and their medusae, *Perarella* for cytaeid hydroids with fixed gonophores and *Stylactella* is restricted to the type species *Stylactis vermicola* Allman, as an insufficiently characterized genus.

2. THE FAMILY CYTAEIDAE

The family Cytaeidae may be defined as follows :

Hydroid (where known). Athecate hydroids with perisarc-covered, anastomosing stolons. Hydranths, naked, tall, columnar, with a group of whorled filiform tentacles around a conical hypostome. Hydranths arising directly from the stolons, often with a short, cup-shaped collar of perisarc. Medusa buds or fixed gonophores borne single on stalks directly from the stolons.

Medusa (where known). Anthomedusae with deep umbrella with four unbranched radial canals and four marginal tentacles. Manubrium, often flask-shaped, with simple mouth with four or more unbranched oral tentacles.[1] Gonads either interradial or forming a continuous ring. No ocelli.

As defined here the family includes the following genera : *Cytaeis*, *Perarella* and the problematic genus *Stylactella*.

3. Genus ***CYTAEIS*** Eschscholtz., 1829

Cytaeis tetrastyla Eschscholtz, 1829

Cytaeis tetrastyla Eschscholtz, 1829, *System der Acalephen* : 104, pl. 8, fig. 2 (medusa).
Kramp, 1959, *Dana Rep.* **46** : pl. 1, figs. 3–6 (medusa with polypoid buds).
Kramp, 1961, *J. mar. biol. Assoc. U.K.* **40** : 63 (in part).

This well-known circumtropic medusa has not so far been linked with a bottom-living hydroid, although either *C. nassa* (Millard) or *C. niotha* (Pennycuik) could be its hydroid.

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[1] In excluding the little known species *Cnidostoma fallax* Vanhöffen, I have followed Picard (in Kramp, 1961 : 444). *Cnidostoma fallax* (syn. *Podocoryne* (*Archaeoceania*) *tournieri*) is placed in the family Clavidae by Picard.

Kramp (1959 : 8) has described " polypoid buds on the proximal portion of the stomach wall ". They are described as somewhat larger than the medusa buds, cylindrical, with a broad proboscis and a whorl of five to seven short tentacles. The author states that these buds are not fully developed, the tentacles being fairly short and the mouth opening not yet broken through. Sections reveal that the polyps are direct outgrowths from the stomach wall produced by asexual budding. These polyps are too young to enable a comparison to be made with benthic colonies of *Cytaeis*.

There is a possibility that *C. tetrastyla sensu*, Kramp (1961), is an aggregate species (see p. 387).

Cytaeis uchidae nom. nov.

Cytaeis japonica, Komai, 1931, *Annot. zool. jap.* **13** : 255, fig. A–C.

The following descriptions are based on colonies kindly sent to me by H.M. The Emperor of Japan. Two fertile colonies were collected at Aburatsubo, Misaki, in Sagami Bay on 28th June, 1960, and it is on these that the main description is based. A further series of 12 shells with fertile colonies were collected in June, 1961, and a batch of newly liberated medusae obtained from them ; these were also forwarded to London and the description contains some additional notes on these and on their medusae.

The colonies obtained in 1960 cover the shells of the gastropod *Nassarius livescens* Philippi. The smooth stolons run in the grooves of the shell, frequently anastomosing at intersections (Text-fig. 1).

The very tall columnar polyps arise basally from thin, but well-developed, perisarcal cups ; the polyps themselves possess a distal whorl of six to ten hispid tentacles around a bluntly-conical hypostome. Medusa buds are borne singly on long stalks arising directly from the hydrorhiza ; they may reach a height of 1·0 mm. Fully-grown medusa buds are about 0·5 mm. long by 0·4 mm. Each medusa bud has four large brownish basal bulbs with equally developed tentacles. There are four capitate tentacles on the manubrium around a single mouth. The manubrium is fusiform reaching to more than half the depth of the bell, and in many examples the ring gonad is well developed.

Medusa buds are plentiful on both shells; in one, the nutritive polyps are as numerous as the medusa buds, but on the other nutritive polyps are few and appear to have been largely resorbed as a result of prolific budding of medusae.

Some typical measurements of the dimensions of the hydroid are given in Table I.

The second series of colonies illustrate the considerable range of variation in the appearance of the colonies (Text-fig. 1) ; in some, polyps are large and densely crowded on the shell (Pl. 10, fig. 2) and on others less crowded (Pl. 10, figs. 3 and 4). In fact the colonies exhibit much the same diversity as *Hydractinia* both as regards the density of polyps on the shell and as regards reproductive exhaustion (Rees, 1956*b*).

It will be seen from Table II that the polyps reach a height of nearly 4 mm. in a well-developed colony. The above description agrees well with that of Komai (1931) except that the polyps reach a much larger size in a well-developed colony.

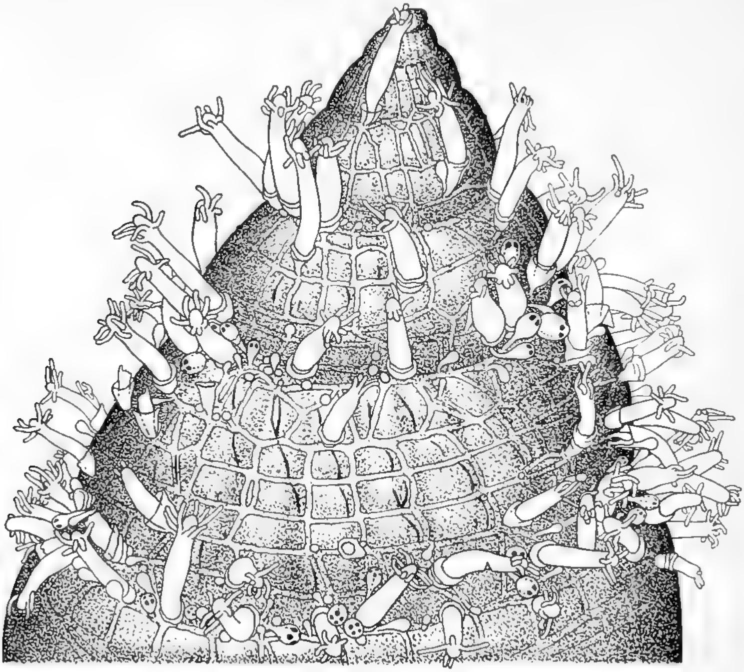

FIG. 1. *Cytaeis uchidae* nom. nov.; general appearance of a colony on the shell of *Nassarius livescens* Philippi from Misaki, June, 1961.

TABLE I.—*The hydroid* Cytaeis uchidae *from Sagami Bay,* 1960

Measurements in mm.

Height of polyp to hypostome	1·28	1·20	1·24	1·3
Diameter of polyp	0·12	0·12	0·12	0·12
Length of hypostome	0·08	0·12	0·12	0·12
Diameter of basal cup	0·10	0·20	0·28	0·3
Total height of medusa bud	0·88	0·88	0·80	1·0
Length of stalk	0·4	0·44	0·40	0·5
Length of medusa bud	0·48	0·44	0·40	0·5
Diameter of medusa bud	0·36	0·36	0·32	0·4

TABLE II.—*The hydroid* Cytaeis uchidae *from Sagami, Bay, June* 1961

Measurements in mm.

Height of polyp	3·85	2·2	3·9	3·85
Diameter of polyp	0·33	0·38	0·4	0·33
Length of tentacles	0·43	0·45	0·45	0·65
Diameter of basal cup	0·44	0·4	0·45	0·35
Diameter of stolon	0·10	0·12	0·14	0·10
Total height of medusa bud	0·9	0·95	0·95	1·0
Diameter of medusa bud	0·55	0·33	0·35	0·33

Komai also described the newly liberated medusa and it is now possible to confirm his description and to add more details.

The umbrella is deep bell-shaped, approximately as high as wide, being 0·55–0·6 mm. high and 0·5–0·7 mm. wide, depending on fixation (Text-figs. 2 and 3). The jelly is uniformly thick, with scattered nematocysts on its exumbrella surface and there is sometimes a slight apical depression with no indication of an apical plate of cells. The stomach is mounted on a short peduncle and varies from half to three-quarters of the height of the subumbrella cavity in length. The mouth is simple and there are four simple perradial oral tentacles, each armed with a battery of nematocysts. There is a well-developed gonad occupying the greater part of the length of the manubrium ; in the male it forms a complete ring round the manubrium (Text-fig. 2). In the female the eggs are large and conspicuous (Text-fig. 3).

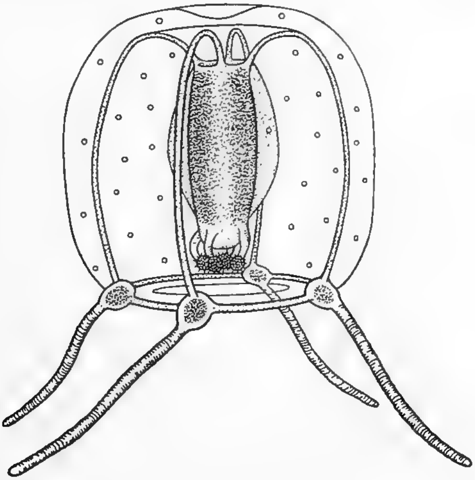

FIG. 2. *Cytaeis uchidae* nom. nov.; newly liberated male medusa obtained from the hydroid, Misaki, June, 1961.

There are four perradial canals and a ring canal. The four perradial tentacles have well-developed rounded bases with an endoderm of a dark brown colour. The tentacles themselves are rather contracted and heavily armed with nematocysts and there is a suggestion that these tend to be grouped in batteries as in *Cytaeis nassa* (see Text-fig. 9). Measurements of typical medusae are given in Table III.

TABLE III.—*Medusae liberated from* Cytaeis uchidae *at Misaki, June,* 1961

Measurements in mm.

Height of bell	0·60	0·55	0·55	0·6
Diameter of bell	0·55	0·5	0·7	0·55
Length of manubrium	0·30	0·30	0·35	0·5
Diameter of manubrium	0·175	0·22	0·20	0·25
Diameter of tentacle bulb	0·075	0·10	0·10	0·10

The problem presented by this species is whether Komai's identification of this species with *Cytaeis japonica* Uchida is justified. The noteworthy feature about the medusa of this hydroid is that, like *Podocoryne carnea*, it is almost sexually mature at liberation, and probably has only a few days of planktonic existence before spawning and dying.

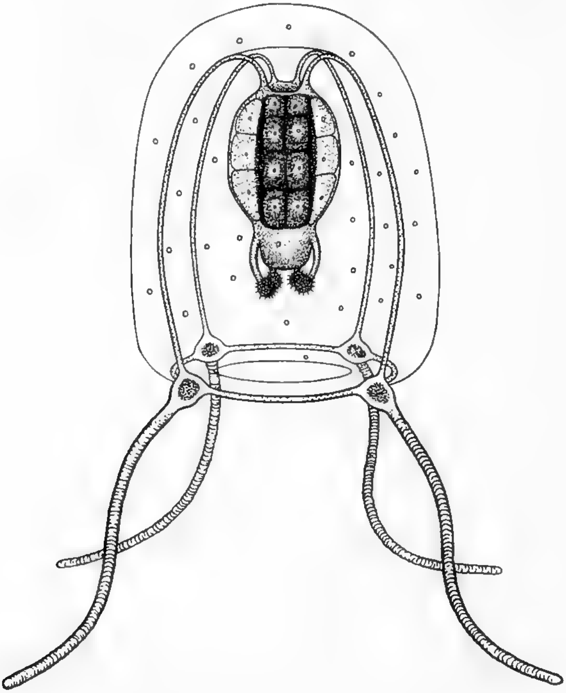

FIG. 3. *Cytaeis uchidae* nom. nov.; newly liberated female medusa obtained from the hydroid, Misaki, June, 1961.

If so, then this medusa probably possesses only the four simple oral tentacles throughout its life.[1] On this assumption it may not be identical with *Cytaeis japonica* Uchida which matures at a much larger size (1·7 mm. × 1·5 mm.) and possesses 5–12 oral tentacles when mature. Uchida (1927) also indicated that he had found juvenile medusae with medusa buds on the stomach and with only four oral tentacles. It would thus appear that *C. japonica* Uchida passes through an asexual phase in which the stomach may possess only four oral tentacles before reaching

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[1] Since this paper was written, Mr. Hatsuki Tsujimura of the Biological Laboratory of the Imperial Household, Tokyo, informs me that in rearing experiments with *C. uchidae* medusae for a period of 40 days, only one medusa increased its oral tentacles to seven. During this period the medusae did not feed and began to shrink after 40 days. The evidence is thus inconclusive but the apparent absence of an asexual budding phase and the presence of a ring gonad justify the retention of *C. uchidae* as a distinct species.

a sexual phase. This is what also takes place in *Cytaeis tetrastyla* Eschscholtz, a species with which *C. japonica* Uchida has been synonymized by Kramp (1961 : 64). The asexual budding phase is known to precede sexual reproduction in medusae such as *Sarsia prolifera, S. gemmifera, Podocoryne minima, Rathkea octopunctata, Lizzia blondina* and many others. Temperature appears to be the deciding factor which initiates the beginning of the sexual phase in some species (Werner, 1956).

From the above it seems highly probable that *Cytaeis japonica* Komai (*non* Uchida) is a distinct species and this view is strengthened from unpublished evidence from cytaeids collected at Singapore by Mr. J. H. Wickstead. Without going into details, some of the small medusae seen have more than four oral tentacles and the developing gonads are small and inter-radial in position ; all this suggests that Kramp (1961 : 63–64) has oversimplified the situation in recognizing only three species of *Cytaeis*.

In *Bougainvillia superciliaris* Werner (1961) has recently discovered that female medusae may be able to produce eggs several times successively, but there is no evidence of this known for *Cytaeis*.

In view of the fact that *Cytaeis japonica* Uchida, 1927, has been synonymized with *Cytaeis tetrastyla* Eschscholtz, 1829, Komai's hydroid and medusa must be regarded as distinct, and therefore must be re-named. I have much pleasure in naming it *Cytaeis uchidae* in honour of Professor Tohru Uchida who has done so much to place our knowledge of Japanese medusae on a sound basis.

Cytaeis nuda sp. n.

The following description of a new hydroid is based on two colonies most kindly sent to me by H.M. The Emperor of Japan who also forwarded notes and some of the illustrations given here. The two host snails were collected by means of the *takotsubo* (a small unglazed pot with a small hole through the bottom) used in a kind of long-line fishing for octopus on the sea bottom. The specimens were taken off Hayama, Sagami Bay on 26th and 31st July, 1934.

The colonies are partly embedded in sponges growing on living gastropods of the species *Fusinus perplexus* (A. Adams). The hydrorhiza forms a close reticulate network a little distance below, and parallel with the surface of the sponge. The reticulate network is not annulated and the periderm of the stolons is very thin and not thickened (Text-figs. 4 and 5).

The cylindrical polyps arise at the junctions of the stolons and there is no indication of any cup-like dilation of perisarc at this point. The hydranth is naked with six to eight tentacles arranged in a whorl around a bluntly-conical hypostome. These hydranths are contracted in preservative, measuring 0·5 mm. in height ; they sometimes project beyond the surface of the sponge through holes in the substance of the sponge (Pl. 10, fig. 1 & Text-figs. 4 and 5).

Medusa buds, as in other cytaeid hydroids, are oval or pear-shaped and borne on distinct, non-annulated pedicels arising directly from the stolons (Text-fig. 6).

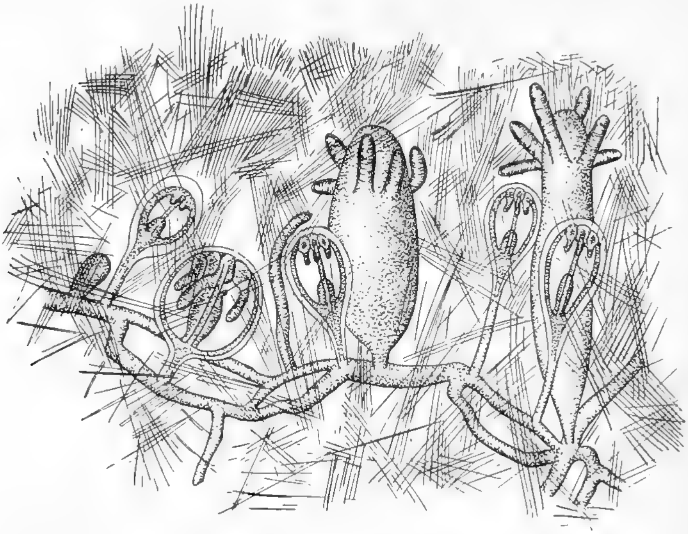


FIG. 4. *Cytaeis nuda* sp.n.; a vertical section of the hydroid colony embedded in the sponge.

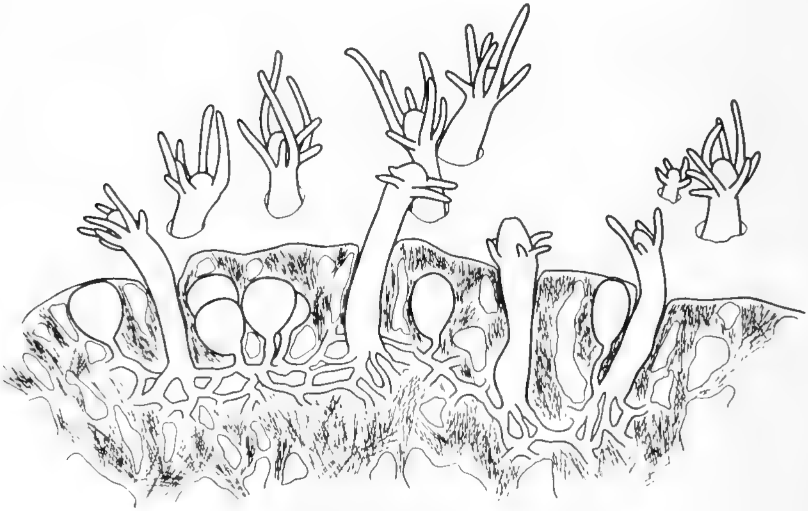
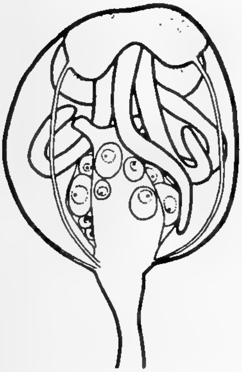


FIG. 5. *Cytaeis nuda* sp.n.; a sketch from a micro-preparation of a small section of the colony; del. H. Daba.

When young the medusa buds are completely enveloped by sponge but with growth the buds push their way to the surface.

A female medusa was obtained from one of the colonies (Text-fig. 7). At liberation this had a deep, bell-shaped umbrella, about 0·3 mm. in height. There were four radial canals, four large perradial bulbs with filiform tentacles of equal size. The tentacles contained reddish brown pigment granules and there were no ocelli. The manubrium, which reached three-quarters of the distance to the bell margin, was fusiform in outline and may have been four-sided in section. The mouth was simple with four, short, capitate oral tentacles. The female gonad appeared to cover the manubrium for the greater part of its length and was best developed interradially. At liberation, the medusa was almost mature and the gonad possessed a small number of large eggs with prominent nuclei.



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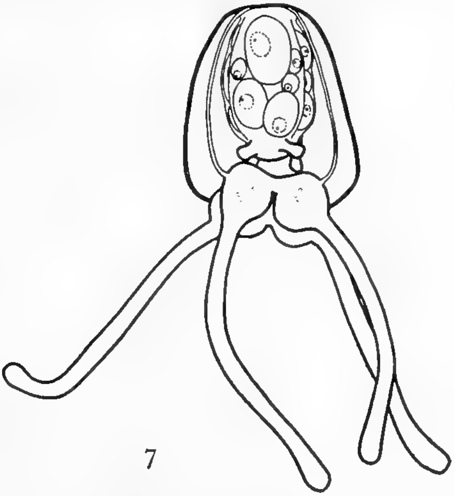

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FIG. 6. *Cytaeis nuda* sp. n.; a female medusa bud; del. H. Daba.
FIG. 7. *Cytaeis nuda* sp. n.; a newly liberated female medusa; del. H. Daba.

The description can be summarized as follows:

Hydroid. Hydrorhiza, forming a reticulate non-annulated network, with perisarc feebly developed embedded in the tissues of a sponge. Hydranths, cylindrical with six to eight filiform tentacles around a conical hypostome, arising from anastomoses in the hydrorhiza. Hydranths project from surface of sponge and are at least 0·5 mm. long. Medusa buds borne singly on pedicels from the hydrorhiza.

Medusa. Newly-liberated ♀ medusa with deep, bell-shaped umbrella with four radial canals, four perradial bulbs without ocelli and with four filiform tentacles. Stomach fusiform with simple mouth, four simple oral capitate tentacles. Gonad best developed interradially, with a few large eggs, almost mature at liberation.

Type locality. Hayama, Sagami Bay, Japan in a sponge on the gastropod *Fusinus perplexus* (A. Adams).

Holotype. British Museum No. 1962.2.12.1; collected 26 July, 1934. *Paratype*, collected 31 July, 1934 in the collections of the Biological Laboratory of the Imperial Household, Tokyo.

There appear to be distinct differences between this species and *Cytaeis uchidae*. In *C. nuda* the absence of a collar of perisarc and the feebly developed perisarc of the stolons may be linked with the habitat of the species within a sponge. However, the much smaller size of the medusa at liberation, its compressed subumbrella cavity and the smaller number of eggs in the gonad (compare Text-fig. 3 with Text-fig. 7) indicate that *C. nuda* is different from *C. uchidae*.

Cytaeis nassa (Millard, 1959)

Podocoryne nassa Millard, 1959, *Ann. S. Afr. Mus.* **44** : 307, fig. 3.

The following description is based on several colonies sent to me by Dr. William Macnae who collected the material between tide levels on Inhaca Island, Lourenço Marques. These colonies are epizooic on the gastropods *Nassa coronata* Brug. and on *Nassa fenestrata* Marratt (Pl. 11).

The perisarc-covered stolons follow the grooves of the shells and the appearance of the colonies which covered the whole of the shells was reminiscent of *Hydractinia* or of *Podocoryne*, but there were differences which indicated that the Inhaca species came nearest to the hydroid described by Komai (1931) as that of the medusa *Cytaeis japonica*.

There are no spines and no encrusting base and the nutritive polyps are fairly evenly distributed at intervals along the stolons as noted by Millard (1959 : 308, fig. 3). The stolons are 0·5–0·10 mm. in diameter and are covered by a thin, distinct, non-annulated, hyaline perisarc; they form a reticulate network.

There is only one type of hydranth, the nutritive kind (Text-fig. 8). These are tall, columnar, slightly thicker near the base than distally. There is a double whorl of 8–16 filiform tentacles around a well-developed conical hypostome; these tentacles are smooth and not hispid as those of *C. niotha*. The base of the hydranth narrows sharply and around this there is a sessile or subsessile cup-like dilation of perisarc which fits closely around it when the hydranth is retracted (as in this preserved material). In the colony noted by Millard the hydranths were only 1·4 mm. high with 8–16 tentacles while those noted here are larger (see Table IV).

The medusa buds are borne singly on pedicels, 0·5–0·64 mm. long, arising directly from the stolons, the total height of gonozooid and stalk being 0·84–1·15 mm. These buds are pyriform, becoming almost globular when fully developed; those measured were 0·34–0·5 mm. long by 0·28–0·4 mm. wide.

No newly-liberated medusae were available, but in the fully developed medusa bud, four perradial bulbs with tentacles, four radial canals and a tubular, slightly fusiform, manubrium with four short oral tentacles can be distinguished (Text-fig. 9). The oral *tentacles* are armed with batteries of nematocysts at their tips. The four perradial tentacle bulbs are well developed and the tentacles themselves are armed with distinct batteries of nematocysts. Gonads are undeveloped.

The following measurements were made from preserved material :

TABLE IV.—*Dimensions of* Cytaeis nassa (*Millard*) *from Inhaca Island*

Measurements in mm.

Total height of polyp	2·1	2·45	2·03	1·55	1·75
Diameter of polyp	0·35	0·35	0·35	0·28	0·3
Diameter of stolon	0·08	0·10	0·08	0·05	0·65
Total height of medusa bud	0·84	1·04	1·05	1·15	0·84
Length of pedicel	0·5	0·64	0·61	0·65	0·4
Length of medusa bud	0·34	0·4	0·44	0·5	0·64
Diameter of medusa bud	0·3	0·3	0·28	0·4	0·32

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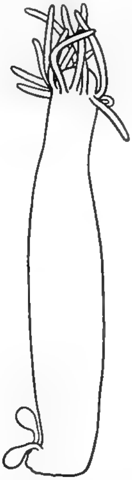

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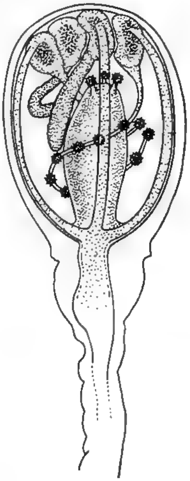

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FIG. 8. *Cytaeis nassa* (Millard) ; hydranth.

FIG. 9. *Cytaeis nassa* (Millard) ; medusa bud.

FIG. 10. *Cytaeis niotha* (Pennycuik) ; a hydranth from the holotype colony (Queensland Mus. No. G. 2392).

The form of the hydranth with its cup-like dilation of perisarc at the base and the characters of the medusa, especially the four oral *tentacles* on the manubrium and the four single marginal tentacles identify the species with the genus *Cytaeis*.

As will be noted the species is very similar to *Cytaeis uchidae* but the latter has far fewer tentacles in the polyp and its medusa is almost mature at liberation. It is possible that this East African species belongs to a known *Cytaeis* medusa, such as *C. tetrastyla*.

The following is a summarized description of the species :

Hydroid with creeping, anastomosing, non-annulated stolon covered with thin hyaline perisarc. Hydranths, tall, columnar, with distinct hypostome and a double whorl of 8–16 solid tentacles. Hydranth sessile, or subsessile, supported by a cup-like dilation of perisarc. Gonozooids borne singly on stalks arising directly from the stolons.

Medusa deep-bell-shaped with four radial canals, ring canal, four perradial marginal bulbs with tentacles armed distally with clusters of nematocysts. Manubrium tubular, with simple mouth, with, at liberation, four oral tentacles armed with nematocyst clusters at their tip. Gonads undeveloped.

Cytaeis niotha (Pennycuik, 1959)

Stylactella niotha Pennycuik, 1959, *Univ. Queensland. Pap. Zool.* **1** (6) : 162, pl. 1, fig. 2.

This species was described from the Great Barrier Reef by Pennycuik. I have been able to re-examine the type colony on the snail *Niotha albescens* Dunker from Heron Island by courtesy of the author and of Mr. George Mack of the Queensland Museum. This colony labelled Queensland Museum G.2392 is here selected as lectotype.

The material is not in very good condition, and although it has not been possible to ascertain some details, it has been possible to establish the relationships of the species with the genus *Cytaeis*.

The hydrorhiza forms a reticulate network running in the groves of snail's shell and the tall, columnar hydranths arise at short intervals along it, and are, as stated by Pennycuik, more concentrated around the mouth of the shell. In view of the condition of the colony it was not possible to ascertain the existence of perisarcal cups round the bases of the hydranths, although the latter are constricted basally. The hydranths have short pointed hypostomes with double whorls of 14–16 tentacles ; the latter are heavily armed with nematocysts and are more hispid than the comparatively smooth tentacles of *C. nassa*. The hypostome, too, seems less developed than in *C. nassa* (Text-fig. 10).

The gonozooids are borne on long stalks arising around the bases of the hydranths. Each is covered by smooth hyaline perisarc and contains a medusa. The latter has four perradial canals, four perradial tentacle bulbs with tentacles equally developed. The slightly-fusiform manubrium has a simple mouth and four, simple, short, capitate tentacles. These are cytaeid characters and the species is therefore referred to *Cytaeis* as *C. niotha*.

It is not possible to unite this species with *C. nassa* in view of the apparent differences in tentacle armature in the hydranths. The species can be distinguished by a greater number of tentacles (14–16 in a double whorl) from *C. uchidae* in which the number is 6–10. There are probably other differences not apparent in this material.

Cytaeis indica (Stechow, 1920)

Stylactis sp., Calman, 1911, *Ann. Mag. nat. Hist.* (8) **8** : 546, text-figs. 1 & 2.
Stylactis indica Stechow, 1920, *Sitz-Ber. Ges. Morph. Phys. München*, **31** : 11.
Stylactella (*Stylactaria*) *indica* Stechow, 1923, *Zool. Jb. Syst.* **47** : 63.

In 1911, Calman described a small hydroid with a creeping stolon and polyps of the "*Stylactis*" type from the carapace and legs of a Xanthid crab. This has recently been re-examined and on one of the stolons, close to a hydranth, a small stalked bud was found. Although the detailed structure of the bud cannot be made out its general appearance (stalked and pear-shaped) strongly recall young medusa buds of *Cytaeis* hydroids. The hydranth, too, has the cup-shaped socket of perisarc at the base as in hydranths of that genus, although this is not immediately obvious because the polyps themselves are much contracted.

Subsequent to Calman's description, Stechow (1920) named this colony *Stylactis indica*, renaming it *Stylactella* (*Stylactaria*) *indica* in 1923. It is now placed in *Cytaeis* as *C. indica*, although better knowledge of *Cytaeis* medusae and their hydroids (as indicated on p. 387) will probably enable the species to be referred to one of the earlier described species of this genus.

The holotype, which is attached to the crab *Xanthias haswelli*, bears the number B.M. (Crustacea) 1911.9.12.36.

4. Genus ***PERARELLA*** Stechow, 1922

Cytaeid hydroids with fixed gonophores.

In selecting this generic name as the best available name for cytaeid hydroids with fixed gonophores (Rees, 1956 : 344), it was obvious, although not stated then, that the confusion caused by many alterations in generic concepts of *Stylactis*, *Stylactella* *Stylactaria* needed clarifying. The only one of these that concerns this paper is *Stylactella* Haeckel which has been restricted in this paper to an ill-defined type species whose gonosome is unknown.

Haeckel's other *Stylactella* spp. are better defined and can be referred to *Perarella*, although micro-preparations prepared by Haeckel have long dried up and the specimens are no longer recognizable.

The type species of *Perarella* Stechow, 1922, is *Perigonimus schneideri* Motz-Kossowska, 1905.

Other species now referred to the genus are: *Hydractinia clavata* Jäderholm, 1905; *Stylactis affinis* Jäderholm, 1904; *Stylactella spongicola* Haeckel (1889) and *S. abyssicola* Haeckel (1889).

Perarella schneideri (Motz-Kossowska, 1905)

Perigonimus steinachi Jickeli, 1883, *Gegenbaurs Jb.* **8** : 617, pl. 27, figs. 1–9.
Perigonimus schneideri Motz-Kossowska, 1905, *Arch. zool. exp. gén.* (4) **3** : 72, fig. VI.
Clavopsis schneideri, Stechow, 1921, *Arch. Naturg.* **87**A : 252.
Perarella schneideri, Stechow, 1922, *Ibid.* **88**A : 145.
Rees, 1956, *Bull. Brit. Mus.* (*Nat. Hist.*) *Zool.* **3** (8) : 344, 346.

I have not seen this species and the following description is based on the work of Motz-Kossowska and of Stechow.

Definition

Hydrorhiza forming an open network of perisarc-covered stolons. Hydranths long and tubular, with a whorl of 12–14 tentacles around a conical hypostome. Hydranths provided with a basal collar of perisarc.

Gonophores, fixed, oval, borne on short stalks, or almost sessile on the hydrorhiza. Male gonophore, cryptomedusoid, with four radial canals and four very rudimentary basal bulbs. Manubrium well developed with ring gonad almost completely filling the subumbrella cavity. ♀ gonophore similar, with numerous eggs.

Motz-Kossowska states that the polyps are extremely contractile but when expanded reach a height of 15 mm. (this is apparently a misprint for 1·5 mm.). The ♂ gonophores are said to be milky-white in colour with the radial canals and tentacle bulbs of a vivid red colour.

Picard (1958 : 190) refers this species to *Perigonimus steinachi* Jickeli, 1883, a species which I regard as insufficiently described (Rees, 1956 : 344). He identifies Stechow's *Stylactella elsaeoswaldae* from Naples also with the present species ; this is probably correct despite the fact that Stechow did not observe the basal collar of perisarc around the base of the hydranth. Stechow gives the height of the hydranths as 0·5–0·75 mm. and the size of the female gonophores as 0·64 mm. by 0·4 mm. The length of gonophore and stalk was 0·96 mm.

Perarella clavata (Jäderholm, 1905)

Hydractinia clavata Jäderholm, 1905, *Wiss. Ergeb. Schwed. Sud-polar Exp.* 1901–05, **5** (8) : 5.
Stylactella clavata, Stechow, 1925, *Wiss. Ergeb. Deutsche Tief-see Exp.* 1898–99, **17** (3) : 401.

This hydroid was referred to *Hydractinia* by Jäderholm who found the species growing on shells dredged from a depth of 360 m. off Ludvig Philip Land, Erebus and Terror Gulf, Antarctica (Swedish Sud-polar Expedition, 1901–03, St. 8).

From a preliminary examination of the material in Stockholm in 1954, it was realized that the species could not be retained in *Hydractinia;* it had no basal crust, no spines, no dactylozooids and no reproductive hydranths (all characteristics of *H. echinata*, the type species). Jäderholm's species possessed stalked gonophores arising directly from the basal stolons and together with the basal cup around the proximal end of the hydranth indicated a relationship with hydroids of the family Cytaeidae. Apart from the fixed gonophores, the species bore a close resemblance to the *Cytaeis* hydroid described by Komai (1931).

This relationship has already been acknowledged by recognizing *Perarella* (Stechow, 1922) as a suitable genus " for cytaeid hydroids in which there are fixed gonophores " (Rees, 1956). Accordingly *H. clavata* is referred to the genus *Perarella.*

The following description of *Perarella clavata* is based on a re-examination of the type material in Stockholm in May, 1959.

Description

The basal stolons form a close, reticulate, anastomosing network, but there are no spines, no dactylozooids or other Hydractinian features. The colony is well developed and extensive on its shell base (*see* Jäderholm, 1905, Taf. 3, fig. 6) so that the network can be assumed to be fully developed.

The hydranths arise from a weakly-chitinized stolon and have thin basal cups of perisarc ; the latter has a height of approximately 0·4 mm. The hydranths are tall, columnar, and are often more swollen distally. There are 10–16 filiform tentacles around a conical hypostome which is not heavily armed with nematocysts.

The gonophores are very characteristic and recall *Cytaeis* rather than *Hydractinia.* They are stalked and arise directly from the stolons (Text-fig. 11). There is, as in the hydranths, a basal ring of perisarc which is only 0·17–0·20 mm. in height. Distal to this, there is a moderately long stalk merging into the gonophore itself, and covered with very thin perisarc. The gonophore is elongate and rather club-shaped in appearance. There were no radial canals described but I have not been able to confirm or deny this from the material. There is a thickening of the wall of the gonophore distally, with apically, a slight protuberance or papilla. The eggs are arranged in a single layer round the well-developed spadix.

Measurements of this type material are given below :

TABLE V.—*Dimensions of the holotype of* Perarella clavata (*Jäderholm*)

Height of hydranth to hypostome .	4·5–6·7
Diameter of hydranth . . .	0·4–1·0
Length of proboscis	0·4–0·6
Diameter of stolons	0·2–0·25
Total height of gonophore . . .	2·15–2·9
Width of gonophore	0·6–0·8
Length of stalk of gonophore . .	0·4–1·0

The chief difference between this species and the closely related type species of *Perarella, P. schneideri* (Motz-Kossowska) lies in the structure of the gonophore. In *P. schneideri* there are four well-developed radial canals and four rudimentary bulbs but in the species *clavata* radial canals are apparently absent and apically there is only a small protuberance.

Perarella spongicola (Haeckel, 1889)

Stylactella spongicola Haeckel, 1889, *Rep. Sci. Res. Challenger Zool.* **32** : 79, pl. 2, figs. 5, 6.
Iwasa, 1934, *J. Fac. Sci. Hokkaido Univ. Zool.* (6) **2** : 254, fig. 5.

Definition

Hydrorhiza consisting of smooth, anastomosing stolons (0·5–0·12 mm. in diameter) forming polygonal or rounded meshes, these giving support to the tissues of the host sponge. Hydranths very small, 0·2–0·3 mm. in diameter, ovate or club-shaped with about eight tentacles around the base of a conical hypostome. Gonophores, fixed, ovate, or club-shaped with distinct stalk. ♀ gonophores are sporosacs with distinct spadix, numerous eggs and no traces of radial canals or of tentacle bulbs (Text-fig. 12*a*).

This species occurs in association with deep-sea sponges of the genera *Psammophyllum*, *Cerelasma*, and *Psammopemma* in the north and central Pacific at depths of 2,300–2,900 fathoms.

The micro-preparations made by Haeckel have long dried up and no additional information can be given on the species.

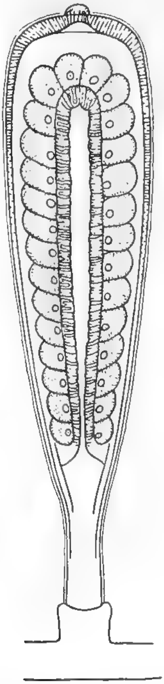

FIG. 11. *Perarella clavata* Jäderholm; a female gonophore from a type slide in the Naturhistoriska Riksmuseum, Stockholm.

Perarella abyssicola (Haeckel, 1889)

Stylactella abyssicola Haeckel, 1889, *Rep. Sci. Res. Challenger Zool.* **32** : 81, pl. 2, fig. 7.
Iwasa, 1934, *J. Fac. Sci. Hokkaido Univ. Zool.* (6) **2** : 255, fig. 6.

Definition

Hydrorhiza of anastomosing stolons of variable thickness. Hydranths fusiform, with hypostome and oral whorl of 12–16 filiform tentacles, borne on short non-annulated stems. Gonophores, fixed, without radial canals or rudiments of tentacles, with prominent spadix, borne on short stalks (Text-fig. 12*b*).

Haeckel states that the hydranths are 0·5–0·6 mm. in diameter, that is nearly twice the size of those of *P. spongicola*. He draws special attention to the fusiform dilations of the stolons between hydranths and the triangular dilations of the anastomosing tubes at nodal points.

This species, like *P. spongicola*, is associated with deep-sea sponges of the genera *Psammophyllum* and *Stannophyllum* from Challenger stations in the north and central Pacific at depths of 2,300–2,900 fathoms.

Haeckel's preparations are in too poor a condition to yield additional information.

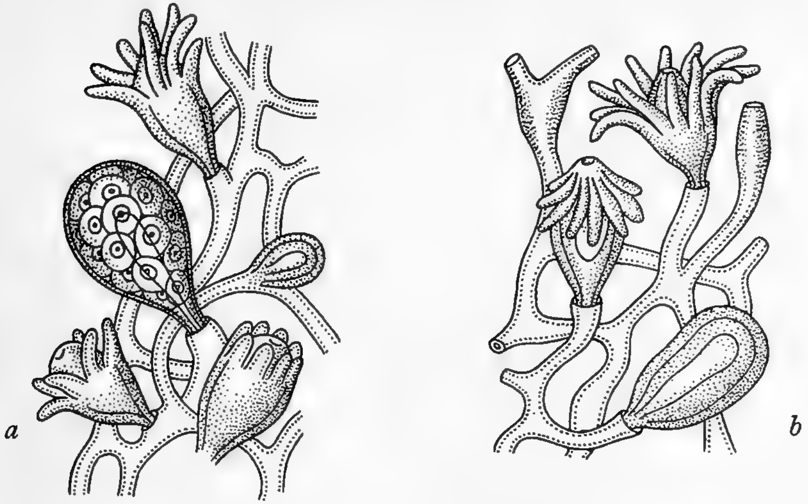

FIG. 12. *a*, *Stylactella spongicola* Haeckel; *b*, *Stylactella abyssicola* Haeckel; both figures redrawn from Haeckel (1889).

Perarella affinis (Jäderholm, 1904)

Stylactis affinis Jäderholm, 1903, *Ark. Zool. Stockholm*, **1** : 264, pl. 12, fig. 1.
?*Stylactis affinis* Stechow, 1912, *Z. Jb.* (*Syst.*) **32** (4) : 348, pl. 13, fig. 9.

This small sterile colony cannot be assigned to any other known species. It was re-examined by me at Stockholm in 1954. The salient features of the colony are a creeping, perisarc-covered hydrorhiza formed of anastomosing stolons 0·10–0·12 mm. in diameter. The hydranths are almost sessile, without enlargement of the perisarc stalk at the base. The distal portion of the hydranth is fusiform and there are 10–14 filiform tentacles of about 0·7 mm. each in length grouped around a conical proboscis. The hydranths are 0·7–2·5 mm. long and 0·25–0·4 mm. in maximum diameter. Reproduction is unknown.

Type locality. Romache Bay, Patagonia, on algae from 11 fathoms.

There is no certainty that the small sporosac figured by Stechow (1912 : 348, pl. 13, fig. 9) belongs to the same species. It may be noted that Stechow mentions four rudimentary marginal tentacles but his figure suggests more than four. This species is placed provisionally in *Perarella*.

5. Genus ***Stylactella*** Haeckel, 1889

Stylactella Haeckel, 1889, *Rep. Sci. Res. Challenger Zool.* **32** : 79.

In his genus Haeckel included three species *Stylactis vermicola* Allman, 1888 and his new species *Stylactella spongicola* and *Stylactella abyssicola*. He defined his genus as follows :

Tubulariae without hydrocaulus, with a reticular hydrorhiza, from which arise single sessile or pedunculate hydranths, and scattered between them single gonophores. Hydranths claviform, naked, with a single circlet of filiform tentacles, which surround the base of a conical hypostome. Gonophores ovate, naked, with a simple central spadix. Chitinous perisarc investing only the tubular branches of the hydrorhiza.

Stylactis vermicola Allman is here designated as type species of *Stylactella.*

Stylactella vermicola (Allman, 1888)

Stylactis vermicola Allman, 1888, *Rep. Sci. Res. Challenger Zool.* **23** : 2, pl. 1, figs. 2, *2a.*
Stylactella vermicola Haeckel, 1889, *Ibid.* **32** : 79.
Stylactella (*Stylactella*) *vermicola* Iwasa, 1934, *J. Fac. Sci. Hokkaido Univ. Zool.* (6) **2** : 253, fig. 4.

The following brief description is based on Allman's text and figure : Hydrorhiza branching with smooth perisarc. Hydranths arising at intervals from extremely short stalks from the stolons. Hydranths clavate with distinct conical hypostome and a whorl of about eight tentacles. Gonophores small, oviform on very short stalks springing from the hydranth close to its proximal end or from the stolons.

Type locality. Challenger St. 244, N. Pacific, 35° 22′ N., 169° 53′ E., 2,900 fathoms on the polychaete *Laetmonice producta.*

A re-examination of the original specimens of the annelid *Laetmonice producta* on which the hydroid was found by Allman, revealed traces of a hydrorhiza and disintegrating fragments of hydranths. There were, however, no other recognizable parts.

Allman thought that the gonophores were adelocodonic (fixed), but in view of their small size there can be no certainty about this, or whether the species is a true cytaeid. Accordingly *Stylactella* (of which *S. vermicola* has already been designated as type species) must be regarded as an insufficiently described genus. It is here restricted to *S. vermicola,* and Haeckel's two species, known to have fixed gonophores, are placed in *Perarella* Stechow.

6. DISCUSSION

It is evident from the above survey that the family Cytaeidae is a well-defined one which can be distinguished from the Hydractiniidae (with which it has been primarily confused), by the complete absence of spines on the hydrorhiza, by the absence of reproductive hydranths, by the direct development of medusa buds on the hydrorhiza and by the characters of the medusa. In the latter the presence of oral tentacles on the manubrium around a simple mouth distinguish it from *Podocoryne* medusae in which the corners of the mouth form oral lips.

The status of those Cytaeid hydroids which liberate medusae cannot be resolved until more is known about the planktonic development of the medusae. In *C. uchidae,* for example, does the medusa shed its gonadial products and die—or does it continue to grow in the plankton and so assume the typical form of *C. tetrastyla* with numerous oral tentacles? The preliminary experiments conducted by Mr. Hatsuki Tsujimura in which one medusa only had increased its oral tentacles to seven after 40 days are inconclusive, but they (and the work of Werner, 1961) suggest profitable lines for future research.

Cytaeis uchidae and *C. nuda*, both liberating medusae with almost mature gonads, appear to be closely related. Likewise *C. nassa* and *C. niotha* are very similar even in the number of tentacles in the hydranth, but there appears to be a distinct difference in the nematocyst armature of the tentacles in the hydranth.

C. uchidae has much fewer tentacles in the hydranth than *C. nassa* and also differs from it in having an almost mature medusa at liberation. The solution of the *Cytaeis* problem thus depends on careful rearing of the medusae to establish their growth and reproductive pattern.

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This report has been made possible through generous gifts and loans of material, and, in particular, I am greatly indebted to H.M. the Emperor of Japan for the gift of specimens of *Cytaeis uchidae* and also for generously placing notes, specimens and drawings of *Cytaeis nuda* at my disposal for description. I also wish to thank: Professor Itiro Tomiyama, Misaki Marine Station, for kindly rearing young medusae of *C. uchidae* from the hydroid ; Dr. Bengt Hubendick for facilities and hospitality when studying the type of *Hydractinia clavata* in Stockholm ; Mr. George Mack and Dr. Pamela Pennycuik for lending the type specimen of *Stylactella niotha* Pennycuik ; Dr. William Macnae for colonies of *Podocoryne nassa* Millard from Inhaca, Island, Lourenço Marques and Dr. N. A. H. Millard for kindly lending the type slides of the same species.

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PLATE 10

FIG. 1. *Cytaeis nuda*, sp. n.: micro-preparation of two nutritive polyps and a young medusa bud.

FIG. 2. *Cytaeis uchidae* nom. nov.: dorsal view of a well-developed fertile colony on a shell on *Nassarius*; Misaki, June, 1961.

FIG. 3. *Cytaeis uchidae* nom. nov.: dorsal view of a young colony on *Nassarius*.

FIG. 4. *Cytaeis uchidac* nom. nov.; ventral view of another colony on *Nassarius*.

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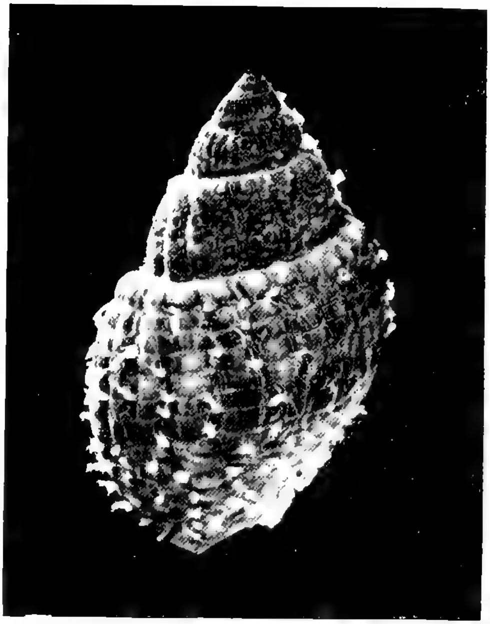

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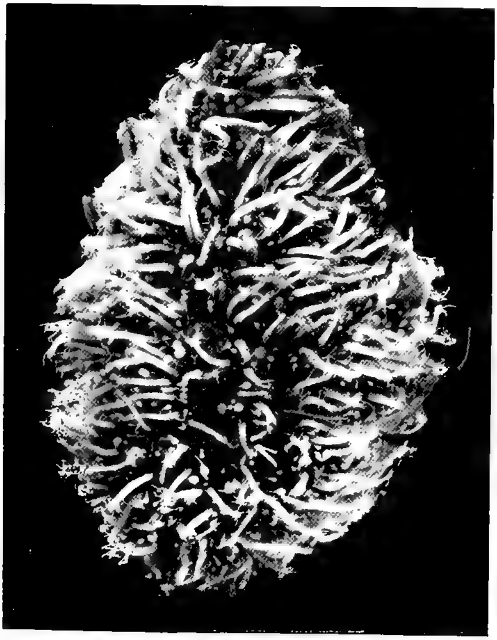

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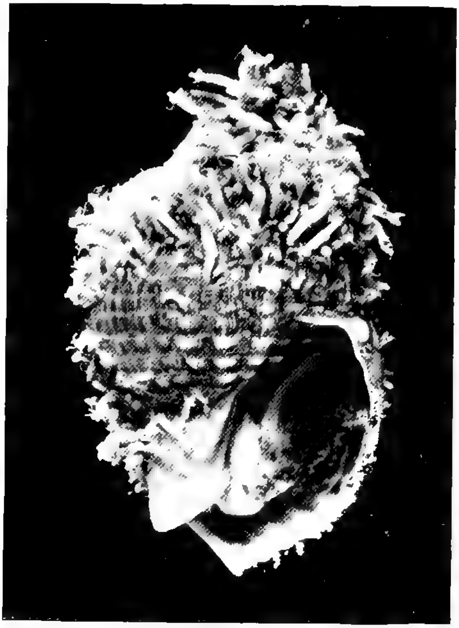

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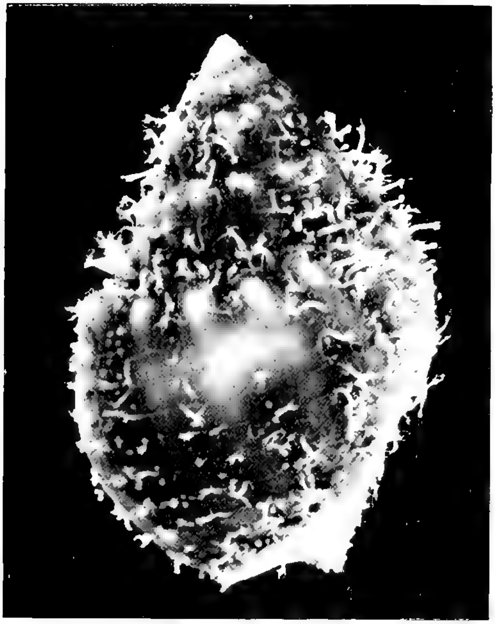
PLATE 11

Cytaeis nassa (Millard)

Figs. 5 and 6. Dorsal and ventral views of the same fertile colony. Note how the stolons follow the grooves of the shell.

Figs. 7 and 8. Dorsal and ventral views of another colony.



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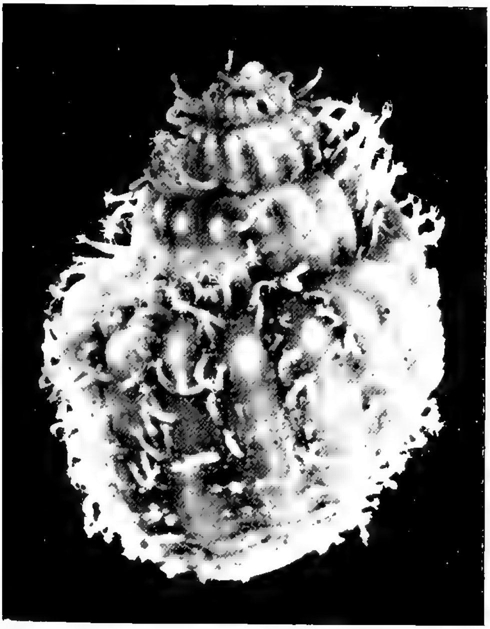

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Pp. 401–418 ; *Plate* 12 ; *3 Text-figures*

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CONTENTS

SYNOPSIS

Caryophyllia smithii is demonstrated to have an extensive distribution in British waters from Portland and the Channel Islands westwards, all around Ireland to the Shetlands. In continental Europe, it is found on the south-west coasts of Norway and on the Bohuslan coast of Sweden. Southwards it reappears in the Channel Islands, extending to the Mediterranean and Madeira. Rossi's belief that the species is cosmopolitan requires further consideration in view of her suggestion that *C. alaskensis* from the North Pacific is the same species.

Pyrgoma anglicum is shown to be restricted to the Western Channel (reaching Exmouth in E. Devon and Roscoff on the Finisterre coast) and the western approaches reaching Pembrokeshire. Its presence on the coral in the Channel Islands has not yet been reported. This species is thought to occur on about one in six *Caryophyllia* in British waters and individual corals may carry from one to twenty-four barnacles. These display some gregariousness in settlement, preferring their own shells to that of the coral for settlement. The species also occurs on *Leptopsammia*, *Dendrophyllia*, *Paracyathus*, *Astroides*, *Psammocora*, *Cladocora*, *Balanophylia* and *Schizoculina*. On the last three genera it is here recorded for the first time.

1. INTRODUCTION

The Devonshire cup-coral, *Caryophyllia smithii*, is, to quote a general belief voiced by Le Danois (1957 : 83) " very common on the continental shelf south of Ireland, and is very occasionally found at low water in south-west England ". However, as will be shown in this paper, the species has a much wider distribution extending northwards on our western coasts to the Shetlands and to the coasts of Norway and Sweden, and southwards at least to the Mediterranean.

On the south coasts of Devon and Cornwall *Caryophyllia* is sometimes found with a commensal barnacle *Pyrgoma anglicum* which lives firmly cemented either to the lip or to the column of the coral. However, its exact distribution in relation to that of *Caryophyllia* needed elucidation, and in this connexion, a remark by Hiro (1936 : 46) that of the cirripedes associated with corals, *Creusia* and *Pyrgoma* " are known to live almost exclusively in tropical waters " seemed significant. It suggested that *Pyrgoma anglicum* might be a warm-water species (like the *Octopus* and many other creatures) which is just able to maintain itself on the western parts of our coasts at the limit of its northward distribution.

Examination of the evidence strongly supports this suggestion.

2. THE DISTRIBUTION OF *CARYOPHYLLIA SMITHII* STOKES & BRODERIP

In the following account I have drawn largely on fauna lists and on the collections of the British Museum which contain much early material associated with Cranch, Leach, Gosse and Norman. Unfortunately, however, much of this early material is lacking in precise details of locality.

(a) *The Status of* Caryophyllia smithii

The following appear to be the principal synonyms of the species :

Caryophyllia cyathus, Fleming, 1828. *Hist. Brit. Animals* : 508 (non Ellis).
Turbinolia borealis Fleming, 1828. *Ibid.* : 509.
Caryophyllia sessilis Bellamy, 1839. *S. Devon Nat. Hist.* : 330, pl. 18.
Caryophyllia smithii Stokes & Broderip, 1828. *Zool. J.* : 486.
    Johnston, 1838. *Brit. Zooph.* : 207, fig. 30.
    Couch, 1844. *Cornish Fauna*, **3** : 72, pl. 12, fig. 3.
    Gosse, 1853. *Devonshire Coast* : 108, pl. 5, figs. 1–5.
    Johnston, 1847. *Brit. Zooph.* Ed. 2 : 198, pl. 35, figs. 4–8.
    Goose, 1860. *Actinologia Britannica* : 310, pl. X, figs. 12–13.
    ?Norman, 1868. *Rep. Brit. Assoc. Norwich* : 319.
Caryophyllia smithii var. *castanea* Gosse, 1860. *Actinologia Britannica* : 312.
Caryophyllia smithii var. *esmeralda* Gosse, 1860. *Ibid.* : 312.
Caryophyllia smithii var. *clara* Gosse, 1860. *Ibid.* : 312.
Caryophillia clavus var. *borealis*, Duncan, 1874. *Trans. zool. Soc. Lond.* **8** : 312, pl. 48, fig. 6.
Caryophyllia clavus var. *smithii*, Duncan, 1874. *Ibid.* **8** : 312, pl. 48, figs. 11–12.
Caryophyllia clavus var. *epitheca* Duncan, 1878. *Ibid.* **8** : 312, pl. 48, figs. 13–16.
Paracyathus inornatus Duncan, 1878. *Ibid.* **10** : 241, pl. 44, figs. 14–16.
Coenocyathus dohrni Doderlein. *Mitth. zool. Sta. Neapel*, **21** : 121, pl. 7, figs. 23–32.

?*Caryophyllia alaskensis* Vaughan, 1941. *J. Palaeont.* **15** : 180, figs. 1–4. Durham & Barnard, 1952. *Hancock Pacific Exped.* **16** : 81, pl. 9, fig. 41*a* + *b*.
Caryophyllia smithii var. *meridionalis* Picard, 1952. *Bull. Lab. Marit. Dinard*, **36** : 6.

There has been some confusion of this species with the Mediterranean species *Caryophyllia clavus* Scacchi notably by Joubin (1928) and Duncan (1874), these errors in identification having been pointed out by Picard (1952) and Rossi (1957). The latter recognizes three distinct species in the Mediterranean, viz., *C. smithii* Stokes & Broderip, *C. clavus* Scacchi and *C. cyathus* Ellis & Solander. She has also examined the type specimens of *Paracyathus inornatus* Duncan, 1878, and *Coenocyathus dohrni* Doderlein, 1913, and concludes that they are identical with *C. smithii*. Picard (1952), who has examined *C. smithii* both from Dinard and the Mediterranean, distinguishes the Mediterranean form as a new variety, because " les calices de la *Caryophyllia* méditerranéenne sont, dans l'ensemble, plus petits et les septes laissent un espace central moins prononcé, cette dernière particularité entrainant une réduction de la prolifération des rubans tordus de la columella chez ces *C. smithii* méditerranéens que je propose de distinguer comme forme *meridionalis* ". Duncan (1874 : 312) who placed *C. smithii* in *C. clavus* as var. *smithii* states " It has a broad base ; but this is the only strong distinction between it and *Caryophyllia clavus*. The gradation of a delicate pedunculated *Caryophyllia clavus* into a broad-based form with all the other peculiarities, depends upon the depth of water and the nature of the bottom ; and the variety *borealis* gradually becomes variety *smithii*, both in the northern seas and in the Mediterranean." Rossi (1957) however, draws distinctions between the two forms. Whether these and the colour differences that have been reported in the living animals are specific or merely ecophenotypic remains to be elucidated. Accordingly I have omitted those records in which there is some doubt about identity, but I have included Norman's records from the Shetlands (Pl. 1, fig. 4) with some reservations, especially as Dr. Rossi (*in litt.*) regards these specimens as *C. clavus*.

Although not stated by Stokes & Broderip (1828) it appears that the type locality of *C. smithii* is the same as noted by de la Beche (1828) in the same paper, that is, " Corbons rocks at the end of Torbay sands ".

(b) *Distribution in the Channel*

Caryophyllia smithii has been recorded from numerous localities in the Western Channel and the distribution as noted in Text-fig. 1 is based on published records and material in the British Museum (Natural History). The latter contains, as noted earlier, much historical material and this has been supplemented with more recent collecting. The old record from the Scilly Isles (North, 1850) has been confirmed from material dredged off Tresco by Mr. W. Fowler (BM. No. 1960.8.4.1).

Canon A. M. Norman's collection contains a fine series with the associated *Pyrgoma* from off Dodman Point, Cornwall. The coral has been frequently recorded in the Plymouth area by the Marine Biological Association (1957 and earlier fauna lists) and notably by Allen (1899) and Forster (1958). Records from deeper water in this area are given by Crawshay (1912) and his positions are plotted in Text-fig. 3. East of Salcombe, there are many records from the Torquay area; these are detailed below. There is also a record from Exmouth in the Gwyn Jeffreys collection in the U.S. National Museum.

It is now possible to add a new record from Portland and others from the central area of the Channel (from the Manihine collections) thus extending the known range eastwards.

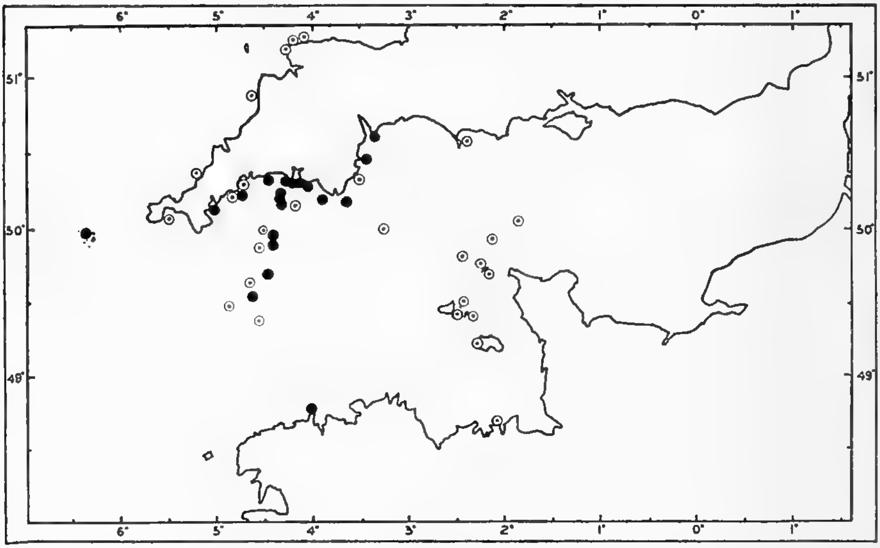

FIG. 1. The known distribution of *Caryophyllia smithii* in the English Channel and the north coasts of Cornwall and Devon; filled (black) circles denote *Caryophyllia* with *Pyrgoma*, and open circles, *Caryophyllia* without *Pyrgoma*. The Pembrokeshire records of *Pyrgoma* complete the known distribution of this species in British waters.

Caryophyllia is also known to occur at all of the Channel Islands (Ansted & Latham, 1862; Sharp, 1909; Sinel, 1906) and on the north coast of France it has been recorded from several localities at Roscoff and several times from one point near Dinard.

There are no records known to me from the eastern half of the Channel. For the English coast, local fauna lists for Bournemouth (Waddington, 1914) and the Isle of Wight (Morey, 1909) contain no records but it is to be expected that aqualung divers will find this species for some distance further east wherever there are suitable substrata offshore.

Channel records of *Caryophyllia smithii*

Scilly Isles: (North, 1850: 180; Hickson, 1909: 398); off Tresco, new record (see p. 405).

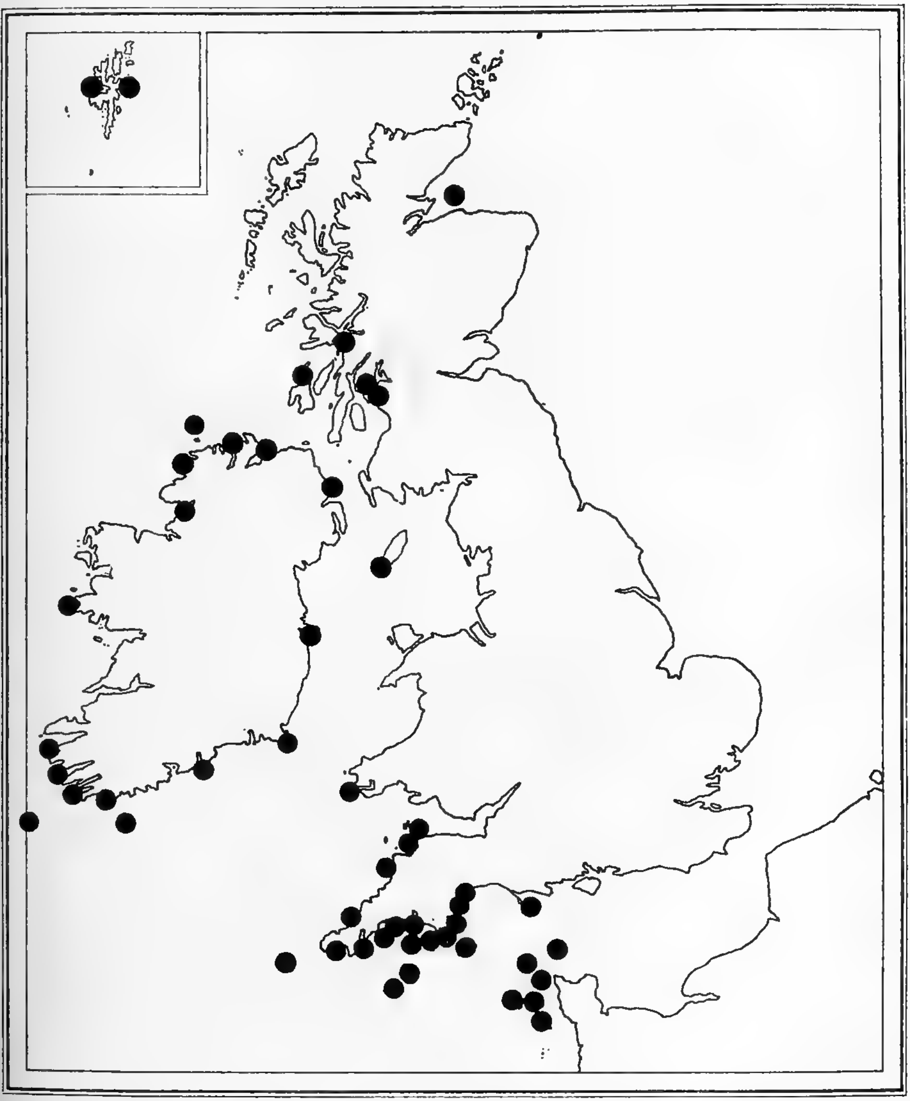

FIG. 2. The recorded distribution of *Caryophyllia smithii* around the British Isles. Western Channel records are more fully represented in Figs. 1 and 3.

South coasts of Cornwall and Devon : Mount's Bay, Penzance (Courtney, 1845 : 43) ; Falmouth, W. P. Cocks (see Norman & Scott, 1906 : 225) ; Veryan Bay (Couch, 1844 : 72, pl. 12, fig. 3) ; Dodman Point, Coll. A. M. Norman (B.M. No. 1905.11.1.7-15) ; Mevagissey (Couch, 1844 : 72) ; Polperro (Couch, 1844 : 72 ; Norman & Scott, 1906 : 225).

Plymouth Sound : various localities, Eddystone area (Allen, 1899) ; Breakwater, Mewstone ledge, SW. of Eddystone, Hand Deeps etc. (*Plymouth Marine Fauna*, Ed. 3, p. 68) : Queener Pt., Whitsand Bay ; 4–7 m., Penlee Pt. ; Eddystone ; Hand Deeps (Forster, 1958 : 474 *et seq.*).

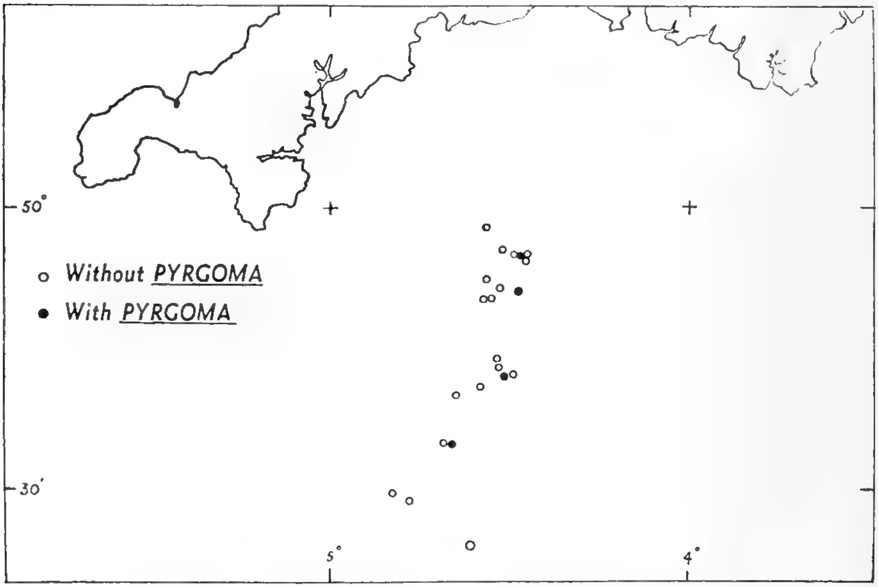

FIG. 3. Stations in the outer Western Channel at which Crawshay (1912) recorded *Caryophyllia* with *Pyrgoma* (filled circles) and *Caryophyllia* only (open circles).

Stoke Point area : N.E. of Stoke Point (Forster, 1958 : 474).

Bolt Head shell gravel (Allen, 1899 : 437).

Prawle stony ground (Allen, 1899 : 439).

Dartmouth (Parfitt, 1866 : 19).

Torquay : Corbons, end of Torbay sands (de la Beche, also Stokes & Broderip, 1828) ; Johnston (1837 : 208), Jones (1858 : 141) ; Templer (1855) ; Parfitt (1866 : 19) ; Anstey's Cove, 28th March, 1961 (Brit. Sub-Aqua Club).

Exmouth : Jeffreys Collection, Smithsonian Institution (Pilsbry, 1916 : 262).

Coast of Dorset :

Portland : Off breakwater, 1st August, 1959, 35–70 ft. Coll. T. Ingram (B.M. 1959.8.5.1–14).

Outer Western Channel :

Various stations extending from the Eddystone to mid-channel (Crawshay, 1912). These records are plotted on Text-fig. 3.

Central Channel Area :

New records from the following Manihine stations :

Manihine St. 9, 50° 03′ 30″ N., 01° 51′ W., 25th July, 1947, 60 m., rocky bottom, 1 specimen, trawled.

Manihine St. 47, 49° 55′ 20″ N., 02° 8′ W., 60 fms., stony bottom, dredge, 1 specimen.

Manihine St. 50, 49° 49′ N., 02° 28′ 45″ W., 31st August, 1948, 70 fms., stony bottom, 2 specimens.

Manihine St. 53, 50° 0′ N., 03° 16′ W., 28·5 fms., dredge, gravel bottom, 4 specimens.

Channel Islands :

Alderney : Sharp (1909 : 93).

Guernsey : Collings (1863 : 173) ; Ansted & Latham (1862 : 240) ; Koehler (1885 : 56) ; Mabbs (1906) ; Tanner (1908 : 283) ; Sharp (1908 : 479 and 481).

Sark : Collings (1863 : 173) ; Ansted & Latham (1862 : 240).

Herm : Ansted & Latham (1862 : 240) ; Koehler (1885 : 56).

Jersey : Sinel (1906 : 31).

North coast of France :

Roscoff : Lacaze-Duthiers (1897 : 73, pl. 4, fig. E) ; Teissier (1950 : 39).

Dinard : Point de Briantais (de Beauchamp, 1929 : 32 ; Lami, 1939 : 33, pl. 1 ; Picard, 1952 : 5).

(c) *Distribution elsewhere in the British Isles*

On the north coasts of Cornwall and Devon, the Ilfracombe district is one of the classical localities for *Caryophyllia* where it has been often reported, and some of P. H. Gosse's material is in the British Museum (B.M. No. 1852.12.9.24–32 and 1853.28.10.10–20). In this area it has been found at extreme low water from Combe Martin to Watermouth (Palmer, 1946). Records from the North Cornish coasts are few, as might be expected, but the *Victoria County History of Cornwall* mentions Newquay and Bude (Clarke, 1906).

Northwards there are no records that I can find for the Bristol Channel north of the Ilfracombe area (Bassindale, 1941) and Fowell (1947) does not record the species from the Gower Peninsular. Pembrokeshire records (see below) are summarized by Bassindale & Barrett (1957), while Chadwick's 1903 record from the Isle of Man has recently been supplemented by new records kindly supplied by Dr. N. S. Jones (personal communication).

Caryophyllia occurs all round the Irish coast. Haddon's early records (1886) from Dalkey Island, north of Dublin have recently been confirmed through the finding of the species on a wreck (Mr. Tom Shakespeare, Irish Sub-Aqua Club, personal communication). The remaining Irish records are noted below and it will be seen that the species occurs all round the coast.

British Records other than Channel Coast

West Wales:

Pembrokeshire: Musselwick, Castle Beach, Gunkel, Gateholm (Bassindale, 1957 : 250); Martin's Haven (Moyse, 1961).

Skokholm: Crab and East Bays (Bassindale, 1957 : 250). Skomer: Mew Stone Basin, North Haven (Bassindale, 1957 : 250); sublittoral, off Skomer (Moyse, 1961 : 372).

Irish Sea (excluding Irish Coast):

Isle of Man: Calf Sound (Chadwick, 1903); (N. S. Jones, *in litt.*).

East Coast of Ireland:

Larne: (Gosse, 1860 : 315).

Belfast Lough: (Williams, 1954).

Dublin Bay, off Dalkey Island: (Haddon, 1886 : 528); Stephens (1908 : 211); T. Shakespeare (*in litt.*).

Wexford Bay: Gosse (1860 : 315).

S. Coast of Ireland:

Youghal: Gosse (1860 : 315).

Off Clonakilty Bay (10 miles S. of Galley Head Light: (Haddon, 1886 : 617).

Lough Ine: Renouf (1931 : 426).

S.W. Ireland:

Position 51° 51′ N., 10° 31′ W.; Mouth of Kenmare River; mouth of Bantry Bay; Haddon (1886 : 617).

Dingle Bay: Beaumont (1900 : 769).

Bantry Bay: Gosse (1860 : 315).

Valencia Harbour: Beaumont (1900 : 769).

Manihine St. 1, 51° 09′ N., 11° 01′ W. 3rd July, 1950, trawl, 3 specimens.

West Coast of Ireland:

Connemara; Bundoran: Gosse (1860 : 315).

North Coast of Ireland:

Lough Swilly; Lough Foyle: Gosse (1860 : 315).

Off Tory Island, 130 fms., July 12, 1935 (H. G. Stubbings *in litt.*).

Scotland:

Millport, Isle of Cumbrae (numerous records).

Oban: Coll. J. Alder (Johnston, 1847 : 198, pl. 35, fig. 4).

Firth of Lorne, 30–50 fms.: Coll. John Murray (B.M. 1887.9.2.2).

Loch Strivan, 20 fms.: Chumley (1918 : 48).

Oronsay, low water: (Oundle School Natural History Society, *in litt.*).

Moray Firth: Gosse (1860 : 315).

Shetlands: off Foulah (Fleming, 1828 : 508); ? Shetland Haaf (Norman, 1868 : 319).

On the west coast of Scotland records are few (see above list) and probably reflect the little attention this coast has received. It is found off Cumbrae in the Firth of Clyde and there is an early record from the Moray Firth, as well as those of Fleming (1828) and of Norman (1868) from the Shetlands. Specimens from the dredgings of the latter are in the British Museum (B.M. No. 1905.11.124–30). One of these is illustrated here (Pl. 12, fig. 4).

(d) *Scandinavian Distribution*

There are no records from Iceland but the species is found on the west coasts of Norway and Sweden as noted below :

Norway : Mandal, Risør, Krageør, Osloford, Hardangerfjord, Korsfjord, Hjeltefjord, Alvaerströmmen (Carlgren, 1945 : 149).

Sweden : Bohuslan (various localities) ; Carlgren (1945 : 149) ; Gullmarfjord (Nilsson & Jägersten, 1961 : 49 and 53).

Records are absent for the Southern North Sea countries of Denmark, Germany, Netherlands and Belgium and for much of the East coast of England, there being, for example, no records for Cullercoats (Bull, 1939), Newcastle-upon-Tyne (Hobson, 1949) and Scarborough (Walsh & Rumington, 1953).

(e) *Distribution in Southern Europe and the Mediterranean*

Caryophyllia smithii is poorly recorded for the Atlantic coast of France and the Iberian peninsular. It has been recorded from Cezimbra, Portugal, by Saville Kent (1870 : 459), and at position 38° 16′ 8″ N., 8° 56′ 43″ W. by Rossi (1958 : 5). Most of the Mediterranean records are from the Western basin, but Rossi (1961 : 36) indicates that the species is found all over the Mediterranean in the " biocoenose coralligène " and Laborel & Vacelet (1958) state that it occurs in " microcavités au plafond des grottes sous-marines ". Rossi (1957*a*, *b* ; 1961) gives the distribution of the species as Banyuls, Marseilles, Prom. di Portofino (Genoa), Naples and Malta ; she also records it from five *Calypso* stations in the general area 37° 10′ N.–37° 50′ N., 11° 02′ 30″ E.–12° 43′ 15″ E. from depths of 20–450 m. The same author (1957) believes the *C. smithii* is probably cosmopolitan in distribution, regarding *Caryophyllia alaskensis* Vaughan (1941 : 180, figs. 1–4) as identical with it ; this suggestion requires careful consideration.

3. THE DISTRIBUTION OF *PYRGOMA ANGLICUM* SOWERBY

It has already been noted that Hiro (1936) considered *Pyrgoma* to be almost an exclusively tropical genus and this suggested to me that our British species was probably at the limit of its northern range on our S.W. coasts.

In British waters *Pyrgoma anglicum* occurs exclusively on *Caryophyllia smithii* and according to Hiro (1936 : 45) both this genus and *Creusia* live always attached to or embedded in corals. In other words, they seem to be obligatory commensals. It was therefore thought desirable to ascertain as far as possible the limits of distribution of this barnacle in relation to its host in British waters. Fifteen species of *Pyrgoma* are known but only *P. anglicum* has been reported from British waters.

(a) *The Recorded Distribution in British Waters*

The British Museum contains some early material without locality labels some of which need not be mentioned here, but others are of historical interest and are included with some other records below.

BM. 1852.4.1.12. One *Caryophyllia smithii* with three large and one minute *Pyrgoma*; Stokes & Broderip (Torquay).

BM. 1855.12.27.22. Locality unknown. Six *Caryophyllia*, two specimens with one *Pyrgoma* each.

BM. 1899.5.24.1–4. Hincks Collection. Five *Caryophyllia*, one only with *Pyrgoma* (twelve large and numerous newly settled young).

BM. 1904.6.27.13. Eddystone. One *Caryophyllia* with *Pyrgoma* (Pl. 12, figs. 1–3). Coll. E. W. H. Holdsworth.

BM. 1905.11.1.7–15. Off the Dodman. Twenty-one specimens, all except seven with *Pyrgoma*. Coll. A. M. Norman.

The type locality of *Pyrgoma anglicum* is given as Devon (Sowerby, 1823, Pl. 3, fig. 7). By 1854, Darwin was able to generalize: "South coast England and of Ireland (12–45 fms., Forbes & MacAndrew)", as well as giving foreign records. However, I have been unable to trace genuine records for the south of Ireland and the distribution in the Channel is more restricted than Darwin would have us suppose.

Channel records as will be seen are confined to the western part. Specimens examined by Stokes & Broderip from Torquay carry *Pyrgoma* (B.M. 1852.4.1.12) and subsequently Holdsworth (quoted by Gosse, 1865 : 282) found the barnacle in Plymouth Sound (B.M. 1904.6.27.13). Allen's survey of the Eddystone fishing grounds (1899) revealed the presence of *Caryophyllia* with *Pyrgoma* over a wide area between Eddystone and Prawle Point, while Norman & Scott (1906 : 255) give additional localities off Polperro and quote W. P. Cocks as finding the species at Falmouth. An unpublished record in 1951, of the association of the two species at Tresco, Scilly Isles, has been kindly supplied by Mr. W. Fowler (B.M. 1960.8.4.1).

More recent records from the Plymouth area have been given by Forster (1958). *The Teignmouth, Dawlish and Torquay Guide* (Anon.) mentions that "beautiful clusters of this shell are found on a madrepore adhering to the rocks at low water at Torquay".. The most easterly report of the species is that of Pilsbry (1916 : 262) from Exmouth from the Gwyn Jeffreys collection in the Smithsonian Institution.

Offshore and extending well into the middle of the Channel from Plymouth, Crawshay found *Pyrgoma* at a number of stations with *Caryophyllia* (see p. 409).

On the south side of the Channel, Lacaze Duthiers (1897) and Teissier (1950) summarize records from the Roscoff area and the former gives an excellent figure (1897, pl. 4, fig. E).

Reports of *Pyrgoma* are lacking from St. Malo and from the Channel Islands although the coral host has been taken at one locality near St. Malo and at all of the Channel Islands.

Apart from the unconfirmed statement by Darwin that *Pyrgoma* is found in Ireland, the records show that *Pyrgoma* is confined to the western Channel and Pembrokeshire, its known easterly distribution being Exmouth on the English side and Roscoff on the south side. The possibility of the species being found at Ilfracombe and along the north coasts of Cornwall and Devon must now be considered. Gosse (1860 and 1865) is not precise about it; he studied both the Ilfracombe and the Torquay areas and his material in the British Museum dating from 1852 gives no clue. The carcinologist, T. R. R. Stebbing, possessed some material of *Caryophyllia* " bought at Ilfracombe " and this is now in the British Museum (B.M. 1927.9.11.1). There are two cemented stones, each with five *Caryophyllia* and the largest specimen bears a large *Pyrgoma*. It is by no means certain that the specimens were collected locally; in view of the fact that there must have been heavy demands for collectors' items during the years when P. H. Gosse held classes in marine zoology at Ilfracombe, it is possible that some supplies at least would be drawn from the Channel coast. Confirmation of the existence of *Pyrgoma* at Ilfracombe is likely as it is known from Pembrokeshire (Moyse, 1961).

(b) *Wider Distribution*

Darwin reported this species from Sicily, Madeira and the Cape Verde Islands (St. Jago). There are specimens on the coral *Cladocora debilis* Milne-Edwards & Haime, 1849, from Madeira (R. Boog Watson collection), this species being hitherto unreported as a host for this barnacle. Along the Biscay coast of France, it has been recorded from Cape Breton (Landes) and Biarritz by Fischer (1872) on *Dendrophyllia* and *Paracyathus*, while Broch (1927) found it on *Dendrophyllia cornigera* on the Moroccan coast. Pérès & Picard (1956) found *Pyrgoma* on *Leptopsammia pruvoti* in the Sicily-Tunis channel and Picard also recorded it on *Astroides calycularis* from Motril, S. Spain. Further afield it has been found at Singapore (Weltner, 1897) and Broch (1931 : 119) mentions its occurrence off the Kei Islands on a fungiid coral. Hiro (1936) names *Psammocora* as its host in Tanabe Bay, Japan.[1]

Hiro was inclined to think that species of *Pyrgoma* are, in general, largely restricted to one species of coral; this may be true for particular localities, but is not so for *P. anglicum*, which, in its wider distribution is now known from more than nine species of coral. So few workers have interested themselves in this association of barnacle and coral, that the list is likely to be extended considerably.

(c) *Frequency and Numbers*

The material available is not suitable for estimating the frequency with which *Pyrgoma* is found on *Caryophyllia*. Gosse, however, writing in 1865 (p. 282) states " so far as my experience goes, extending over a very extensive series of specimens, I think about one in six of these corals carries the parasite, generally situated either on, or just without the margin of the cup ". This estimate agrees reasonably well with Crawshay's records of four positive stations (i.e., *Caryophyllia* with *Pyrgoma*) out of twenty-five stations at which *Caryophyllia* was taken, but the frequency probably varies greatly locally because gregariousness in settlement may ensure denser settlement in some places.

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[1] For additional coral hosts see Addendum p. 415.

Gosse (1860 : 315) states that sometimes two *Pyrgoma* are found on the same coral, but a single *Caryophyllia* may carry a surprising number of barnacles. This author mentions in 1865 (p. 282) that he possessed specimens " one of which carries nine, the other eleven " and adds " Mr. Holdsworth mentions however that he had seen fourteen Pyrgomata attached to a single *Caryophyllia* dredged in Plymouth Sound".[1]

One *Caryophyllia* of unknown locality, from the Cuming Collection, attached to a *Millepora*, carries twenty-four barnacles, and this heavy infestation bridges the gap across the disk of the corallite.

A series of nineteen *Caryophyllia* from off the Dodman Point, Cornwall, in the collection of the Rev. A. M. Norman, carried *Pyrgoma* in varying numbers as noted below :

1 with 14 *Pyrgoma*.
1 with 11 *Pyrgoma* (one on the flat base of the corallite).
1 with 9 *Pyrgoma*.
1 with 6 scars of *Pyrgoma*.
1 with 5 *Pyrgoma*.
3 with 4 *Pyrgoma*.
1 with 2 *Pyrgoma*.
3 with 1 *Pyrgoma* (two with one barnacle each and one with scar).
7 without *Pyrgoma*.

Another specimen from the Eddystone (B.M. 1904.6.27.13) bore nine large *Pyrgoma* and three minute ones on the larger barnacles.

On some *Caryophyllia*, notably a specimen from the Hincks collection and presumably Devon in origin, it is possible to recognize at least five settlement classes of *Pyrgoma* according to size and the manner of settlement. It is not however suggested that these are year classes as *Caryophyllia* is long lived and it is by no means improbable that settlement over a period up to twenty years or more may be represented.

Pyrgoma exhibits some gregariousness in settlement as later arrivals seem to exhibit preference for the hard surface of their own kind to that of the coral.

4. DISCUSSION

Caryophyllia smithii has been shown to have a wide distribution along the south-west and west coasts of Britain, extending round the Orkneys and Shetlands to the west coast of Norway and southwards to the deep-water fjords of the Bohuslan coast of Sweden. It appears to be absent along the east coast of England and in the countries bordering the southern N. Sea.

In the Eastern Channel records are wanting but this does not rule out the possibility of finding the specimens on hard substrata off shore.

The commensal barnacle has a much more restricted distribution in British waters, being confined to the western half of the Channel, and the Bristol Channel to Pembrokeshire ; this suggests that its distribution is limited by temperature as it is

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[1] This specimen (B.M. 1904.6.27.13) presented by Holdsworth to the British Museum actually carries ten large and medium *Pyrgoma* as well as seven young including scars ; it is illustrated on Pl. 12, figs 1–3).

for many other warm-water species which just reach this area. Surprisingly, on the south coasts of the Channel it has not been recorded further east than Roscoff, and, if it is truly absent from the Channel Islands, then it does not follow the expected pattern of distribution.

Pyrgoma anglicum is probably an obligatory commensal on corals of the genera *Caryophyllia*, *Dendrophyllia*, *Leptopsammia*, *Paracyathus*, *Astroides*, *Cladocora* and *Psammocora*.[1] Nothing is known of its relationship with the coral but it is reasonable to assume that heavy infestations must restrict the disk movements of the coral and possibly rob it of much of its food. It is noted too that the barnacles appear gregarious, preferring to settle on each other than on the column of the *Caryophyllia*.

Acknowledgments

For the additional records of *Caryophyllia*, I wish to thank members of the British and Irish Sub-Aqua Clubs, Oundle School Natural History Society, Dr. N. S. Jones and Dr. H. G. Stubbings. I am indebted to Dr. J. P. Harding for access to specimens from the Cuming and Boog-Watson collections mentioned in the text. I also wish to thank Mr. Ernest White for much assistance in the identification of various corals, Dr. J. W. Wells for confirming the identification of *Oculina* (*Schizoculina*) *fissipara* and Mr. P. J. Green for the remarkably good photographs reproduced on Pl. 12.

5. ADDENDUM

Since this paper was written, Dr. H. G. Stubbings has forwarded corals from the Atlantic coast of Africa for identification and on these *Pyrgoma* has been found on *Balanophyllia formosa* Gravier, 1915, and *Oculina* (*Shizoculina*) *fissipara* Milne Edwards & Haime, 1850, from the Ghana coast and on *Dendrophyllia cornigera* (Lamarck, 1816) taken in the Cape Verde Islands by the *Calypso*. Further details will be given in a forthcoming paper by Dr. Stubbings to whom I am much indebted for these records.

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[1] See Addendum p. 415.

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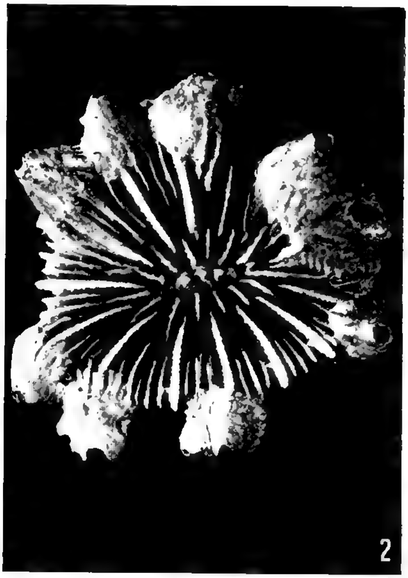
PLATE 12

Figs. 1–3. Different views of *Caryophyllia smithii* with the commensal barnacle *Pyrgoma anglicum* from the Eddystone. Coll. E. W. H. Holdsworth (B.M. 1904.6.27.13).

Fig. 4. *Caryophyllia* from the Shetlands. Coll. A. M. Norman (B.M. 1905.11.1.24).

1



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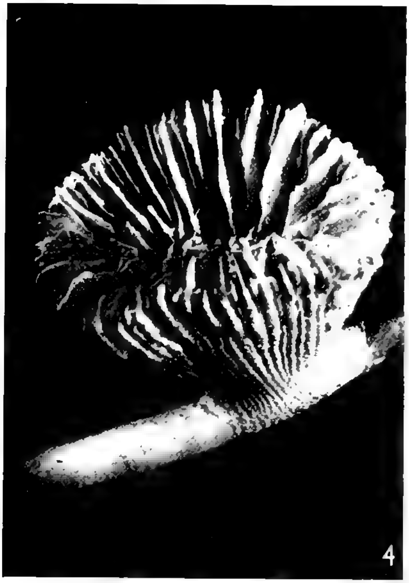

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THE IDENTIFICATION OF CEPHALOPOD "BEAKS" AND THE RELATIONSHIP BETWEEN BEAK SIZE AND TOTAL BODY WEIGHT

MALCOLM R. CLARKE

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BY
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National Institute of Oceanography

Pp. 419–480 ; *Plates* 13–22 ; 25 *Text-figures*

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By MALCOLM R. CLARKE

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CONTENTS—(*contd.*)

I. INTRODUCTION

LIVING Cephalopoda have two tough, horny mandibles generally called beaks because of their superficial resemblance to bird beaks.[1] They are embedded in a mass of muscle connected with the cephalic cartilages. Its hardness and horny nature makes a beak extremely durable when subjected to mechanical and chemical action and accounts for the widespread occurrence of isolated beaks in the stomachs of numerous species of whales, seals, fish and birds as well as on the ocean floor. Indeed, beaks are far more frequently found than other parts of cephalopods and beak identification is of considerable interest to ecologists concerned with many animal groups as well as to students of Mollusca.

Literature on cephalopod beaks is scattered and fragmentary and no separate study of the beak has been undertaken although many workers have included figures of beaks in their description of some species (see Table IV). Naef (1923) published several careful drawings of beaks from a variety of families in such a way that they can be easily compared but he gave no details of variation or growth changes within each species and omitted to designate criteria for identification. Beaks are included in only a small proportion of taxonomic descriptions. The present paper shows that it is probably impossible to identify the species from a beak (unless some chemical means is found), but families may be identified by reference to quite distinct characters. The work has been based upon a detailed study of over 500 beaks removed from identified specimens, that were selected to give as big a size range as possible within any one family. It is remarkable that, although measurements were taken from cephalopods which had been variously stored in ice, formalin and alcohol for different periods, it was possible to find relationships between beak size and total

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[1] The term "beak" is applied to one mandible in cephalopods but in birds it is used to describe both the upper and lower structures together. For cephalopods it is not misleading to use "beak", "jaw" and "mandible" as synonyms.

body weights for each family. Thus identification of the family to which a beak belongs allows an estimation of the total weight of the animal whose beak is under consideration. The accuracy of such an estimate is influenced by several factors which are discussed below (p. 473).

Stable criteria described below provide a basis for relating loose beaks with complete cephalopods found in the same stomach. Thus, workers should not only be able to identify the family to which beaks in a stomach belong, but, by comparing beaks present with identifiable cephalopods also present, they should get a good idea of the likely species represented by the beaks.

Squids are the main food of many large oceanic animals and this study is principally concerned with the beaks of the oceanic squids (i.e., Oegopsida). To complete such a study, it has been necessary to examine beaks of the more neritic squids and cuttlefish (Myopsida) and the Octopoda so that these may be distinguished from oegopsids when they occur. Myopsid and octopod beaks are relatively rare in stomachs of oceanic predators and I have not studied them in the same detail as the beaks of oegopsids. No attempt has been made to find criteria to distinguish octopod families. The smaller (young) beaks of large species dissolve to some extent in digestive juices and may become unidentifiable. Beaks of small species could probably be identified but their study demands different techniques and I have therefore only considered larger species which may occur in stomachs of whales, seals, the larger fish and the larger birds, and beaks with a rostral length of over 1 mm.

II. METHODS

First, beaks differ in their relative proportions and, by comparing selected dimensions, it is possible to express such differences in objective terms. Secondly, when a developmental series is studied, it is possible to find stages of darkening[1] which differ in different species. Thirdly, some sculpturing such as ridges or grooves may be present in some species and absent in others. All these features are frequently of value for identification.

Methods used in this investigation are restricted by several practical considerations. Although beaks from adult squids are largely unaffected by digestive juices, the non-darkened region of young stages often dissolves. This may make identification difficult by removing some of the features used for identification (e.g., dark patches on the wings—see p. 435) and makes any very accurate examination of relative dimensions pointless. To be of practical value, dimensional differences between families must be clear-cut with little, if any, overlap in the distribution of measurements because purely statistical differentiation cannot help in the identification of a few beaks and would be extremely tedious for the investigator. For these reasons no attempt was made to measure with a greater accuracy than can be obtained with a pair of finely adjustable dividers and a metal ruler. With these it is possible to estimate within ± 0·2 millimetres.

It is very difficult to find a standard method of weighing animals such as cepha-

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[1] The horny material of beaks becomes dark as it ages as if a tanning process takes place but no analysis has been carried out.

TABLE I.—*List of Beaks which were Removed from Cephalopods for this Work. Many more Beaks were Examined* in situ *and are not included in this List but Some of the measurements were used.*

Family	Genus and species	Number of speci-mens	Region	B.M. Registration No.	Date of collection	Preserva-tive	Source of material	Identified
Ommastrephidae	*Sthenoteuthis caroli*	25	NE. Atlantic	—	1951–59	Formalin (F)	" Discovery "	Author.
	S. pteropus	8	Madeira	—	1959	F	,,	,,
	? *S. pteropus*	1	Japan	—	1952	F	Whale Res. Inst. Tokyo	,,
	Todarodes sagittatus	16	Iceland	—	1960	Ice	" Discovery "	,,
	,, ,,	7	Madeira	—	1959	F	,,	,,
	,, ,,	1	G. Britain	1937.6.91	—	Alcohol (A)	B.M.	,,
	,, ,,	1	,, ,,	1933.5.27.1	—	A	,,	,,
	Todaropsis eblanae	13	,, ,,	—	1932–38	F	A. M. Bidder	A. M. Bidder.
	,, ,,	2	Plymouth	Not registered	1947	A	B.M.	W. J. Rees.
	Illex coindeti	3	Banyuls	—	1929	F	A. M. Bidder	A. M. Bidder.
	,, ,,	5	Gibraltar	—	1954 and 1959	F	" Discovery "	Author.
	,, ,,	6	NE. Atlantic	—	1955 and 1959	F	,,	,,
	Illex illecebrosus	9	NW. Atlantic	—	1959 and 1960	F	,,	,,
	Ommastrephes sloanei	3	N. Pacific	—	1952	F	,,	,,
	Hyaloteuthis pelagica	4	Ascension Is.	—	1958	F	B. Stonehouse	,,
	Symplectoteuthis oualaniensis	1	—	1947.7.8.25	1925	A	B.M.	G. C. Robson.
Onychoteuthidae	*Onychoteuthis banksi*	15	W. Coast of Canada	—	1957	F	" Discovery "	Author.
	,, ,,	1	NE. Atlantic	—	1959	F	,,	,,
	Ancistroteuthis lichtensteinei	1	,, ,,	—	1959	F	,,	,,
	Moroteuthis ? ingens	1	—	Not registered (No. 1636)	—	F	B.M.	,,
	Moroteuthis sp.	4	Antarctic	—	1958–59	F	" Discovery "	,,
	Moroteuthis (heads only)	4	,,	—	1959–60	F	,,	,,
	? *Moroteuthis* (head only)	1	Madeira	—	1959	F	,,	,,
Histioteuthidae	*Histioteuthis bonelliana*	8	,,	—	1959	F	,,	,,
	,, ,,	1	,,	—	1956	F	,,	,,
	Calliteuthis sp.	1	,,	—	1959	F	,,	,,
	Calliteuthis reversa	3	NE. Atlantic	—	1958 and 1959	F	,,	,,
	Calliteuthis dōfleini (after Sasaki, 1929)	11	W. Canada	—	1957 ?	F	,,	,,

Family	Genus and species	Number of speci-mens	Region	B.M. Registration No.	Date of collection	Preserva-tive	Source of material	Identified
Architeuthidae	*Architeuthis* sp.	1	Madeira	—	1959	F	Discovery	Author
	,, ,,	1	Azores	—	1955	A	,,	W. J. Rees.*
	A. clarkei	1	Newfoundland	—	1933	A	B.M.	G. C. Robson.
Enoploteuthidae	*Abraliopsis morisi*	1	Off Portugal	—	1959	F	"Discovery"	Author.
	Enoploteuthis leptura	2	NE. Atlantic	—	1961	F	,,	,,
	Pyroteuthis margaritifera	1	Off Morocco	—	1959	F	,,	,,
Octopodoteuthidae	*Octopodoteuthis* sp.	2	13° 25′ N, 18° 22′ W.	—	1925	A	,,	,,
	Cucioteuthis unguiculata	1	Madeira	—	1959	F	,,	,,
Thysanoteuthidae	*Thysanoteuthis rhombus*	1	,,	—	1959	F	,,	,,
	,, ,,	1	NE. Atlantic	—	1958	F	,,	,,
	,, ,,	1	S. of Sagami	1938.9.11.1	?	A	B.M.	,,
Gonatidae	*Gonatus antarcticus*	4	Antarctic	—	1955–56 and 1959	F	"Discovery"	,,
	,, ,,	1	48° 26′ S, 22° 10′ W.	—	1930	A	,,	,,
	Gonatopsis borealis	1	N. Pacific	—	1959	F	,,	,,
Chiroteuthidae	*Chiroteuthis imperator*	1	NE. Atlantic	—	1959	F	,,	,,
	Mastigoteuthis magna or *flammea*	1	,, ,,	—	1959	F	,,	,,
	M. magna	1	,, ,,	—	1959	F	,,	,,
	Lepidoteuthis grimaldi	2	Madeira	—	1959	F	,,	,,
Cranchiidae	*Euzygaena* sp.	1	NE. Atlantic	—	1959	F	,,	,,
	Helicocranchia sp.	1	,, ,,	—	1959	F	,,	,,
	Phasmatopsis cymoctypus†	1	,, ,,	—	1959	F	,,	,,
	Taonius megalops†	1	West coast of Canada (new to region)	—	1956	F	,,	,,
	Mesonychoteuthis hamiltoni	1	Antarctic	—	1959–60	F	,,	A. M. Bidder
Loliginidae	*Loligo forbesi*	9	Plymouth	—	1960	F	,,	Author.
	,, ,,	1	Cornish Coast	1922.11.28.1	—	A	B.M.	?
	,, ,,	1	Azores	1953.4.22.1	1952	A	,,	W. J. Rees.
	,, ,,	1	Hebrides	1937.9.3.1	—	A	,,	Author
	Loligo vulgaris	1	NW. Scotland	1912.11.26.1	?	A	,,	,,
	,, ,,	1	Milford Haven	1915.11.24.1	—	A	,,	,,
	,, ,,	7	52° 48′ N., 3° 14′ E.	—	1960	A	Platessa B.M.	,,
	,, ,,	2	Falmouth	98.5.21.273	—	A	,,	,,
	Loligo sp	1	NE Atlantic	—	1955	F	"Discovery"	,,
	,, ,,	2	Gibraltar	—	1959	F	,,	,,
	,, ,,	1	Madeira	—	1959	F	,,	,,
	Sepioteuthis sp.	1	?	—	—	A	B.M.	,,

TABLE I—(*contd.*)

Family	Genus and species	Number of Specimens	Region	B.M. Registration No.	Date of collection	Preservative	Source of material	Identified
	Speioteuthis lessoniana	1	Cocos-Keeling Is.	B.M. Ref. No. 1623	1941	A	B.M.	W. J. Rees.
	,, ,,	1	Senafir	—	1949	F	,,	,,
Sepiolidae	*Rossia macrosoma*	1	Scarborough	1933.6.15.1	—	A	,,	,,
	,, ,,	1	Norway	98.5.21.375	1882	A	,,	,,
	,, ,,	1	,,	1925.10.13.17	—	A	,,	,,
	,, ,,	1	N. Wales	1915.12.1.1	—	A	,,	,,
	,, ,,	1	Scarborough	—	1928	A	,,	,,
Sepiidae	*Sepia officinalis hierreda*	2	Gambia river estuary	1947.10.14.1–2	1947	A	,,	W. Adam.
	Sepia officinalis	1	Southampton water	1908.12.22.21	? 1908	A	,,	W. J. Rees
	,, ,,	1	Corunna	95.8.1.1–2	? 1895	A	,,	W. Adam.
	,, ,,	1	Lanzarote	60.5.4.4	?	A	,,	,,
	,, ,,	3	St. 52	B.M. Ref. No. 1650	1948	A	"Manihine" Coll.	Author
	,, ,,	2	—	B.M. Ref. No. 1638	1948	A	B.M.	?
	,, ,,	1	Dale roads	Acc. No. 2029	1960	A	,,	?
	,, ,,	2	—	—	1960	A	Platessa	Author
	Sepia latimanus	1	Singapore	1947.5.16.1	? 1947	A	B.M.	W. Adam.
Octopodidae	*Octopus vulgaris*	1	Bermudas	72.9.2.5	?	A	,,	G. E. Pickford.
	,, ,,	2	—	65.5.23.1	—	A	,,	?
	,, ,,	1	Brighton	Cat. 1927 No. 18	1901	A	,,	?
	,, ,,	1	Madeira	—	? 1936	A	,,	?
	Octopus ? indicus	1	Selangor	1928.4.1.1	—	A	,,	?
	Octopus vulgaris	1	Pt. Isabel, Texas	1948.6.21.6	—	A	,,	G. E. Pickford.
	Octopus macropus	1	Villefranche	1952.4.1.43	—	A	,,	W. J. Rees
	Octopus arcticus	2	60° 3′ N., 5° 51′ W.	89.4.24.35–6	—	A	,,	?
	Eledone cirrhosa	1	Sound of Sanda	88.3.25.35	1888	A	,,	G. C. Robson.
	,, ,,	1	?	79.1.20.8	—	A	,,	,,
	,, ,,	1	Denbigh	1931.6.29.1	? 1931	A	,,	?
	,, ,,	2	Plymouth	1929.11.13.1–2	? 1925	A	,,	?
	,, ,,	1	SW. Ireland	1951.10.1.3	1951	F	,,	?
	Pareledone charcoti	1	S. Georgia	1951.4.26.13	1926	A	,,	G. C. Robson.
Argonautidae	*Argonauta hians*	1	—	68.6.8.52	—	A	,,	?
	Argonauta argo	2	—	64.2	—	A	,,	?

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* This was described by R. Clarke (1955) and he weighed it fresh and preserved the beak which I have been able to study.

† A paper is being published discussing the validity of these names.

lopods, which vary greatly in weight. When weighing small cephalopods (up to 200 g.) I used a letter scales which was accurate to ± 0·5 g. Larger cephalopods (from 200 to 7,000 g.) were weighed on kitchen scales which were accurate to 30 g. The largest cephalopods were weighed on a heavy duty scale (Standard Avery accurate to 100 g.). Before weighing, the mantle cavity was allowed to drain and the outside of the animal was wiped over with a cloth to remove excess preservative.

A list of specimens used in this investigation is given in Table I. To avoid undue taxonomic discussion, I have not provided trivial names for some specimens listed. Some rare families, considered here are only represented by very few individuals (e.g., Architeuthidae and Thysanoteuthidae).

A key has been given to aid preliminary sorting and all criteria for identification is included under each family heading.

III. GENERAL DESCRIPTION OF BEAKS

Beaks are usually described as either " upper " or " lower " with respect to the upper (morphological anterior) and the lower sides of the head. Here both upper and lower beaks will be orientated in the same way in order to aid comparison ; i.e., the " outer " side of both the beaks is that side which lies at the top of Text-fig. 1 and the " anterior " end lies to the left of these figures. Surfaces of the beak facing the sagittal plane have been termed " medial " and those facing away from it, " lateral ".

Both beaks have many features in common and for clarity the same basic nomenclature will be used. Table V gives the nomenclature used by Verrill, Steenstrup and Naef, compares it with that used here, and gives reasons for any changes made.

1. *The Upper Beak*

This has an anteriorly-directed, hardened extension which I have called the rostrum (Text-fig. 1). It is pointed (except when worn down), hardened, and usually curved downwards at the tip. Transverse sections (at right angles to its anterior-posterior plane) show that the inner surface is flat or slightly concave and the sides and outer surface, together approximate to a semi-circle. To avoid the previous term " cutting edge " I have used the terms inner side of the rostrum and inner edges of the rostrum in both beaks.

The outer side of the rostrum expands towards the posterior end of the beak, separates from, and extends beyond, the inner edges of the rostrum. The term " hood " has been used to describe the whole structure from the tip of the rostrum to the posterior end.

The inner side of the rostrum also expands towards the posterior end of the beak. At the jaw angle it joins a broad sheet which is folded so that the lateral edges almost touch one another on the beak's inner side and for convenience when dealing with surface modification of the lower beak I have treated the left and right sides as separate entities (left and right " lateral walls " joined in the sagittal plane at the " crest ").

There is a " wing " at each side of the hood. The wing's outer border is attached to the hood and its anterior border is attached to some cartilage which covers the front edge of the lateral wall. This cartilaginous layer is often very thin and is sometimes absent near the jaw angle resulting in fusion of the wing with the lateral wall. From the jaw angle to the inner end of the cartilage has been called the " shoulder " in the following description. This region is constantly worn during growth and probably functions as a cutting edge.

2. *The Lower Beak*

This has essentially the same components as the upper-beak but their relative size is different. The inner edges of the rostrum extend inwards so that the inside of the rostrum is very deeply concave. The lower rostrum, therefore, is much broader at the base, when viewed from the side, than the upper rostrum (Text-fig. 1). The hood is relatively shorter from front to back than it is in the upper beak and it often has a median concavity in its posterior border.

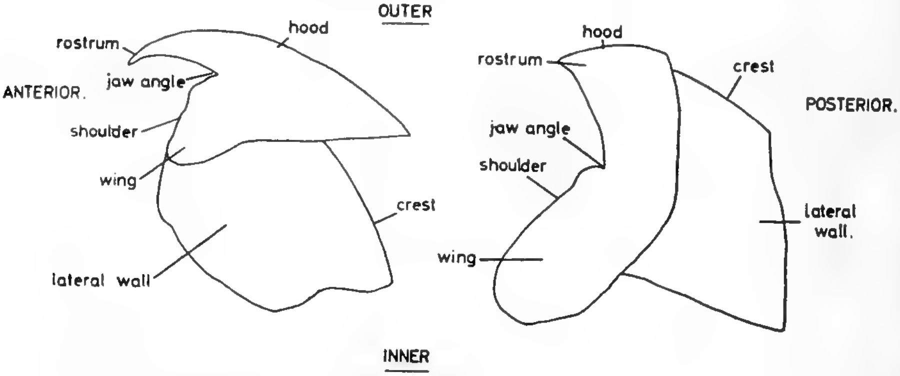

FIG. 1. A summary of the terms used in this paper, to describe the parts of both beaks. For a full description of the various parts consult the text.
Left: upper beak; right: lower beak

The lateral walls are nearly flat and meet one another at a clearly defined crest. From the side they resemble a rough parallelogram or sometimes a triangle as opposed to the semicircular shape of the walls of the upper beak.

The wings of the lower beak are far more developed than in the upper beak and extend beyond the free edges of the lateral walls. A small extension of the lateral wall lies medial to the wing and is often separated from the rest of the lateral wall by a ridge or transparent strip; I have called it the " medial side of the wing " because it is often useful to distinguish it from the rest of the lateral wall.

IV. DEVELOPMENT OF THE CEPHALOPOD BEAK

Progressive darkening of the beak has proved useful for identification in a few families which are well represented in this collection.

Some idea of change in proportions during increase in beak size can be obtained if several dimensions are plotted against one another. If plotted on an arithmetic scale the points sometimes fall on a straight line. This is illustrated when the dorsal mantle lengths of squids are plotted against the rostral lengths of the beaks (Text-

TABLE II.—*Table of Comparison of the Beak Dimensions*

The general equation has the form $y = mx + c$ and is fitted to the logarithmic values of the original data. Dimensions compared are 1 = rostral length; 2 = hood length; 3 = crest length; 4 = wing length; 5 = rostral width (see Text-figs. 2 and 3 for explanation).

	Dimensions								
Beak	x	y	Family	Genus	Species	No. of specimens	m	c	Standard Deviation
Lower	1	2	Ommastrephidae	..	..	94	0·94	−0·02	0·038
				Sthenoteuthis	*caroli*	24	0·91	0	0·033
				Todarodes	*sagittatus*	25	0·95	−0·03	0·023
			Cranchiidae	..	..	5	0·86	−0·18	0·050
			Chiroteuthidae	..	..	4	0·83	−0·22	0·052
			Gonatidae	..	..	2	0·76	−0·17	..
			Thysanoteuthidae	..	..	3	0·64	0·07	0·015
			Architeuthidae	..	..	3	1·34	0·13	0·018
			Octopodoteuthidae	..	..	3	1·02	−0·22	0·006
			Onychoteuthidae	..	..	25	0·99	−0·06	0·052
			Histioteuthidae	..	..	24	0·79	−0·14	0·043
			Sepiolidae	..	..	5	0·88	0·05	0·058
			Sepiidae	..	..	7	0·98	0·05	0·073
			Loliginidae	..	..	30	1·03	0·18	0·052
			Octopodidae	..	..	22	1·09	0·11	0·070
	1	4	Ommastrephidae	..	..	93	0·96	0·23	0·038
				Sthenoteuthis	*caroli*	24	1·03	0·24	0·022
				Todarodes	*sagittatus*	25	0·97	0·21	0·026
			Cranchiidae	..	..	4	0·93	0·19	0·016
			Chiroteuthidae	..	..	4	0·83	0·03	0·061
			Gonatidae	..	..	2	0·92	0·13	..
			Thysanoteuthidae	..	..	2	0·92	0·43	..
			Architeuthidae	..	..	3	1·11	0·41	0·036
			Octopodoteuthidae	..	..	3	1·19	0·15	0·015
			Onychoteuthidae	..	..	25	1·09	0·28	0·052
			Histioteuthidae	..	..	24	0·91	0·19	0·043
			Sepiolidae	..	..	5	1·10	0·45	0·033
			Sepiidae	..	..	8	1·04	0·38	0·036
			Loliginidae	..	..	30	1·06	0·48	0·054
			Octopodidae	..	..	19	1·02	0·32	0·082

TABLE II.—*Table of Comparison of the Beak Dimensions* (contd.)

	Dimensions					No. of specimens			Standard Deviation
Beak	x	y	Family	Genus	Species		m	c	
	3	2	Ommastrephidae	..	..	93	0·95	−0·25	0·030
				Sthenoteuthis	*caroli*	24	0·93	−0·25	0·028
				Todarodes	*sagittatus*	25	0·94	−0·24	0·028
			Cranchiidae	..	..	5	0·87	−0·36	0·057
			Chiroteuthidae	..	..	4	0·94	−0·31	0·058
			Gonatidae	..	..	2	0·98	−0·34	..
			Thysanoteuthidae	..	..	2	0·74	−0·26	..
			Architeuthidae	..	..	3	1·18	−0·39	0·016
			Octopodoteuthidae	..	..	3	0·89	−0·32	0·024
			Onychoteuthidae	..	..	25	0·85	−0·33	0·037
			Histioteuthidae	..	..	24	0·81	−0·32	0·036
			Sepiolidae	..	..	5	0·86	−0·35	0·029
			Sepiidae	..	..	10	1·07	−0·35	0·026
			Loliginidae	..	..	29	0·94	−0·36	0·040
			Octopodidae	..	..	26	0·96	−0·35	0·046
			Argonautidae	..	..	3	1·31	−0·27	0·003
Upper	1	2	Ommastrephidae	..	..	94	0·97	0·48	0·035
				Sthenoteuthis	*caroli*	24	0·89	0·50	0·024
				Todarodes	*sagittatus*	25	1·00	0·47	0·025
			Cranchiidae	..	..	5	1·10	0·46	0·037
			Chiroteuthidae	..	..	5	0·89	0·35	0·023
			Gonatidae	..	..	2	0·92	0·46	..
			Thysanoteuthidae	..	..	2	0·88	0·58	..
			Architeuthidae	..	..	2	1·15	0·58	..
			Octopodoteuthidae	..	..	3	1·17	0·42	0·018
			Onychoteuthidae	..	..	25	0·99	0·51	0·034
			Histioteuthidae	..	..	24	1·05	0·51	0·048
			Sepiolidae	..	..	5	0·94	0·57	0·037
			Sepiidae	..	..	10	0·99	0·60	0·032
			Loliginidae	..	..	28	1·00	0·62	0·035
			Octopodidae	..	..	12	0·67	0·23	0·051
	1	4	Ommastrephidae	..	..	94	1·00	−0·10	0·047
				Sthenoteuthis	*caroli*	24	0·98	−0·07	0·026
				Todarodes	*sagittatus*	24	1·01	−0·14	0·028
			Cranchiidae	..	..	4	1·10	−0·13	0·019
			Chiroteuthidae	..	..	5	0·91	−0·18	0·066
			Gonatidae	..	..	2	1·09	−0·06	..
			Thysanoteuthidae	..	..	2	1·00	0·16	..
			Architeuthidae	..	..	2	1·12	0·05	..
			Octopodoteuthidae	..	..	3	1·22	−0·17	0·002
			Onychoteuthidae	..	..	25	0·93	0·02	0·065
			Histioteuthidae	..	..	24	1·24	0·03	0·084
			Sepiolidae	..	..	5	1·06	0·18	0·056
			Sepiidae	..	..	11	1·28	0·22	0·045
			Loliginidae	..	..	29	1·11	0·19	0·051
			Octopodidae	..	..	12	0·91	0·15	0·068

TABLE II.—*Table of Comparison of the Beak Dimensions* (contd.)

	Dimensions								
Beak	x	y	Family	Genus	Species	No. of specimens	m	c	Standard Deviation
Upper	1	5	Ommastrephidae	..	..	95	0·92	—0·10	0·046
				Sthenoteuthis	*caroli*	25	0·84	—0·07	0·034
				Todarodes	*sagittatus*	25	0·94	—0·13	0·016
			Cranchiidae	..	..	5	0·92	—0·19	0·085
			Chiroteuthidae	..	..	5	0·87	—0·23	0·016
			Gonatidae	..	..	2	0·97	—0·15	..
			Thysanoteuthidae	..	..	2	1·01	0·01	..
			Architeuthidae	..	..	2	0·96	—0·07	..
			Octopodoteuthidae	..	..	3	1·16	—0·18	0·015
			Onychoteuthidae	..	..	25	0·87	—0·16	0·038
			Histioteuthidae	..	..	24	1·15	—0·04	0·051
			Sepiolidae	..	..	5	0·95	—0·05	0·037
			Sepiidae	..	..	11	0·88	—0·06	0·024
			Loliginidae	..	..	30	0·91	—0·03	0·037
			Octopodidae	..	..	12	1·03	0·14	0·055
	3	2	Ommastrephidae	..	..	92	1·04	—0·11	0·020
				Sthenoteuthis	*caroli*	24	0·98	—0·07	0·017
				Todarodes	*sagittatus*	25	1·02	—0·11	0·011
			Cranchiidae	..	..	5	1·03	—0·11	0·046
			Chiroteuthidae	..	..	5	0·99	—0·16	0·030
			Gonatidae	..	..	2	1·04	—0·11	..
			Thysanoteuthidae	..	..	2	0·99	—0·12	..
			Architeuthidae	..	..	2	0·98	—0·13	..
			Octopodoteuthidae	..	..	3	0·99	—0·11	0·005
			Onychoteuthidae	..	..	25	1·04	—0·15	0·022
			Histioteuthidae	..	..	24	0·98	—0·11	0·020
			Sepiolidae	..	..	5	0·98	—0·19	0·014
			Sepiidae	..	..	10	1·03	—0·12	0·017
			Loliginidae	..	..	25	1·00	—0·13	0·021
			Octopodidae	..	..	29	0·78	—0·38	0·048
			Argonautidae	..	..	2	1·27	—0·25	..

fig. 11). On the other hand, when weights of squids are plotted against rostral lengths the points do not fall on a straight line (Text-fig. 12).

However, as I have shown below, if any of the dimensions being compared are plotted on double logarithmic paper, the points tend to lie on straight lines and this method has been adopted for all comparisons made here. The formula for these mean lines is $\log y = m \log x + \log c$. Values for m and c, number of specimens measured and the standard deviations are given in Table II. The reliability of the mean values m and c depends upon the number of specimens available but in view of the conformity to the straight line relationship found in all the better represented families I think it is reasonable to assume that similar rules also govern the growth of beaks in poorly represented families. The standard deviations indicate the spread of points about the regression and the relative reliability of judgements based upon measurements of beaks of the different families. The m and c values and the standard deviations were calculated by a "Mercury" electronic computer. By judicious use of the parameters *m* and *c* and the standard deviations ($\pm 1\cdot96$ standard deviations include 95% of the measurements) it should be possible for some beaks to be tentatively grouped in families but this method should only be adopted when other methods fail. However, the method is of use in identifying beaks of families in which the *m* or *c* values differ markedly from the values of other families (e.g. Thysanoteuthidae and Architeuthidae can be distinguished from other families, Text-figs. 9 and 10). Little importance should be attached to the actual values of *m* and *c* when such a small number of specimens are being compared.

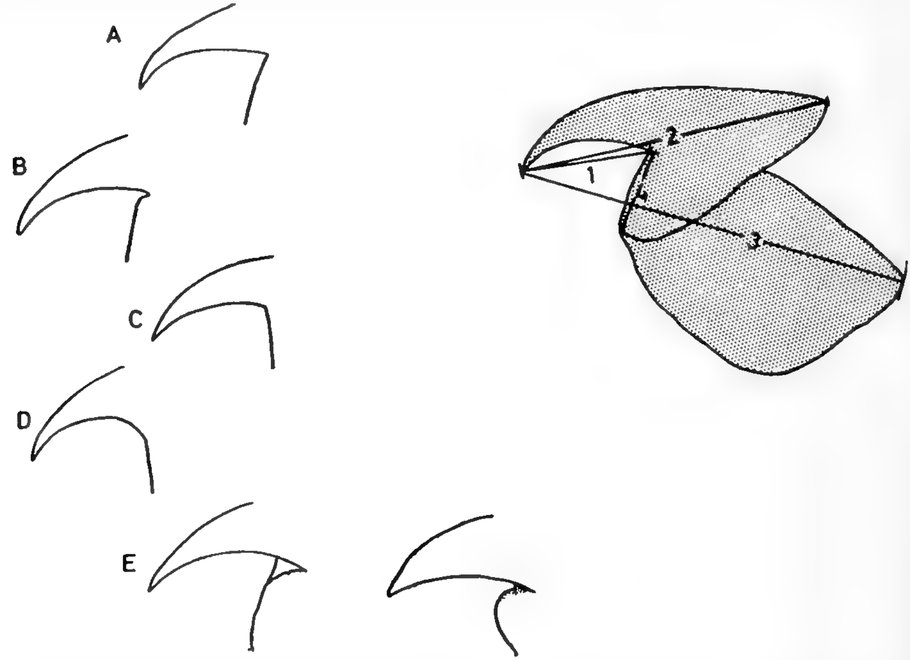

FIG. 2. Diagram to illustrate some of the variations in the jaw angle of the upper beak and to show the dimensions compared in this paper. A = acute angle; B = recessed; C = obtuse; D = curved; E = two types of false angle—left, the broken edge of wing forms the posterior border of the false angle and right, the shoulder is "rounded into" the angle to form a small false angle. 1 = length of rostrum (measured to corner of false angle if present); 2 = hood length; 3 = crest length; 4 = wing length; 5 = width of rostrum at the angle (not illustrated).

Text-figs. 2 and 3 show positions at which measurements were made on upper and lower beaks.

The points and calculated regressions were plotted on a double logarithmic scale for every relationship for which a regression was calculated (i.e., 140 regressions) and

I was satisfied that they could all be regarded as having a simple allometric relationship. Figures of these plots are given for two ommastrephid species (Text-figs. 4–7) and for the sparsely represented families (Text-figs. 9 and 10).

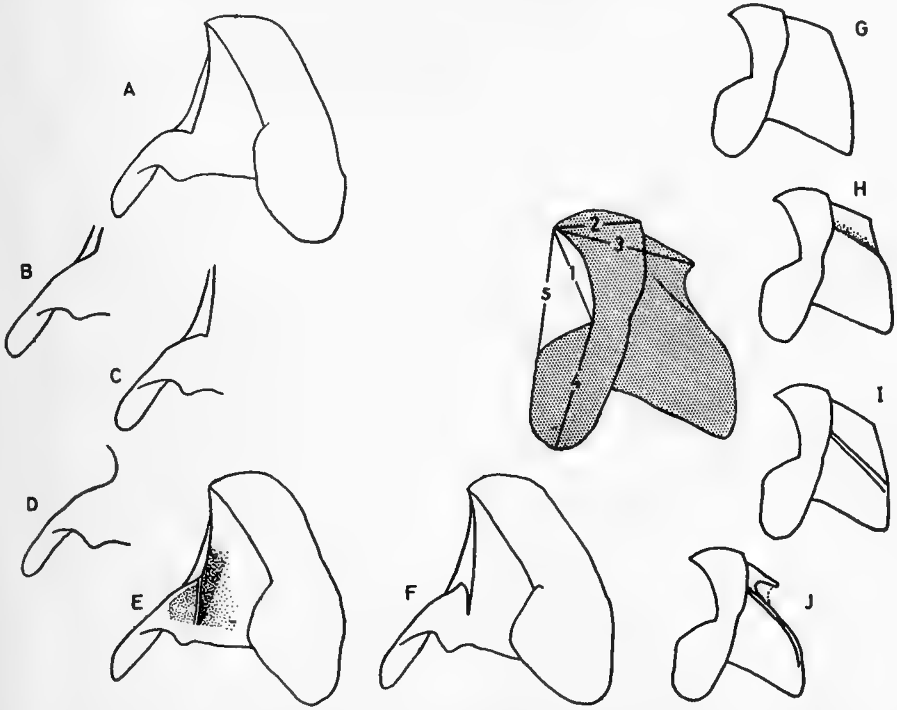

Fig. 3. Diagram to illustrate some of the variations in the lower beak and to show the dimensions compared in this paper. A = acute angle; B = obtuse angle; C = recessed angle; D = curved; E = light area between darkened areas at inside of wing and the anterior part of the lateral wall; F = " step " found below the jaw angle (as seen in the Onychoteuthidae); G = no ridge on lateral wall; H = fold or weak ridge of lateral wall; I = clear ridge running to a position half-way between the crest and the inner corner of the lateral wall; J = clear ridge and reduction of dark area outside the ridge. 1 = length of rostrum (measured to where shoulder is inserted against rostrum in the Onychoteuthidae); 2 = hood length; 3 = crest length; 4 = wing length; 5 = rostral gap.

DECAPODA

OEGOPSIDA

1. Ommastrephidae

This family is well represented in the " Discovery " collections. Figures showing changes of beak dimensions in *Todarodes sagittatus* (Text-figs. 4 and 5) and *Sthenoteu-*

this caroli (Text-figs. 6 and 7) indicate that the relationship between the selected dimensions is allometric. The difference between the dimensions of the two species is only very slight except for the width of the upper rostrum when compared with its length (Table II). This difference could be used to distinguish between the species if only one was present in a population but, if both were present, individual beaks could not be assigned to one or other species.

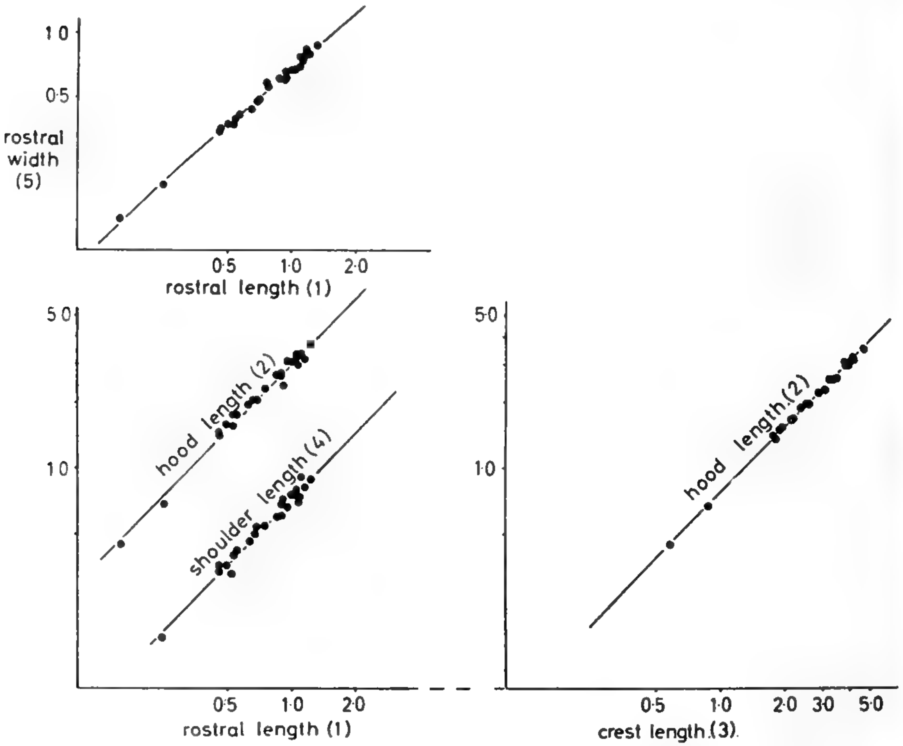

FIG. 4. *Todarodes sagittatus.* The relationships between various dimensions of the upper beak plotted on double logarithmic scales. The numbers in brackets are given to the named dimensions throughout the paper. The meaning of these may be seen from Figs. 1 and 2. The lines have been calculated using the formula $\log y = m \log x + \log c$.

Very similar allometric relationships are found when all the other members of the family are examined. Calculated regressions for all the ommastrephids in the present collection (considered together and including *T. sagittatus* and *S. caroli*) are given in Table II and a general formula for each allometric relationship can be given to include the several species within the family. The young beaks of *Sthenoteuthis* *caroli* have dark brown or black rostra with transparent edges to the lateral walls and transparent wings (Pl. 13). The largest beaks (A and G) are dark brown all over except for a narrow transparent region near the growing edges. Between these two extremes, the dark region shows various degrees of extension over the beak; this is irregular and an isolated patch darkens on the wings (in the lower beak) or lateral walls (in the upper beak) prior to becoming linked with the main darkened area (Pl. 13). This intermediate stage, when isolated areas appear and join with the main dark areas, is accompanied by only a small increase of rostral length. Therefore, the intermediate stage is either of short duration or a period of slow growth. Similar stages are found in all the ommastrephid species which are represented by a good size range in the collection available. Text-fig. 8 shows rostral lengths at which the intermediate darkening stage was found in species of the family.

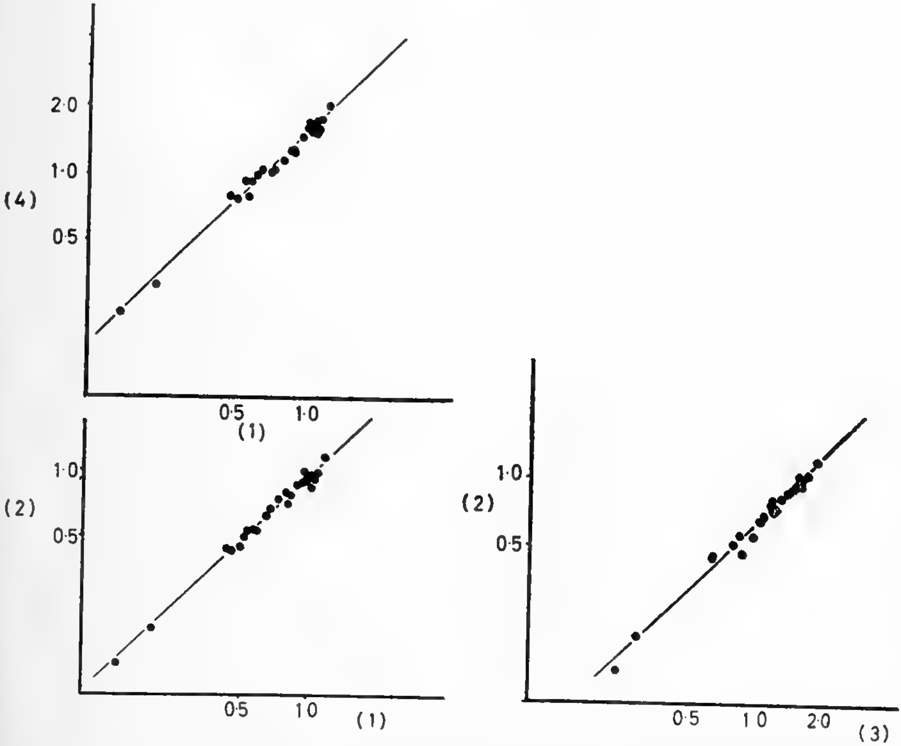

Fig. 5. *Todarodes sagittatus.* The relationships between various dimensions of the lower beak plotted on double logarithmic scales. 1 = rostral length; 2 = hood length; 3 = crest length; 4 = wing length. The lines have been calculated using the formula $\log y = m \log x + \log c$.

A beak can often be identified by comparing this rostral length with the stage of darkening. Thus, for example, it would be possible to distinguish between many specimens of *Illex coindeti* and many specimens of *Sthenoteuthis caroli* on the basis of the darkening process (Text-fig. 8). Identifications of this nature can only be used for a proportion of the squids in a family but, by combining the method with a knowledge of geographical distribution, identification is facilitated because any one region is inhabited by few species of the family.

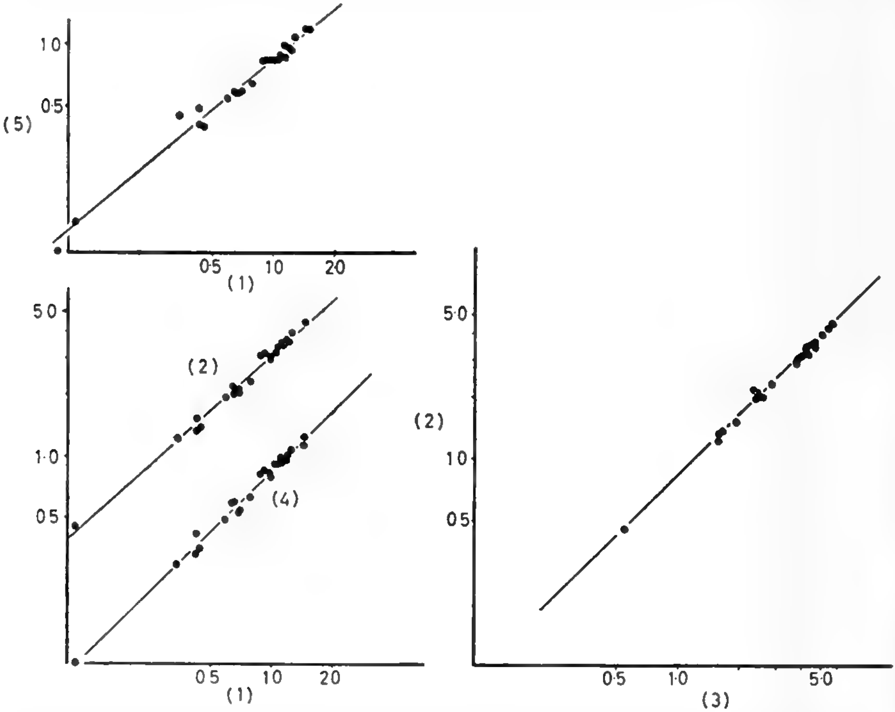

FIG. 6. *Sthenoteuthis caroli.* The relationships between various dimensions of the upper beak plotted on double logarithmic scales. The numbers in brackets are given to the named dimensions throughout this paper. The meaning of these may be seen from Figs. 1 and 2. The lines have been calculated using the formula $\log y = m \log x + \log c$. 1 = rostral length; 2 = hood length; 3 = crest length; 4 = wing length; 5 = rostral width.

The size at which darkening takes place differs in the two sexes of species adequately represented in the collection, and the onset of maturity (dotted line in Text-fig. 8) nearly coincides with the intermediate stage of the beak. This suggests a relationship between darkening and sexual development. Specimens usually referred to *Todarodes sagittatus* fall into two groups in respect of the darkening process and they are treated separately in Text-fig. 8.

The problems involved in distinguishing *Sthenoteuthis pteropus* from *Sthenoteuthis caroli* are complex and, for the present, I have called the specimens caught in Madeira *S. pteropus* and those caught elsewhere in the North Atlantic *S. caroli* (these are also caught at Madeira but specimens from this region were not considered here). These two groups differ in several respects[1] and the names applied here may have to be revised after further work. One of the differences between the species is in the size of the beak at the intermediate stage of darkening (Text-fig. 8).

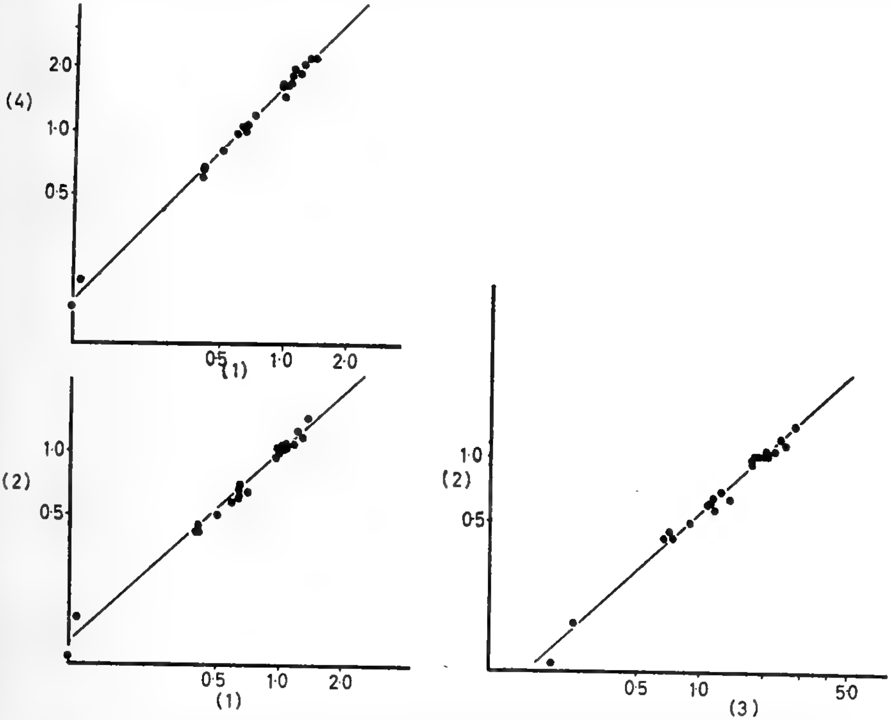

FIG. 7. *Sthenoteuthis caroli.* The relationships between various dimensions of the lower beak plotted on double logarithmic scales. 1 = rostral length; 2 = hood length; 3 = crest length; 4 = wing length. The lines have been calculated using the formula $\log y = m \log x + \log c$.

2. ONYCHOTEUTHIDAE

Species of the family represented in the collection are *Ancistroteuthis lichtensteinei*, *Moroteuthis* sp. and *Onychoteuthis banksi*. In one specimen of *Moroteuthis* (weight 357 g. and lower rostral length 0·5–1·0 cm.) the wings of the lower beak were not

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[1] A separate paper is in preparation.

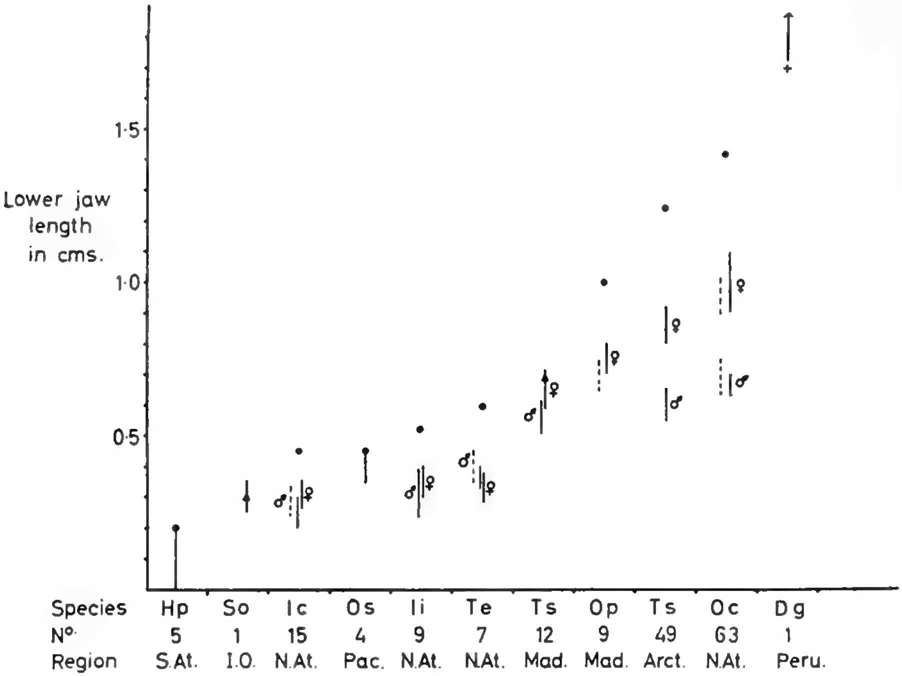

Fig. 8. The species of the Ommastrephidae arranged in order (from left to right) of increasing lower rostral length of the largest specimen in the available collections.

● = the largest specimen (in the final stage of darkening).
▲ = the largest specimen (in the stage when the extension of darkening takes place).
+ = the largest specimen (before the dark area has extended).
——— = approximate lower rostral length at which the darkened area extends.
- - - - - = approximate lower rostral length at which the males (♂♂) and females (♀♀) become sexually mature (spermatophores present or enlarged nidamental glands).

The species are *Hyaloteuthis pelagicus* (Hp) ; *Symplectoteuthis oualaniensis* (S. o.) ; *Illex coindeti* (I. c) ; *Ommastrephes sloanei* (O. s) ; *Illex illecebrosus* (Ii); *Todaropsis eblanae* (Te) : *Todarodes sagittatus* (T. s) ; *Sthenoteuthis pteropus* (O. p) ; *Sthenoteuthis caroli* (O. c) ; and *Dosidicus gigas* (D. g).

The number of specimens examined in each species is given below the species symbols. The regions from which the specimens came are also noted for each species and are : the South Atlantic (S. At) ; Indian Ocean (I.O) ; North Atlantic (N.At) ; Madeira (Mad) ; Arctic ocean (Arct) ; and the Peru current (Peru).

darkened, but they were partly in all other specimens of the family. Unlike the ommastrephids, stages of a progressive spread of darkening from the jaw angle over the wing are found and there is no club-shaped stage (cf. Pls. 13 and 14). Therefore, in this family there is probably no isolated patch stage during the lower beak development. All upper beaks examined have completely darkened lateral walls but in the smallest *Moroteuthis* darkening is rather faint.

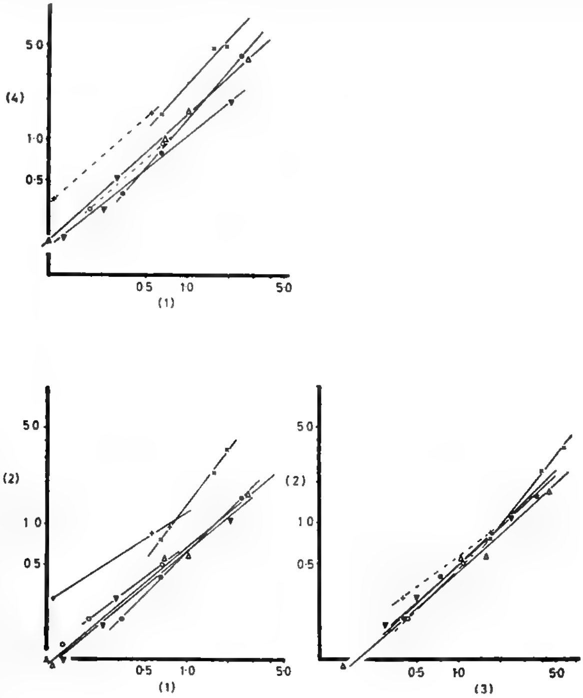

FIG. 9. The sparsely represented families. The relationships between various dimensions of the lower beak plotted on double logarithmic scales. 1 = rostral length; 2 = hood length; 3 — crest length; 4 = wing length. The lines have been calculated using the formula $\log y = m \log x + \log c$.

Key: + Thysanoteuthidae.
× Architeuthidae.
○ Gonatidae.
● Octopodoteuthidae.
▼ Chiroteuthidae.
△ Cranchiidae.

3. HISTIOTEUTHIDAE

Representatives of this family examined were *Histioteuthis bonelliana*, *Calliteuthis reversa* and *Calliteuthis döfleini*. A good size range of each species was included.

The wings of the smallest lower beaks are not darkened, and no stage has been found in which isolated dark patches are present on the wings. However, medium-sized beaks of both *Calliteuthis döfleini* and *Histioteuthis bonelliana* have club-shaped patches and the larger beaks form a series where the darkening spreads from the posterior edge of the wing to the anterior edge (Pl. 15). This suggests that isolated dark patches are found on the wings at some stage. Darkening finally extends entirely over the wing until it reaches the outer side of the cartilage on the shoulder. The dark region of the wing then extends towards the jaw angle thus encroaching on the exposed shoulder cartilage which decreases until it may disappear

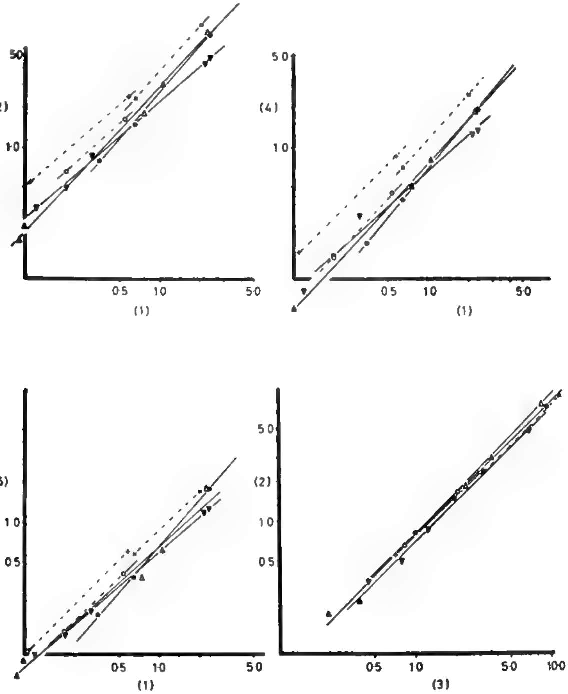

Fig. 10. The sparsely represented families. The relationships between various dimensions of the upper beak plotted on double logarithmic scales. 1 = rostral length; 2 = hood length; 3 = crest length; 4 = wing length; 5 = rostral width. The lines have been calculated using the formula $\log y = m \log x + \log c$.

Key: + Thysanoteuthidae.
× Architeuthidae.
○ Gonatidae.
● Octopodoteuthidae.
▼ Chiroteuthidae.
△ Cranchiidae.

altogether. As in the Ommastrephidae the various stages of darkening take place at different rostral lengths in the different species and genera.

Upper beaks are dark on the outer half of the lateral walls in the smallest specimens examined. The darkening extends progressively towards the anterior edge of the lateral walls with its " leading edge " in a straight line. As all the stages of the forward spread of the dark area are present it is unlikely that these beaks pass through an isolated patch stage.

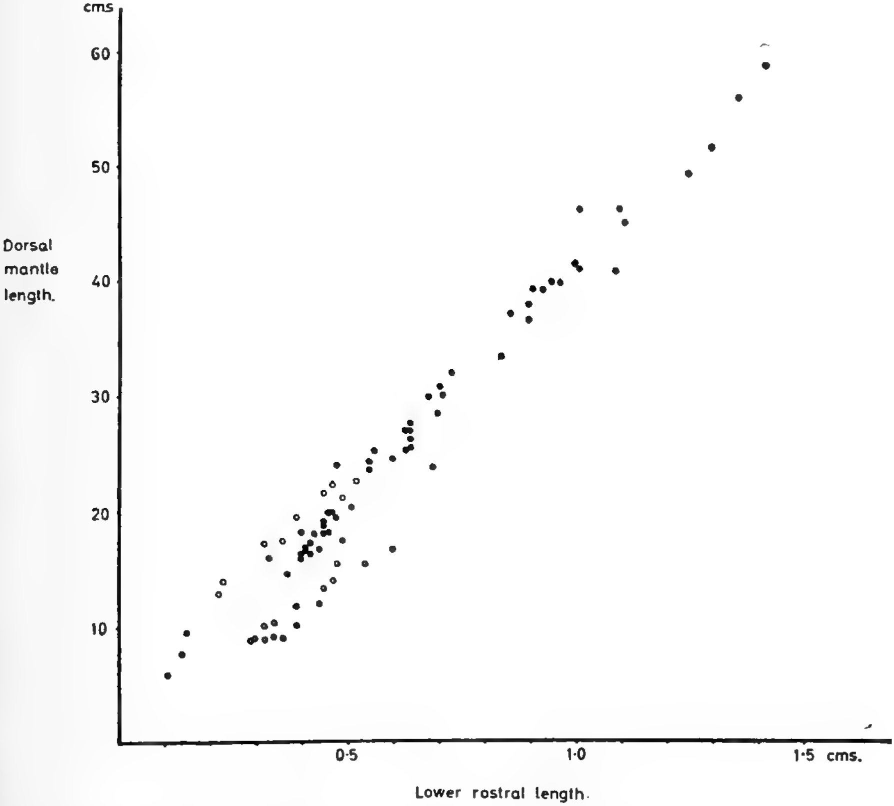

Fig. 11. The relationship between the dorsal mantle lengths and the lower rostral lengths in three species of the Ommastrephidae. ○ = *Illex illecebrosus* ; ● = *Sthenoteuthis caroli* ; ◑ = *Todaropsis eblanae.*

4. Architeuthidae

The upper beak has transparent lateral walls and a dark crest and the lower beak wings are completely transparent at a lower rostral length of 0·65 cm. The dark crest reaches a maximum width of 0·65 cm. at the posterior end and if viewed from below, a constriction of the dark crest can be seen just behind the jaw angle. Beaks of both the other specimens examined (with lower rostral lengths of 1·94 cm. and 1·56 cm.) were fully darkened.

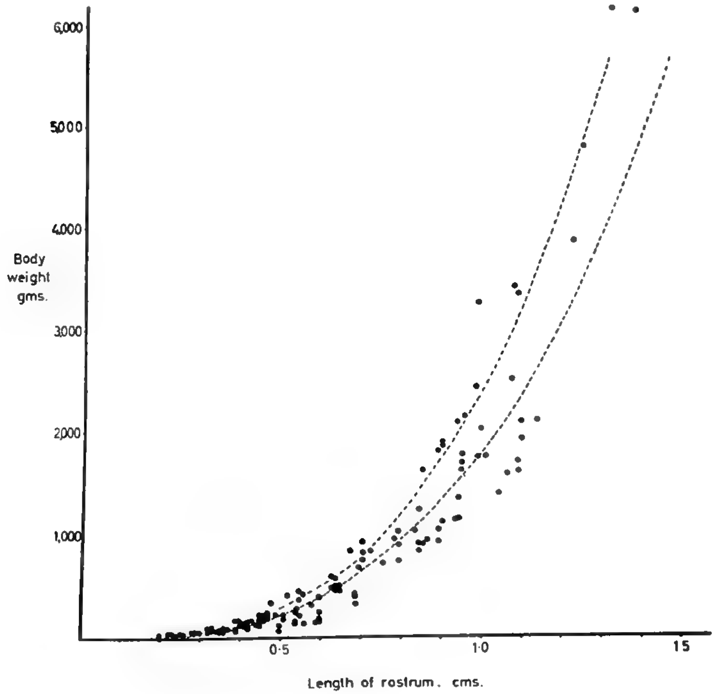

FIG. 12. The relationship between the body weight and the lower rostral length in the Ommastrephidae. Upper broken line is the regression for *Sthenoteuthis caroli*. Lower broken line is the regression for all the ommastrephids taken together. These lines are the arithmetic plots of the straight lines shown in Figs. 13 and 14.

5. ENOPLOTEUTHIDAE

This family is represented by one *Abraliopsis morisi*, one *Pyroteuthis margaritifera* and two *Enoploteuthis leptura* specimens. The *Abraliopsis* and *Pyroteuthis* are both known to mature at a small size and their beaks are fully darkened at a lower rostral length of 0·09 cm. and 0·13 cm. respectively. *Enoploteuthis* reaches a larger size and the smaller beak examined (lower rostral length of 0·2 cm.) has undarkened lower wings and upper lateral walls while the larger beak examined (lower rostral length of 0·34 cm.) is in an advanced stage of darkening.

6. Octopodoteuthidae

Six specimens of *Octopodoteuthis* were examined. Those with a lower rostral length of 0·34, 0·47, 0·18, 0·23 cm. had lower beaks with transparent wings and those with a lower rostral length of 0·65 and 0·47 cm. had lower beaks with club-shaped, dark areas on the wings which suggests that an isolated patch may be present at some stage. Thus, the extension of the dark area appears to take place at a lower rostral length of about 0·47 cm. I have less information concerning the upper beak because only two were removed and the sides of the upper beak cannot be seen *in situ*. When the lower rostral length is 0·34 cm. the lateral walls of the upper beak are transparent but the crest is darkened at a rostral length of 0·65 cm. and the lateral walls are completely darkened. The darkening of both beaks, therefore, takes place at about the same time. In the genus *Cucioteuthis*, beaks are in the final stage of darkening at a lower rostral length of 2·5 cm., but the smaller stages are not known at present.

7. Thysanoteuthidae

Lateral walls of both beaks and the wings of the lower beak of the smallest specimen of *Thysanoteuthis* (lower rostral length of 0·11 cm.) are not darkened. The beaks are extensively darkened in the specimen with a lower rostral length of 0·56 cm. This darkening, however, is incomplete and its form in the lower beak suggests that darkening spreads over the wing from the outer side as if preceded by a straight " leading edge " pivoted at the jaw angle (Pl. 16B). The upper beak has a broad transparent region adjacent to the crest and the posterior border of the lateral walls (Plate 16A).

8. Gonatidae

Beaks from five *Gonatus* and one *Gonatopsis* were examined. The smallest *Gonatus* (lower rostral length of 0·2 cm.) and the *Gonatopsis* (lower rostral length of 0·1 cm.) had undarkened lower wings and upper lateral walls. The other specimens (lower rostral lengths of 0·59, 0·65, 0·65 and 0·67 cm.) had beaks in an advanced stage of darkening. As the undarkened region of the lower hood-wing structure is opposite the jaw angle it seems unlikely that there is ever a club-shaped stage or an isolated patch stage of darkening.

9. Chiroteuthidae

In the *Mastigoteuthis magna* specimen (lower rostral length of 0·13 cm.) the outer half of each lateral wall is darkened and the inner half is transparent. Wings of the lower beak are transparent at this stage. In the large specimen, which is apparently of the same species (lower rostral length of 0·31 cm.) the upper beak has almost completely darkened lateral walls but the lower beak has transparent wings.

Beaks of a specimen of *Chiroteuthis imperator* (lower rostral length of 0·25 cm.) are in the same stage of darkening as those of *Mastigoteuthis magna* with a rostral length of 0·13 cm.

In *Lepidoteuthis grimaldi* beaks are in an advanced stage of darkening. The shoulder cartilages of both the upper and lower beaks are exposed and the posterior part of the lateral wall of the lower beak is not darkened between the rib and the crest (Pl. 18c).

10. CRANCHIIDAE

Beaks of both the two smallest specimens examined (*Euzygaena* sp. and *Helicocranchia* sp.) are at a very early stage of darkening. Only the rostra are darkened in *Euzygaena* (lower rostral length of 0·1 cm.) and only the edge of the rostra in *Helicocranchia* (lower rostral length of 0·11 cm.).

Other specimens of the family examined belonged to the species *Taonius megalops* (lower rostral length of 0·69 cm.), *Phasmatopsis cymoctypus* (lower rostral length of 1·02 cm.) and *Mesonychoteuthis hamiltoni* (lower rostral length of 2·75 cm.). These were all in an advanced stage of darkening.

MYOPSIDA

LOLIGINACEA

11. LOLIGINIDAE

Specimens of *Loligo vulgaris*, *L. forbesi* and *Sepioteuthis lessoniana* were examined. The darkening process appears to be similar in all species considered but I was unable to find if it is precisely the same because the later stages of *L. vulgaris* and the early stages of *L. forbesi* are not represented in this collection. There is some evidence of geographical variation in the size at which darkening extends to the wings and lateral walls.

In *Loligo vulgaris* the lateral walls of the upper beak and the wings of the lower beak are transparent at a lower rostral length of 0·1 cm. A small brown fleck appears on the wings of the lower beak at a rostral length of 0·14 cm. This fleck enlarges and finally (at a lower rostral length of about 0·2 cm.) becomes continuous with the darkened region of the shoulder. The darkening then extends over the rest of the lower beak wing and over the upper beak lateral wall. The darkening of the lateral walls of the upper beak progresses from under the hood towards the periphery of the walls, and there are no isolated patches or prior darkening of the crest. In this species the largest specimen (lower rostral length of 0·35 cm.) has reached a stage where darkening of the upper beak lateral walls has extended half-way to the periphery from the hood. A specimen from Milford Haven does not conform to this general plan of development and has a beak in an early stage of development and a lower rostral length of 0·3 cm. The other specimens were from the east coast, NW. Scotland and Falmouth, and this could be a difference between populations.

In *Loligo forbesi* all the specimens, except one, with lower rostral lengths of more than 0·29 cm. (i.e. twelve) are in the same stage as *L. vulgaris* specimens of the same length. The exception is a large squid whose beaks were collected in Madeira; the lower rostral length is 0·64 cm. and the beaks are extremely pale brown except for the rostra and shoulders. This could be another example of a difference between populations.

All three specimens of *Sepioteuthis* (lower rostral lengths of over 0·26 cm.) are in the stage which was attained at a lower rostral length of about 0·3 cm. in the two species of *Loligo*.

SEPIACEA

12. SEPIOLIDAE

Rossia macrosoma was examined because this grows to a larger size than most other members of the family.

The smallest specimen (lower rostral length of 0·1 cm.) has transparent wings on the lower beak and almost transparent lateral walls on the upper beak. A slight darkening is present in the crest region of the upper beak. Other specimens examined (with lower rostral lengths of 0·2–0·32 cm.) have lower beaks with darkened wings and upper beaks with at least half the lateral walls darkened.

13. SEPIIDAE

The smallest specimens of *Sepia officinalis* examined (upper rostral length of 0·19 cm. and 0·23 cm. ; the lower rostral length is less reliable) had lower beaks with partly darkened lateral walls. The form of the darkened area suggests that darkening starts along the crest and spreads forward and inward over the lateral walls. All specimens with an upper rostral length of between 0·35 cm. and 0·5 cm. (i.e., four specimens) had upper beaks in which this darkening of the lateral walls had almost reached the anterior edge of the walls. A specimen with an upper rostral length of 0·5 cm. and those with larger rostra, had beaks with completely dark lateral walls. One specimen (the only one from the Canary Islands) differs from the others in having beaks in the final stage of darkening and an upper rostral length of only 0·29 cm. This could be a difference between populations.

OCTOPODA

INCIRRATA

14. OCTOPODIDAE

Specimens of *Pareledone*, *Octopus* and *Eledone* species were examined. Allometric relationships are not as clear as in the Decapod families and standard deviations of the regressions are larger (Table II) because the jaw angle is usually indistinct and rostral length cannot be accurately determined. The lower rostral length could rarely be measured at all so that the length of the " rostral gap " (Text-fig. 3) was plotted instead and the wing length was then measured from the anterior end of the shoulder instead of from the jaw angle. The upper rostral length could not be measured in *Eledone* and some species of *Octopus*. Exactly the same stage of darkening is found in all the *Octopus vulgaris* beaks (i.e. lower gap lengths from 0·19 cm. to 0·65 cm). Both beaks are brown except for a narrow border at the growing edges and the anterior edge of the lower wings. This transparent border is slightly broader on the distal (posterior) wing edge opposite the shoulder.

The beaks of *Octopus rugosus*, *O. macropus*, *O. robustus*, *O. bairdi*, *O. indicus* and *O. arcticus*[1] are all darkened the same as *O. vulgaris*.

The smaller *Eledone cirrhosa* specimens (lower rostral gap of 0·63 cm.) have lower wings that are darkened over about one-half of their area. In larger specimens each wing is dark except for a narrow border. In *Pareledone* the lower beak is in the earlier stage of darkening (lower rostral gap of 0·67 cm.).

15. ARGONAUTIDAE

Two specimens of *Argonauta hians* and one of *A. argo* were examined. In each the lower beak has darkened wings and the upper beak has a little darkening of the lateral walls. A rather unusual feature is that the lateral walls of the lower beak of each specimen are largely transparent; only the crest and the outer anterior part of the walls are darkened.

The largest beaks and some of the smallest beaks of octopods are black or nearly so and this noticeable feature is often useful for a preliminary identification.

V. THE IDENTIFICATION OF BEAKS

On the whole, lower beaks can be more readily identified than upper beaks. For clarity, the numbers appended to the features used for identification correspond to those on the plates. Subjective observations concerning the impression of the general proportions which one gets after numerous beaks have been examined are included as these express, in words, the values of the calculated regressions which are given in Table II.

DECAPSODA

OEGOPSIDA

1. Rostral tip is not worn down in either beak and there is nearly always a slight indentation in the periphery of the lateral wall of the upper beak (arrow in plates).

1. OMMASTREPHIDAE

The Upper Beak (Pl. 13)

2. The jaw angle is clearly defined and usually recessed (Text-fig. 2B).

3. The wing extends in front of the front margin of the lateral walls so that the shoulder gives the impression of a cutting edge when viewed from the side. This edge may be curved and smooth in outline or may be slightly jagged.

4. The inner end of the wing is transparent in most beaks but becomes dark in the later stages of development. The outer edge of the transparent region is straight.

5. Darkening includes (*a*) a stage when there is an isolated patch of brown on each lateral wall; (*b*) an earlier stage when part of the crest is dark but the lateral walls are transparent.

6. The hood appears to be rather large compared with the rostral length.

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[1] Names given here are those used in the collection of the British Museum; it is recognized that *Octopus rugosus* is an aggregate species.

The Lower Beak (Pl. 13)

2. The lateral walls have no sharply defined ridge running across them (as seen in the Histioteuthidae, p. 449) but a broad, indistinct fold may be present. This is not a constant feature and seems to arise by slight buckling of the lateral wall. It is easily distinguishable from the narrow, constant and clearly-defined ridges seen in some other families (see Text-fig. 3).
3. The jaw angle is always acute and usually recessed (Text-fig. 3C).
4. In all but the oldest specimens there is a narrow, undarkened zone between the darkened regions of the lateral wall and the medial side of the wing. This has the characteristic appearance indicated in Text-fig. 3E and Pl. 13E.
5. A narrow wedge of cartilage on the anterior end of each shoulder is partly exposed even in the oldest beaks.
6. Darkening includes (*a*) a stage when there is an isolated dark patch on the wing, and (*b*) a stage when the patch on the wing is attached to the dorsal darkened region by an isthmus which lies near the free posterior edge of the wing.
7. In profile the beak looks rather " square " and the rostrum is about equal in length to the wing.

Identification of Species within the Family

As mentioned above (p. 436) some lower beaks may be identified from their stage of darkening and rostral length. This does not make possible identification of beaks from all squids of a species but only those beaks in particular stages of darkening. In practice this identification is aided by some knowledge of the squid fauna of the geographical location concerned. Text-fig. 8 summarizes my data on the darkening process in this family and may prove helpful when comparing ommastrephids of a particular area.

As mentioned above (p. 434) *Sthenoteuthis caroli* and *Todarodes sagittatus* differ in the relationship between upper rostral width and upper rostral length (i.e., *S. caroli* specimens have a broader upper rostrum than *T. sagittatus* specimens of the same size). As some overlapping between the species occurs this is of little value for the identification of a few beaks but it could be used to show the predominance of one of the species if enough beaks were examined to allow a statistical analysis.

2. ONYCHOTEUTHIDAE

The Upper Beak (see Pl. 14)

2. The jaw angle may be clearly acute or may be obtuse and have a false angle (Text-fig. 2 and Pl. 14A).
3. From the side, the shoulder appears to be a cutting edge but, from the front, it is seen that the edge is blunt with a false angle, and consists of two horny layers (lateral wall and wing) separated by a cartilaginous layer.
4. The inner end of the cartilage is often covered by a transparent area of the wing which is much more restricted than in the Ommastrephidae.
5. It seems unlikely that an isolated dark patch is ever present on the lateral wall.

The Lower Beak (Pl. 14)

2. There is usually a ridge on the lateral wall which is narrow anteriorly and becomes broader and less distinct posteriorly. This ridge, or outward fold, of the lateral wall intersects the posterior edge of the wall at a point about half-way between the free posterior corner and the crest and this, coupled with the broadness of the ridge, makes confusion with the ridges found in the Histioteuthidae and the Chiroteuthidae unlikely (see below).

3. The jaw angle is nearly always obtuse and the shoulder slopes from its point of insertion with the edge of the rostrum. The outer part of the wing, which lies directly to the side of the jaw angle, often protrudes forwards slightly so that the angle is hidden when viewed from the side.

4. The proximal end of the rostral edge lies inside and medial to the point where the shoulder is inserted into the rostral wall so that there is a slight step between the medial surface of the wing and the anterior end of the lateral wall (see Text-fig. 3F).

5. There is usually a short, narrow wedge of cartilage at the front end of the shoulder which remains exposed during growth.

6. An isolated dark patch or a club-shaped area is probably never present on the wings.

7. The hood is rather short from front to back.

Identification of Species within the Family

I have been unable to find criteria for the separation of *Onychoteuthis banksi* from *Ancistroteuthis lichtensteinei*. Both these, however, appear to be separable from the *Moroteuthis* considered here on the basis of three features in each.

The upper beaks of *Moroteuthis* specimens have a false angle, an obtuse jaw angle and the shoulder looks three-layered from the front. The two other species considered have no false angle (or at most a very small one), a recessed jaw angle and a shoulder which forms a single cutting edge.

In the lower beaks of *Moroteuthis*, the indistinct ridge of the lateral wall intersects the posterior side of the wall at, or above, the point midway between the crest and the free, posterior corner (Text-fig. 3H). In the other species considered, the intersection usually lies at the free, posterior corner of the wall but may lie almost up to the midway point.

In addition *Onychoteuthis* and *Ancistroteuthis* probably never approach the size of mature *Moroteuthis*.

One *Moroteuthis* specimen (with a lower rostral length of 0·51 cm.) has transparent wings and at the same size the *Onychoteuthis* and *Ancistroteuthis* specimens all have darkened wings and this provides an additional means of identifying some beaks.

3. HISTIOTEUTHIDAE

The Upper Beak (see Pl. 15)

2. The jaw angle is usually obtuse and a very distinct, false angle is present. The shoulder is irregularly broken and has no constant form.

3. The shoulder cartilage is exposed on the anterior side and contributes to the rear border of the false angle.

4. Part of the wing which covers the cartilage is transparent in these specimens but it never has the characteristic shape of that seen in the Ommastrephidae (Pl. 13).

5. The dark region has a straight anterior edge during its progressive extension towards the anterior of the lateral wall and no isolated dark patch is found on the lateral walls.

The Lower Beak (Pl. 15)

2. A very distinct narrow ridge on each lateral wall runs to the free, posterior corner of the wall (Pl. 15 and Text-fig. 3).

3. The jaw angle is obtuse.

4. There is no transparent area between the dark regions of the anterior lateral wall and the medial side of the wing and there is no " step " between these regions.

5. There is an extensive area of exposed cartilage on the shoulders which becomes much smaller in the later stages of growth (see Pl. 15D–F showing *Calliteuthis*).

6. There is probably a stage in which a dark isolated patch is present on each wing and there is certainly a stage during which the dark region of the wing is connected to the main darkened region by an isthmus which lies near to the free edge of the wing (Pl. 15D).

Identification of Species within the Family

Beak size at particular stages of darkening varies between some of the species examined. In *Histioteuthis bonelliana* only half the wing of the lower beak is darkened at a lower rostral length of 0·85–1·05 cm. a stage found in *Calliteuthis döfleini* at 0·45 cm. and 0·51 cm. In *Histioteuthis bonelliana* more than half the wing is darkened but a large area of shoulder cartilage is exposed at a lower rostral length of from 0·86 cm. to 1·18 cm. In *Calliteuthis döfleini* this stage and the final stage, when the cartilage is greatly reduced, may be reached at 0·5 cm. A *Calliteuthis* specimen found with *Histioteuthis bonelliana* in a whale's stomach had a lower beak in the " reduced cartilage " stage although it had a rostral length of only 0·63 cm. A *Calliteuthis reversa* specimen had a lower beak with wings in the " half-way " stage of darkening although it had a lower rostral length of only 0·17 cm. Thus, although the present material is insufficient to obtain an accurate idea of the mean rostral lengths at which the stages of darkening take place in the various species, it seems clear that species of *Calliteuthis* considered, pass through these stages when the beaks are smaller than the beak of *Histioteuthis bonelliana*. I have already found this difference of practical value when sorting beaks found in a whale's stomach.

4. ARCHITEUTHIDAE

The Upper Beak (Pl. 16)

2. The jaw angle is acute and there is no suggestion of a false angle.

3. The horny layer of the wing is thickened at its anterior edge and extends further forward than the anterior limit of the lateral wall, to form a strong, sharp cutting edge.

4. Cartilage of the inner end of the shoulder is not covered by a transparent area of the wing.

5. The upper beak passes through a stage when the crest is darkened and the lateral walls are transparent. Although a number of figures of architeuthid beaks have been published (Verrill, 1880–82; Voss, 1956) they give little information concerning the darkening of the beak because they are all in an advanced stage of development. In passing I feel that it is important to mention that large beaks from stomachs of whales have sometimes been attributed to this family which clearly belong elsewhere. For example, Joubin (1900) figured two beaks as the upper and lower mandibles of *Architeuthis* sp. and while the upper beak is almost certainly from a squid of this genus, the lower beak is clearly from a squid of the genus *Cucioteuthis* (see p. 451).

6. Rostral length is small in comparison with hood length and total beak length. The rostrum is wide and the shoulder is long relative to the rostral length.

The Lower Beak (Pl. 16)

2. There is no indication of a ridge on the lateral wall.

3. The jaw angle is acute and lies behind an upgrowth of the shoulder.

4. There is no transparent region between the medial surface of the wings and the anterior limit of the lateral walls (Text-fig. 3E) even in the smallest specimen available.

5. The exposed cartilage of the shoulder is very small in area.

6. I have no evidence whether or not there is ever an isolated dark patch on the wings.

7. The rostrum is relatively short compared with the length of the wings. The hood extends backwards at each side of the midline. The wings are relatively broad.

5. Enoploteuthidae

The Upper Beak (Pl. 18)

2. Very recessed jaw angle. There is a very marked prominence of the shoulder next to the angle and this may be rounded in such a way that a small false angle is formed (see Text-fig. 2E).

3. Cartilage at the inner end of the shoulder may be covered by darkened (*Abraliopsis* and *Enoploteuthis*) or undarkened wing (*Pyroteuthis*).

4. There may be an indentation in the periphery of the lateral wall (*Enoploteuthis* and *Abraliopsis*) or this may be absent (*Pyroteuthis*).

5. The darkening process includes a stage when the lateral walls of the upper beak and the wings of the lower beak are transparent but nothing is known concerning an isolated patch stage.

The Lower Beak (Pl. 18)

2. Either there is no distinct ridge on the lateral walls (*Pyroteuthis*) or a ridge is present which intersects the posterior edge of the lateral wall, half-way between the crest and the inner edge (*Abraliopsis* and *Enoploteuthis*).

3. Jaw angle recessed (*Pyroteuthis* and *Enoploteuthis*) or obtuse (*Abraliopsis*).

4. Medial side of the wing is not separated from the lateral wall by a transparent strip or a ridge.

5. There is a small wedge of cartilage at the inner end of the shoulder.

6. A very slight fold of the hood-wing structure hides the jaw angle when seen in profile.

7. From the form of the dark region of the wing in *Enoploteuthis* it seems unlikely that there is a " club " stage during darkening.

8. The hood covers more than half of the crest. The beak has a squat appearance with broad wings and a rostrum about half as long as the wing. In *Enoploteuthis* the crest is very short (Pl. 18).

6. OCTOPODOTEUTHIDAE

The Upper Beak (Pl. 17)

2. The jaw angle is curved. There is a false angle but this is rounded off so that the anterior end of the lateral wall does not form a broken cutting edge.

3. Cartilage of the shoulder is very well developed, and is not covered completely by the horny wing and actually forms the leading edge of the shoulder.

4. The inner end of the wing is transparent even in the largest specimen considered.

5. There is no indentation in the periphery of the lateral wall.

6. The darkening process involves a stage at which the crest is darkened while the lateral walls are transparent but it is not known whether an isolated dark patch is ever present on the lateral walls.

7. The rostrum is relatively long and narrow when compared with some families (e.g. Ommastrephidae and Architeuthidae).

The Lower Beak (Pl. 17)

2. A very clearly defined ridge runs to the posterior edge of each lateral wall.

3. The jaw angle is about 90°.

4. Part of the medial surface of the wing darkens and this part is much narrower from front to back than in, for example, the Ommastrephidae. There is an ill-defined transparent strip between this area and the anterior edge of the lateral wall in the smallest specimens.

5. The shoulder consists of exposed cartilage along the whole length.

6. There are no furrows lateral to the mid-line of the hood.

This feature may not be constant within a family but it has been found of value for the separation of beaks of *Cucioteuthis* from those of *Lepidoteuthis*.

7. There is a stage when a narrow isthmus near the posterior edge of the wing connects the dark areas of the wing and hood and probably there is an isolated dark patch on the wing at an earlier stage.

8. The rostrum is long in comparison with the wing and hood lengths. The border of the hood extends backwards at each side of the mid-line, and the wings are very broad.

In *Octopodoteuthis* the lateral wall is not darkened between the exposed crest and the ridge of the lateral wall but it is in the much larger *Cucioteuthis*.

7. THYSANOTEUTHIDAE

The Upper Beak (Pl. 16)

2. The jaw angle is distinct and forms a slightly-recessed, acute angle. There is no false angle.

3. The shoulder is a cutting edge which is formed by the thickened horny wing layer. The anterior limit of the lateral wall lies behind the anterior edge of the wing and is connected to it by a very thin layer of cartilage.

4. A small area of the cartilage at the inner end of the shoulder is covered by undarkened wing.

5. No characteristic stages in the darkening process are present in these specimens.

6. The rostrum is relatively very broad and short and the shoulder is relatively long when compared with the other dimensions.

The Lower Beak (Pl. 16)

2. There is no indication of a ridge on the lateral wall.

3. The jaw angle is acute and slightly recessed.

4. The smallest beak (lower rostral length of 0·11 cm.) has a narrow transparent strip between the darkened area of the medial surface of the wing and the darkened area of the lateral wall (Text-fig. 3).

5. There is a small wedge of cartilage at the front end of the shoulder which is covered by transparent wing material.

6. There is no indication of any stage during which an isolated dark patch is present on the wings.

7. The rostrum is relatively very short and the wing and crest relatively very long. The wings are very broad when compared with squids in other families.

Squids of this family are likely to be confused with members of the Architeuthidae but are almost fully darkened at a much smaller size (lower rostral length of 0·56 cm.) and probably never attain such a large size. Thus, a large specimen with a dorsal mantle length of 76·4 cm. (the largest record with a mantle length of 80·0 cm. was noted by Pfeffer, 1910) had a lower rostral length of only 0·75 cm.

8. GONATIDAE

The Upper Beak (Pl. 14)

2. The jaw angle is obtuse in the smallest beaks (lower rostral length of 0·1 and 0·2 cm.). In the larger beaks (lower rostral lengths of 0·59—0·67 cm.) the jaw angle is curved. The outer anterior edge of the wing layer lies behind the anterior edge of the lateral wall so that a distinct false angle is formed which is similar in profile to the jaw angle (i.e., it is also curved).

3. In the smaller specimens the wing of the shoulder forms a cutting edge but in the larger specimens the anterior wing edge lies behind the anterior edge of the lateral wall for most of the shoulder length.

4. The wing is narrow from front to back. The inner half of the wing is transparent in the small specimens but this is darkened in the larger specimens.

5. There is no indentation in the periphery of the lateral walls in the small specimens but this is present in the larger specimens.

6. No characteristic details of the darkening process can be ascertained from this material.

7. To judge from these specimens there is a change in the form of the shoulder and wing during development. The jaw angle becomes more curved and its exact position less clear so that the rostrum appears to become longer and the shoulder shorter.

The Lower Beak (Pl. 14)

2. There is a slight fold but no well-defined ridge on the lateral wall.

3. There is no light strip or ridge between the dark region of the medial surface of the wing and the anterior limit of the lateral wall.

4. The jaw angle is clearly obtuse.

5. There is no exposed cartilage on the shoulder in the larger specimens.

6. These specimens do not reveal any characteristic stage in the darkening process but the larger beaks suggest that there is not a stage where the dark area on the wing is connected to the main dark area by an isthmus lying near the free edge of the wing.

7. The most striking feature of the beak is the relatively narrow rostrum and this feature is of use when separating this family and the Cranchiidae from other families. The hood is short and the wings are narrow in comparison with the crest length. The rostrum is about the same length as the wing. The smaller beaks could be confused with those of the Ommastrephidae but may be distinguished on the grounds of feature 3 above.

9. CHIROTEUTHIDAE

The Upper Beak (Pl. 18)

2. Except in the smallest specimen (*Mastigoteuthis magna* with a lower rostral length of 0·13 cm.) the jaw angle is curved and there is a clearly defined false angle. The anterior part of the wing does not reach the jaw angle or the anterior edge of the shoulder.

3. The shoulder consists of exposed cartilage which extends a little over the lateral surface of the wing and the medial surface of the lateral wall so that it covers the anterior edges of these horny layers.

4. The inner part of the wing is not darkened even in the largest specimens examined.

5. There is no indentation in the edge of the lateral wall in the large specimen (*Lepidoteuthis*) but there are slight indentations in the smaller specimens (*Chiroteuthis imperator*, *Mastigoteuthis magna* and *Mastigoteuthis* spp.).

6. It seems unlikely that there is a stage in which an isolated dark patch is present on the lateral wall. A straight, well-defined line borders the anterior limit of the dark area of the lateral walls during its progressive extension forwards.

7. The rostrum is long in relation to the hood length and in the largest specimens (*Lepidoteuthis*) it is narrow at the base compared with its length.

The Lower Beak (Pl. 81)

2. An extremely well-defined ridge on the lateral wall intersects the posterior edge of the wall below the half-way point between the free corner and the crest. The lateral wall between the posterior end of the crest and the ridge never becomes darkened and remains soft in *Lepidoteuthis* and *Chiroteuthis*. This is an aid in identification but a similar condition is found in the small octopodoteuthids which were examined (see p. 452).

3. The jaw angle is acute.

4. There is neither a transparent strip nor a " step " between the anterior limit of the lateral wall and the dark region of the medial side of the wing.

5. The shoulder is formed from cartilage which covers the anterior edge of the wing layers.

6. In *Lepidoteuthis* (but not in the other species of this family which were examined) there is a furrow running from the point of the jaw, across the hood.

7. Nothing of value for identification can be seen in the darkening process of these specimens.

The rostrum is long in proportion to the wing length and the hood length (particularly in the larger specimens, i.e. *Lepidoteuthis*). The beaks have the appearance of being rather high in relation to their length.

Identification of Species within the Family

It is not possible to separate the effects of growth from the differences between species because the specimens of the different species are of different sizes.

Note. Members of this family may be confused with those of the Octopodoteuthidae. Specimens of *Cucioteuthis* and *Lepidoteuthis* may, however, be separated by the furrow in the hood, the extent of the undarkened region near the crest and the relative width of the wings.

10. CRANCHIIDAE

Species of this family appear to be very diverse in structure and this diversity is reflected in the beaks considered here although only five species are considered. Although this should be borne in mind, some common features for identification can be found and, in practice, the larger ones can be distinguished from the beaks of species in other families.

The Upper Beak (Pl. 19)

2. In the smaller beaks the jaw angle is acute and recessed (*Phasmatopsis cymoctypus*, *Helicocranchia* and *Euzygaena*).

In *Taonius megalops* the jaw angle is slightly obtuse.

In *Mesonychoteuthis* the angle is very clearly recessed and there is a false angle.

3. The shoulder is straight in all but *Mesonychoteuthis* in which the jaw angle is so recessed that the shoulder forms a " bulge " forward. The lateral wall layer of the shoulder may extend a little more anteriorly than the edge of the wing layer (*Mesonychoteuthis*), may lie alongside it (*Taonius megalops*) or may lie behind it (*P. cymoctypus*).

4. In the larger beaks there is no transparent region of the wing.

5. There may be (*P. cymoctypus*) or may not be (*T. megalops*) an indentation in the periphery of the lateral walls.

6. No characteristic features of the darkening process have been found.

7. The only really noticeable features of these beaks are the relatively long hood when compared with the crest length, and the relatively narrow rostrum.

The Lower Beak (Pl. 19)

2. A distinct broad ridge on the lateral wall intersects the posterior edge of the wall at a point about half-way between the crest and the free corner in *Taonius megalops* and *P. cymoctypus* but this ridge is completey absent in *Mesonychoteuthis*. Its presence cannot be determined in these *Helicocranchia* and *Euzygaena* which have very incompletely darkened beaks.

3. The jaw angle is obtuse.

4. There is no line of separation between the darkened area of the medial side of the wing and the anterior of the lateral wall in the three larger species (*Taonius megalops*, *P. cymoctypus* and *Mesonychoteuthis*).

5. The shoulder is not prominent, lies at an obtuse angle to the rostrum and it bears little or no exposed cartilage. The jaw angle is hidden from a profile view by a fold of the hood-wing structure.

6. There is a furrow in the wing of these beaks running from the shoulder region to the inner edge of the wing.

7. No characteristic details of the darkening process are present in these specimens.

8. The beaks all present a very large expanse of lateral wall in side view and the crest is long in comparison to the hood length. Although the rostrum is about the same length as the wing, in profile it appears to be only about half the length because of a fold of the hood-wing structure near to the jaw angle. These beaks give a striking impression of being relatively tall and narrow.

Identification of Species within the Family

A few structural distinctions between the species considered have been given.

MYOPSIDA

LOLIGINACEA

1. The rostral tip is not worn down and there is a slight indentation in the periphery of the lateral wall of the upper beak (arrow—in plates).

11. Loliginidae

The Upper Beak (Pl. 20)

2. The jaw angle is recessed and there is no false angle.

3. The shoulder is straight in profile—except for secondary minor indentations, apparently caused by wear-and forms a cutting edge in which the three layers (wing, cartilage and lateral wall) cannot be distinguished.

4. There is no distinct, transparent area near the inner end of the wing.

5. The darkening process probably does not include a stage in which there is an isolated patch on the lateral wall.

6. The rostrum is very short in comparison to the hood length and the shoulder length.

The Lower Beak (Pl. 20)

2. There is no suggestion of a ridge on the lateral wall.

3. The jaw angle is distinct, obtuse and not recessed.

4. There is no dividing line between the darkened area of the medial side of the wing and that of the lateral wall. In many of the beaks there is a very dark area which extends along the rostrum and the shoulder without any discontinuity near the jaw angle. This region is always (in these specimens) much darker than the rest of the beak (Pl. 20E).

5. The shoulder is nearly straight and bears no exposed cartilage. The jaw angle can be seen from the side because there is no prominence of the hood-wing structure (as is found in the Cranchiidae).

The shoulder is slightly sculptured in the largest specimens.

6. There is probably no stage during which there are isolated dark patches on the wings.

7. The hood and the rostrum are short in comparison with the crest and wing lengths.

Identification of Species within the Family

There are no clear differences between the species considered here (*Loligo forbesi*, *L. vulgaris* and *Sepioteuthis lessoniana*). However, hood length of *L. vulgaris* is rather larger in comparison with the crest length than in the other two species. As seen above (p. 444) quite marked differences in the darkening process seem to exist even among specimens of one species from different geographical regions.

SEPIACEA

1. Rostral tip of upper beak is not worn down but that of the lower beak is worn so that it is broad and blunt. There is a distinct indentation in the periphery of the lateral wall of the upper beak.

12. Sepiidae

The Upper Beak (Pl. 21)

2. The jaw angle is acute and there is no false angle.

3. The shoulder forms a blunt cutting edge in which the three layers (wing, cartilage

and lateral wall) cannot be distinguished. In profile the shoulder is slightly curved so that the two ends lie a little posterior to the middle.

4. There is sometimes a clear area near the inner end of the wing but this does not have a straight, clearly-defined outer limit.

5. This material suggests that the darkening spreads progressively from the crest over the lateral walls.

6. These beaks have relatively long hoods and shoulders when compared with the crest and rostral lengths.

The Lower Beak (Pl. 21)

2. There is no ridge on the lateral wall.

3. The position of the jaw angle cannot be determined because the inner edge of the rostrum curves round and is continuous with the shoulder. The rostral length, therefore, cannot be measured.

4. There is no indication of any limit between the dark area of the medial side of the wing and that of the lateral wall.

5. The shoulder bears no exposed cartilage. The edge of the rostrum is continuous with the shoulder and the form of this region is characteristically double edged (Pl. 21G, 6).

6. There is a distinct furrow in the sides of the hood, just above the level of the shoulder; this is more distinct than the slight hollows sometimes seen in the oegopsids or the Loliginidae.

7. There is no indication of a stage in which isolated dark patches are present on the wings.

8. Rostral length and wing length cannot be measured because of the indistinct jaw angle. The crest is long in comparison with the hood length. The wings and the hood are long compared with the rostral length.

13. Sepiolidae (Pl. 21)

Beaks of members of this family are very similar to those of the Loliginidae. Lower beaks differ, however, in having a blunt, worn tip to the rostrum and a curved jaw angle. Upper beaks have an obtuse instead of a recessed jaw angle.

OCTOPODA

1. Rostrum in upper beak is worn down and it may be worn down in the lower beak. Deep indentation in the periphery of the lateral wall of the upper beak.

INCIRRATA

14. Octopodidae

The Upper Beak (Pl. 22)

1. The rostral tip is worn down so that it is broad and blunt.

2. There is no false angle and the jaw angle may be either obtuse or rounded and very indistinct.

3. The shoulder forms a cutting edge in which the three layers (wing, cartilage

and lateral wall) cannot be distinguished. In profile, this edge may be straight or may be more prominent in the centre. It may blend imperceptibly into the rostrum.

4. A transparent area of the inner part of the wing is present in some beaks but this does not have a straight and distinct outer limit.

5. The indentation in the periphery of the lateral wall is usually deeper than is seen in the oegopsids.

6. Any rapid extension of the dark area must take place at a small size. The beaks of octopods are often very dark brown or black and this is often useful for a preliminary sorting.

7. The outstanding feature of these beaks is the relatively very short hood.

The Lower Beak (Pl. 22)

1. The rostrum may be very clearly worn so that it is either flat across the anterior end or it may even have a slight indentation in the mid-line. On the other hand the rostrum may be pointed.

2. There is no ridge on the lateral surface of the lateral wall. Near the inner edge of the lateral wall, there is often an undarkened region and the outer border of this is limited by a ridge on the medial surface of the wall which extends from the region of the jaw angle, to the posterior end of the inner edge of the lateral wall. This limit seems to be homologous with the limit between the medial side of the wing and the lateral wall which is seen in the oegopsids (Pl. 22C and D).

3. The jaw angle is very indistinct because the inner edge of the rostrum curves round and becomes continuous with the shoulder.

4. The medial part of the wing extends backwards far more than in the squids so that much of it lies inside the lateral wall.

5. There is no exposed cartilage on the shoulders which form a blunt cutting edge.

6. The smallest beaks examined are completely darkened.

7. The lateral walls are strikingly narrow between the inner and outer edges compared with their length.

Identification of Species within the Family

The considerable variation among octopod beaks suggests that a detailed study could help taxonomists and ecologists in their search for criteria to distinguish species and populations.

Some species have blunt lower rostra (*Octopus vulgaris, O. bairdi* and *Eledone cirrhosa*) while others have pointed lower rostra (*O. indicus*, and *O. arcticus*).

15. ARGONAUTIDAE

The Upper Beak (Pl. 22)

1. The rostral tip is slightly worn down.

2. The anterior edge of the wing and hood curves to the tip of the rostrum so that no division into rostrum and shoulder is apparent and no jaw angle can be seen.

3. The region probably corresponding with the shoulder is straight or slightly concave in profile. It forms a sharp cutting edge.

4. There is no well-defined undarkened region at the inner end of the wing.

5. There is an indentation in the periphery of the lateral wall.

6. In these specimens only the outer part of the lateral walls is darkened.

7. The region which probably represents the rostrum of other cephalopods is very short in comparison with the rest of the beak. The lateral walls lie very far apart from one another so that the beak is very broad.

The Lower Beak (Pl. 22)

1. The rostral tip is pointed. There is no dividing line between rostrum and shoulder and therefore no jaw angle.

2. There is no ridge on the lateral wall.

3. There is no clear limit between the dark region of the medial side of the wing and the dark region of the lateral wall (either ridge or clear region).

4. The shoulder bears no exposed cartilage and it forms a sharp cutting edge.

5. The inner posterior part of the lateral wall is not darkened even in the largest specimen. This undarkened region extends over more than half the wall.

The darkened region of both beaks is nearly black.

6. The region which probably represents the rostrum of other cephalopods is minute compared to the wing, hood and crest. The hood is about half the length of the crest. The wings and the inner edges of the lateral walls lie very much apart from one another so that the beak has the appearance of being rather flattened.

VAMPYROTEUTHIDAE

Beaks of this family have not been examined here but were illustrated by Pickford, 1949*a*. They resemble beaks of octopods in having no distinct jaw angle but their form seems to be quite different from Octopoda and Decapoda considered here.

VI. BODY WEIGHT AND BEAK SIZE

Total body weight of each specimen was determined and is shown plotted against lower rostral length (Text-figs. 13–24). Families are treated separately.

The animals had been stored in alcohol, formalin or ice for very variable periods. Some specimens had lost tentacles or arms, and in some, the total weight was estimated from the weight of the head and a knowledge of the ratio of head weight to total weight in other specimens. When such an estimate is made it is clearly indicated in the figures. Although all these factors contribute to making the values for total weight rather inaccurate, the relationship between rostral length and body weight is clearly allometric within the families which are well represented (Text-figs. 13, 15, 16). I think that it is quite reasonable to assume a similar relationship in the more poorly represented families and I have, therefore, included parameters for these in Table III.

Text-fig. 24 gives the calculated lines of most of the families of squids and also a line (x) obtained by finding the regression of points, taken along each of the family lines (3 points per line). This "general" line for squids may be of some use if some beaks cannot be identified to family. However, the wide spread of the family

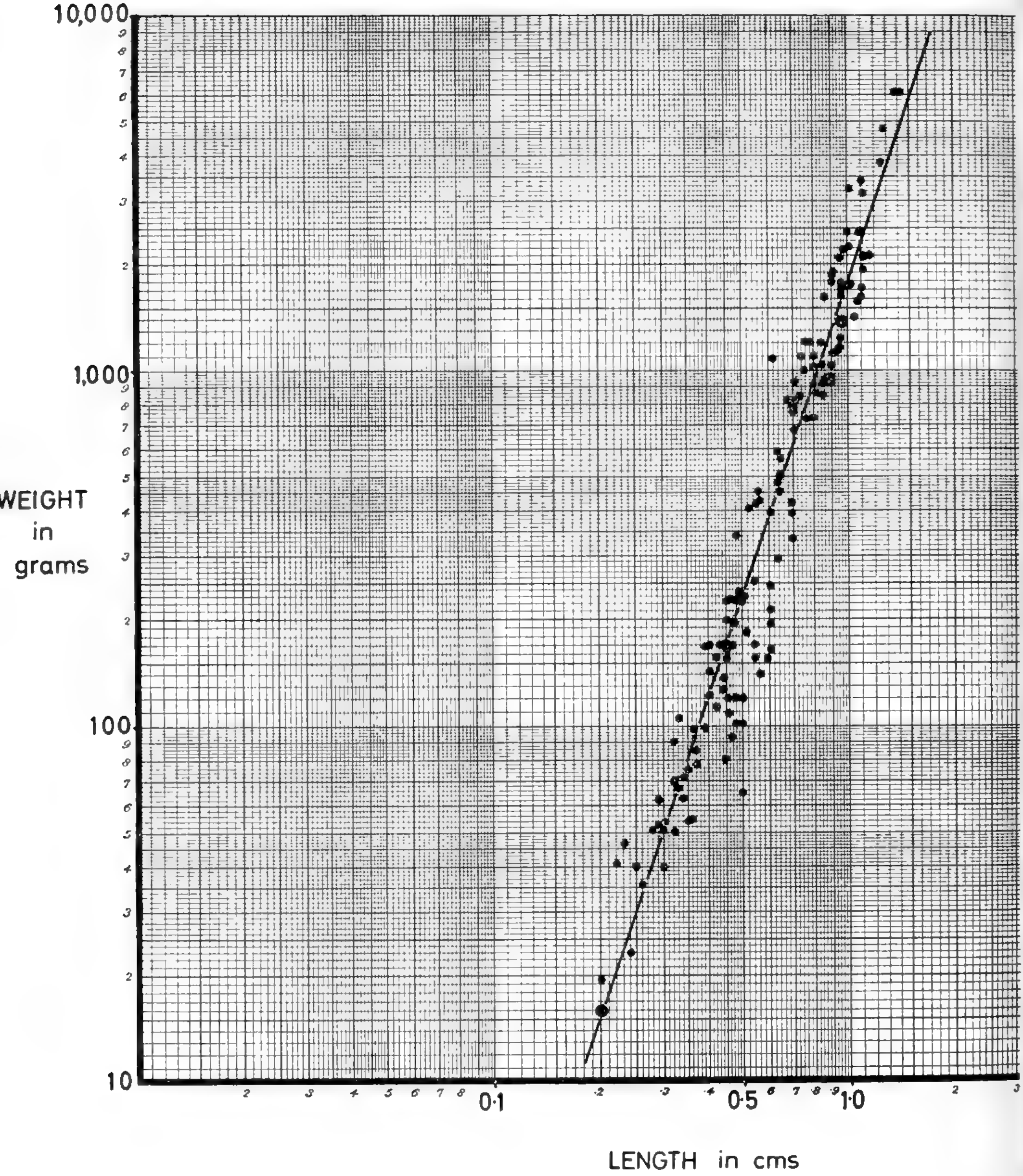

FIG. 13. The Ommastrephidae. Total weight plotted against the lower rostral length. The calculated line is included (see Table III).

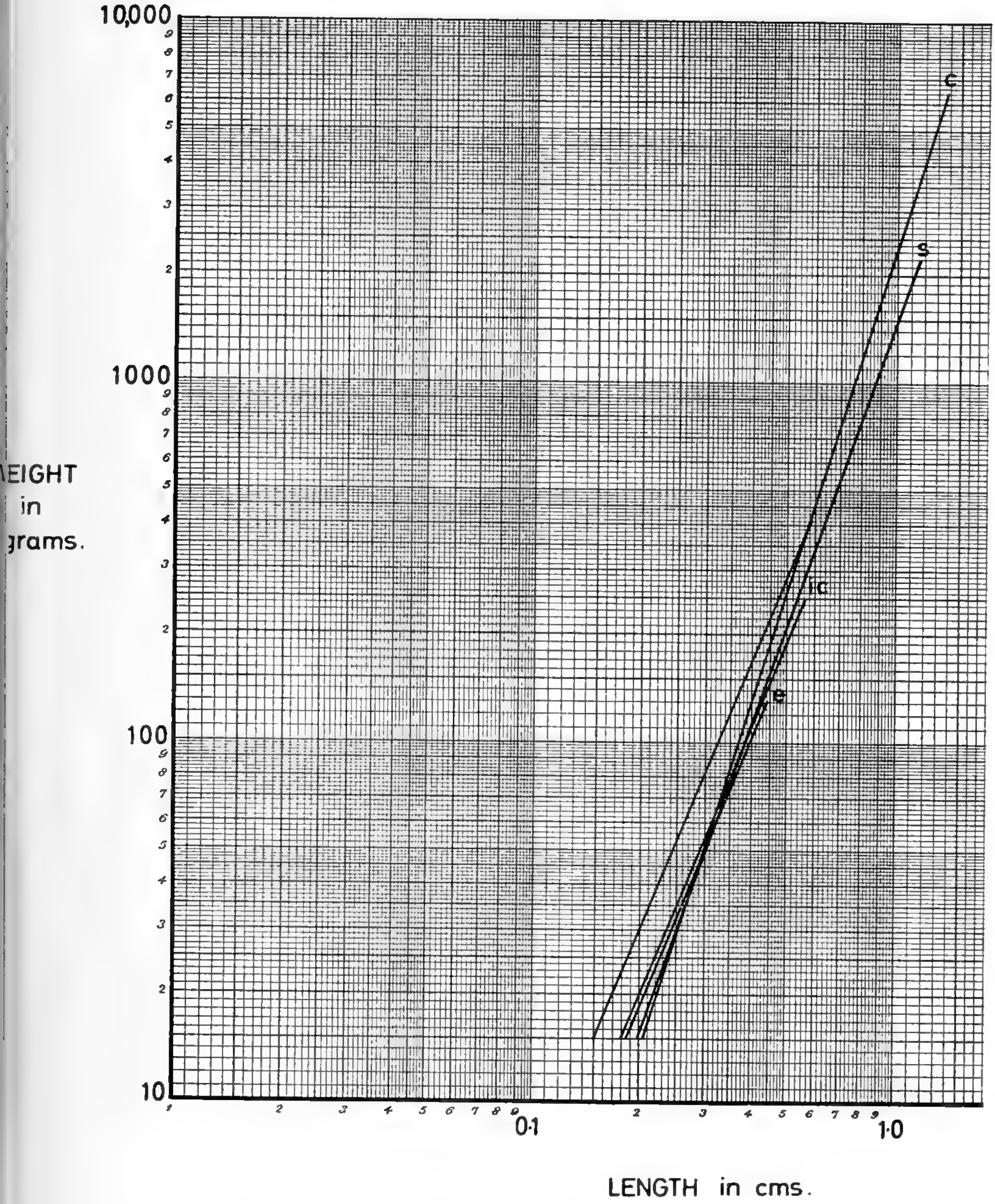

FIG. 14. The calculated lines of the species of the Ommastrephidae which are well represented in this collection. The upper ends of these lines lie at the maximum weight of the specimens in the collection (see Table III). Total body weight plotted against lower rostral length.

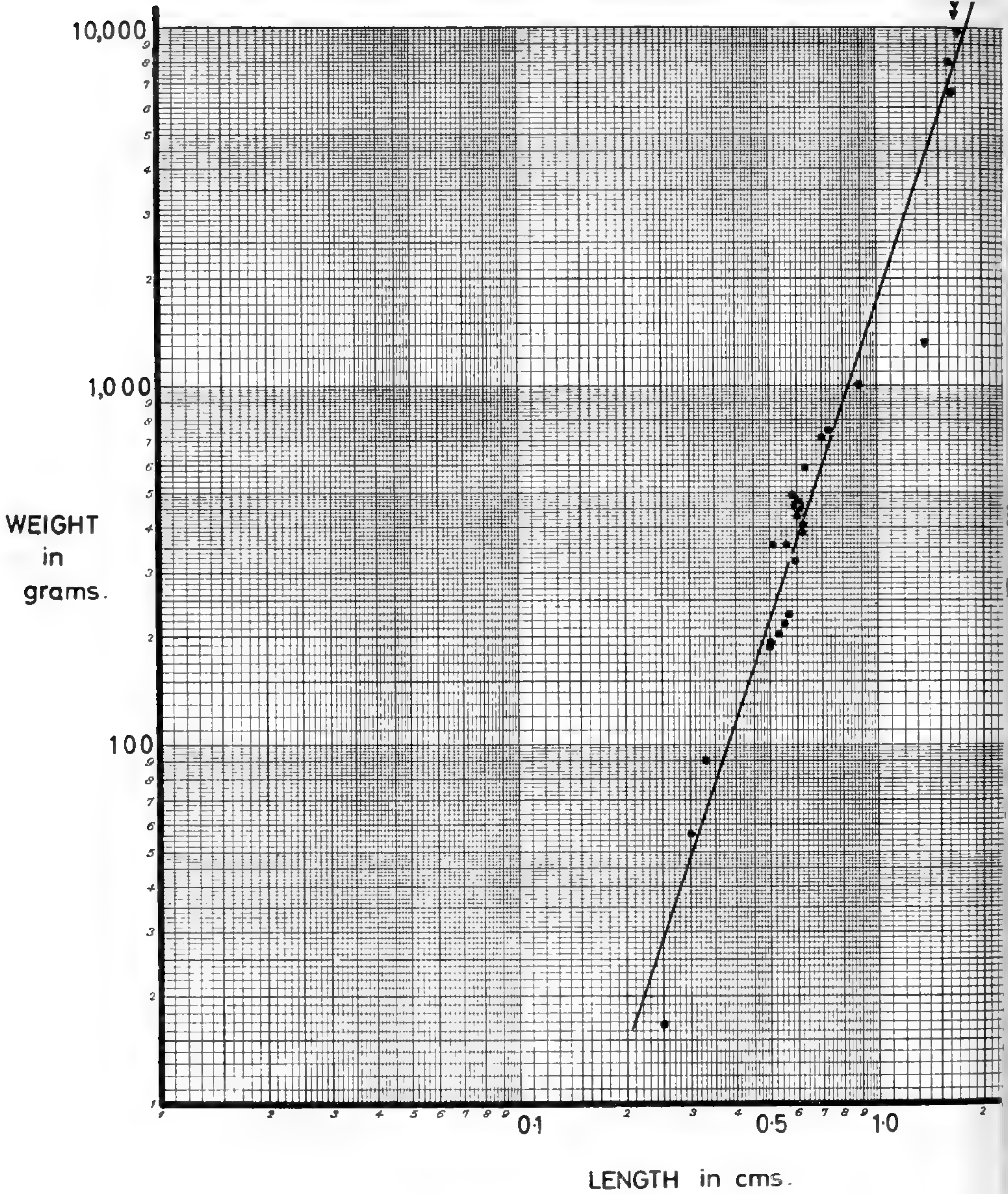

FIG. 15. The Onychoteuthidae. Total weight plotted against the lower rostral length. The calculated line is included. Triangles represent values estimated from the weight of the head and a knowledge of the head weight to total weight ratio found in other specimens of the same species. These were not used in the calculation of the line (see Table III).

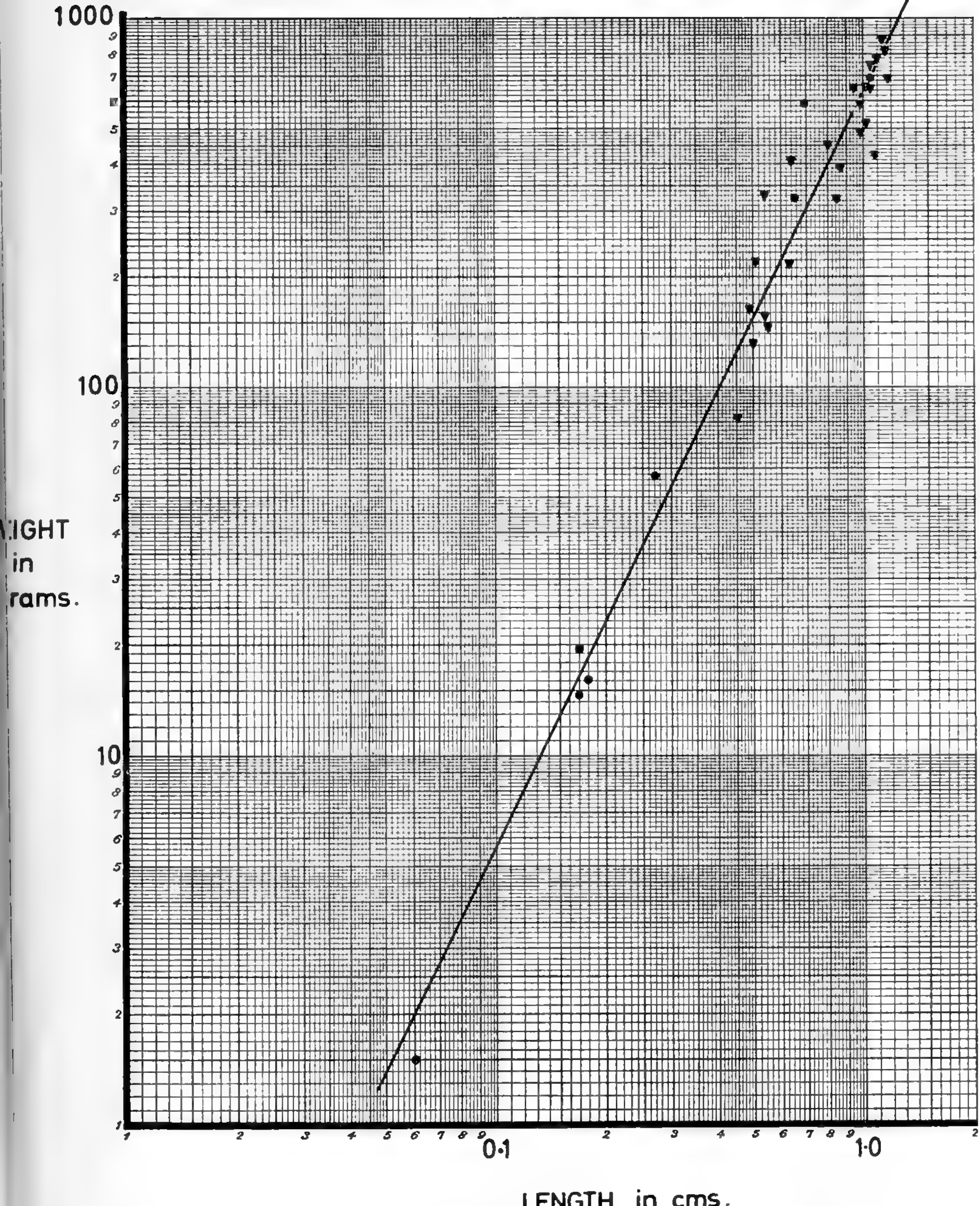

Fig. 16. The Histioteuthidae. Total weight plotted against the lower rostral length. The calculated line is included. Triangles represent values estimated from the weight of the head and a knowledge of the head weight to total ratio found in other specimens of the same species. These were used in the calculation of the line (see Table III).

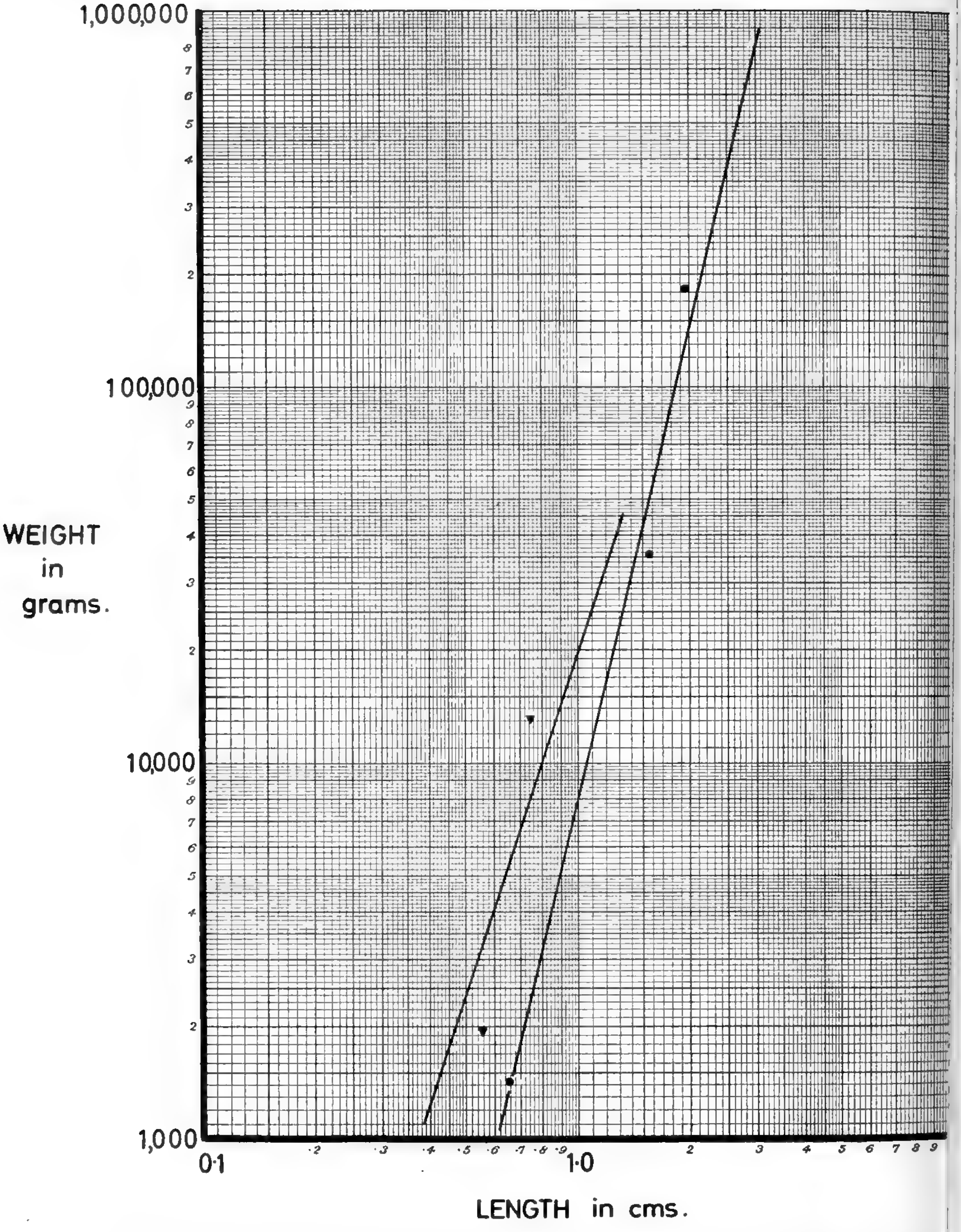

FIG. 17. The Architeuthidae (solid circles) and the Thysanoteuthidae (solid triangles). Total weight plotted against the lower rostral length. The calculated line is included (see Table III). The line for the Thysanoteuthidae was calculated from three values but one value falls below the range of the graph.

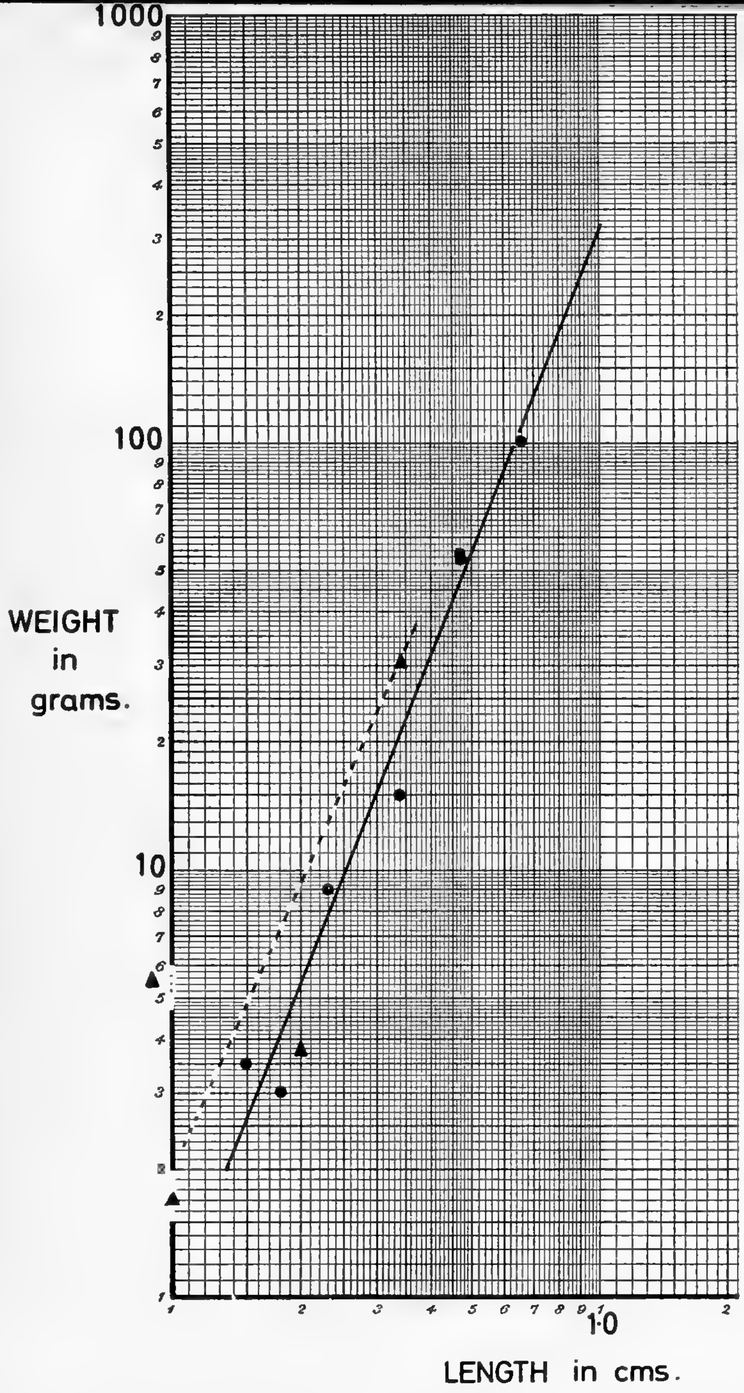

FIG. 18. The Octopodoteuthidae (solid circles) and the Enoploteuthidae (solid triangles and broken line). Total weight plotted against the lower rostral length. The line for the Octopodoteuthidae was calculated and that for the Enoploteuthidae was drawn in by eye.

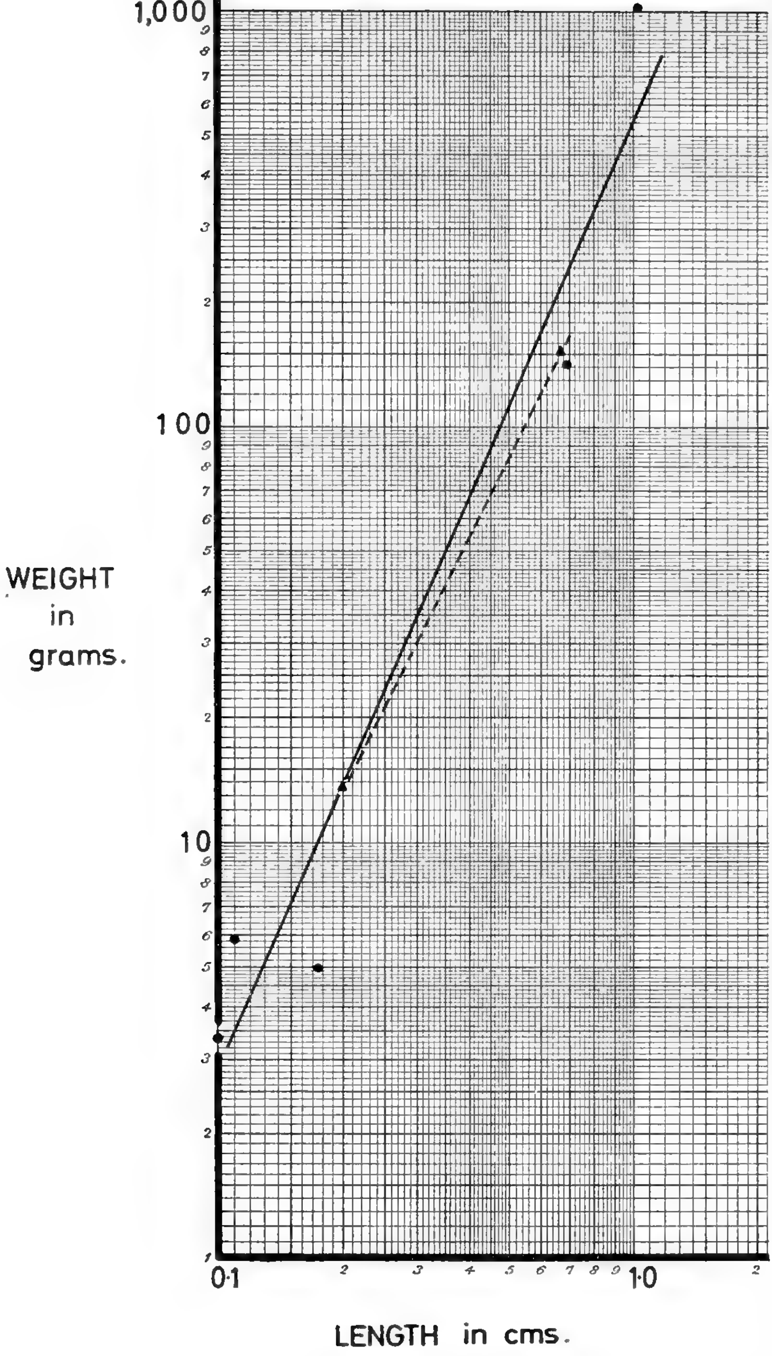

FIG. 19. The Cranchiidae (solid circles) and the Gonatidae (solid triangles and dotted line). Total weight plotted against the lower rostral length. The calculated lines are included (see Table III).

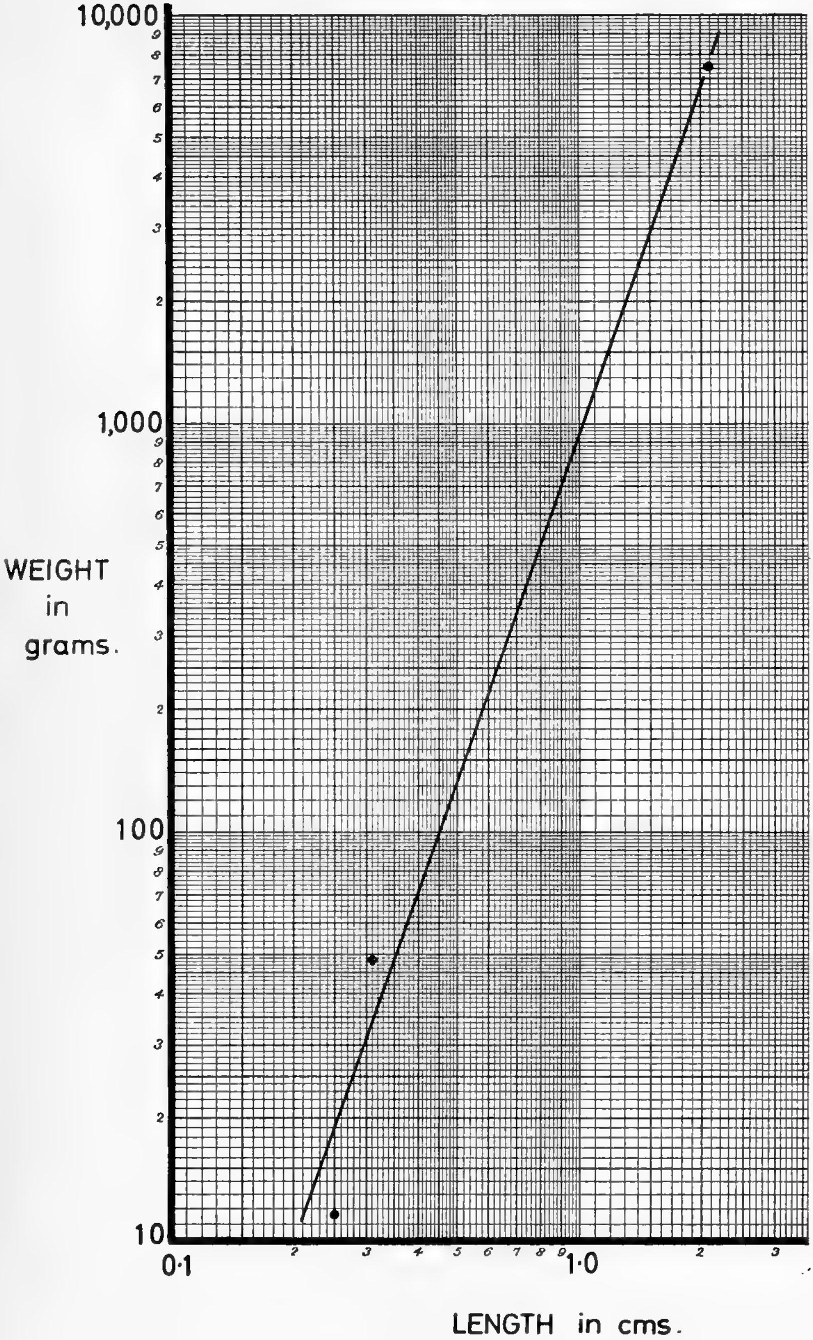

FIG 20. The Chiroteuthidae. Total weight plotted against the lower rostral length. The calculated line is included (see Table III).

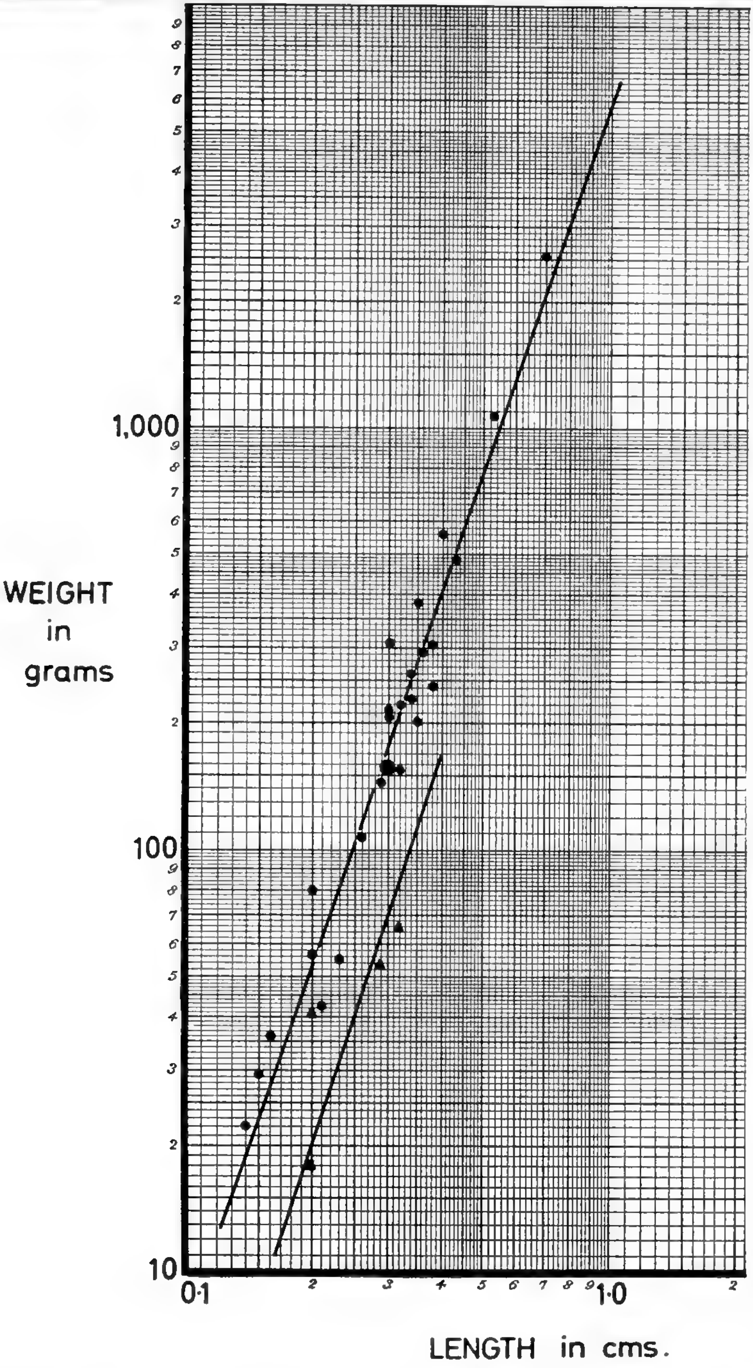

FIG. 21. The Loliginidae and the Sepiolidae (solid triangles). Total weight plotted against the lower rostral length. The calculated lines are included (see Table III). Three points for the Loliginidae and two points for the Sepiolidae are below the range of the graph but were included in the calculation.

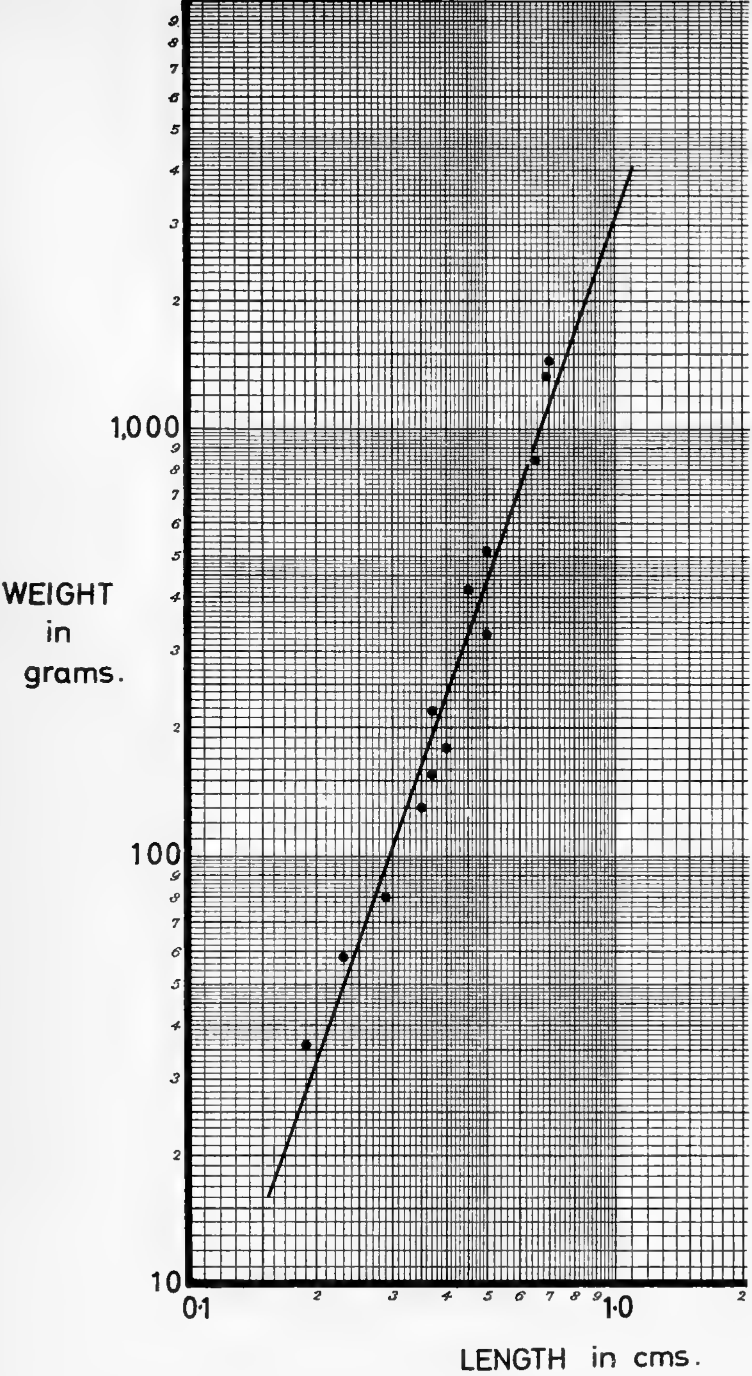

FIG. 22. The Sepiidae. Total weight plotted against the *upper* rostral length. The calculated line is included (see Table III).

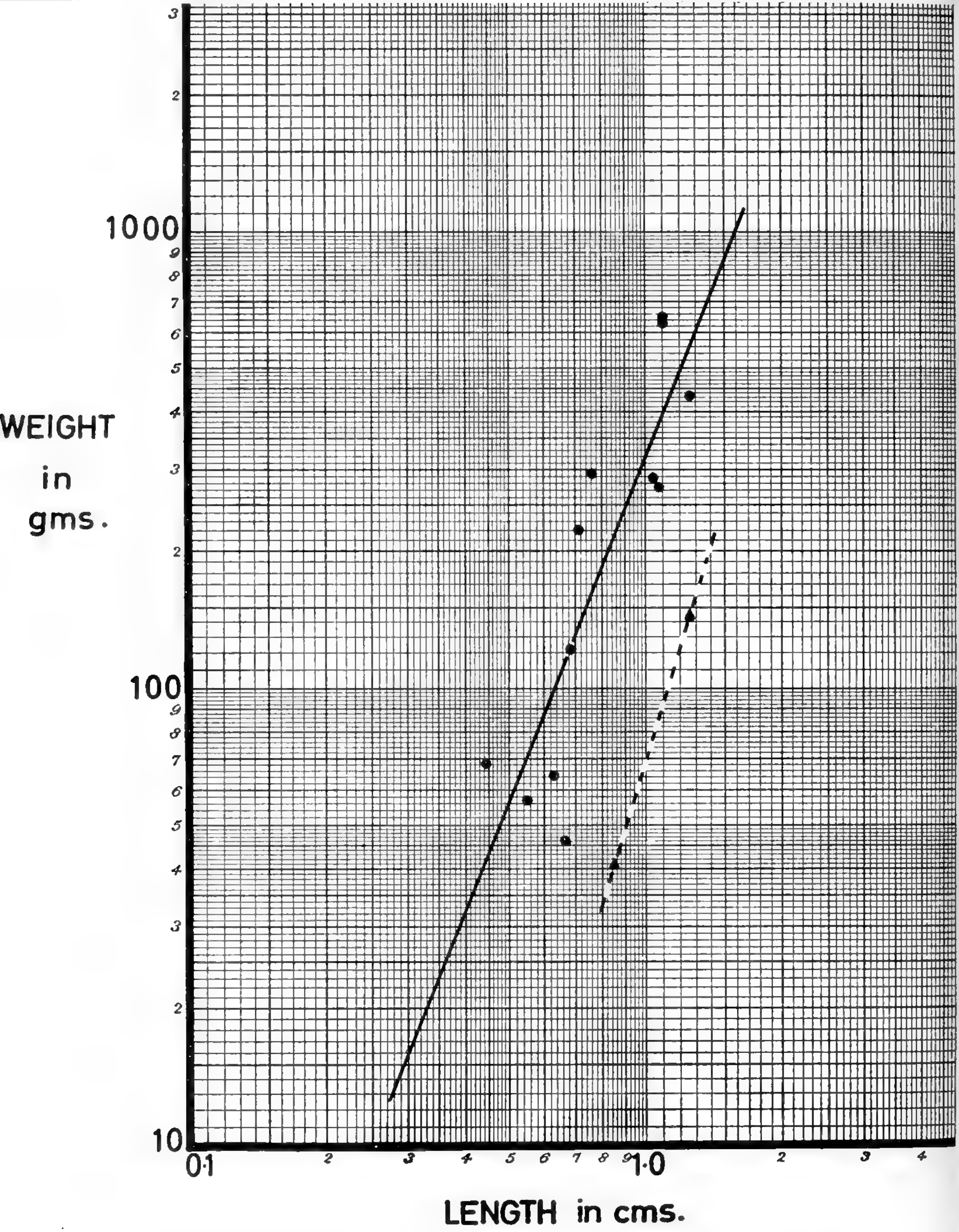

FIG. 23. The Octopodidae and the Argonautidae (solid triangles). Total weight plotted against the *lower crest* length (measurement 3 of Fig. 3). The calculated line is included (see Table III).

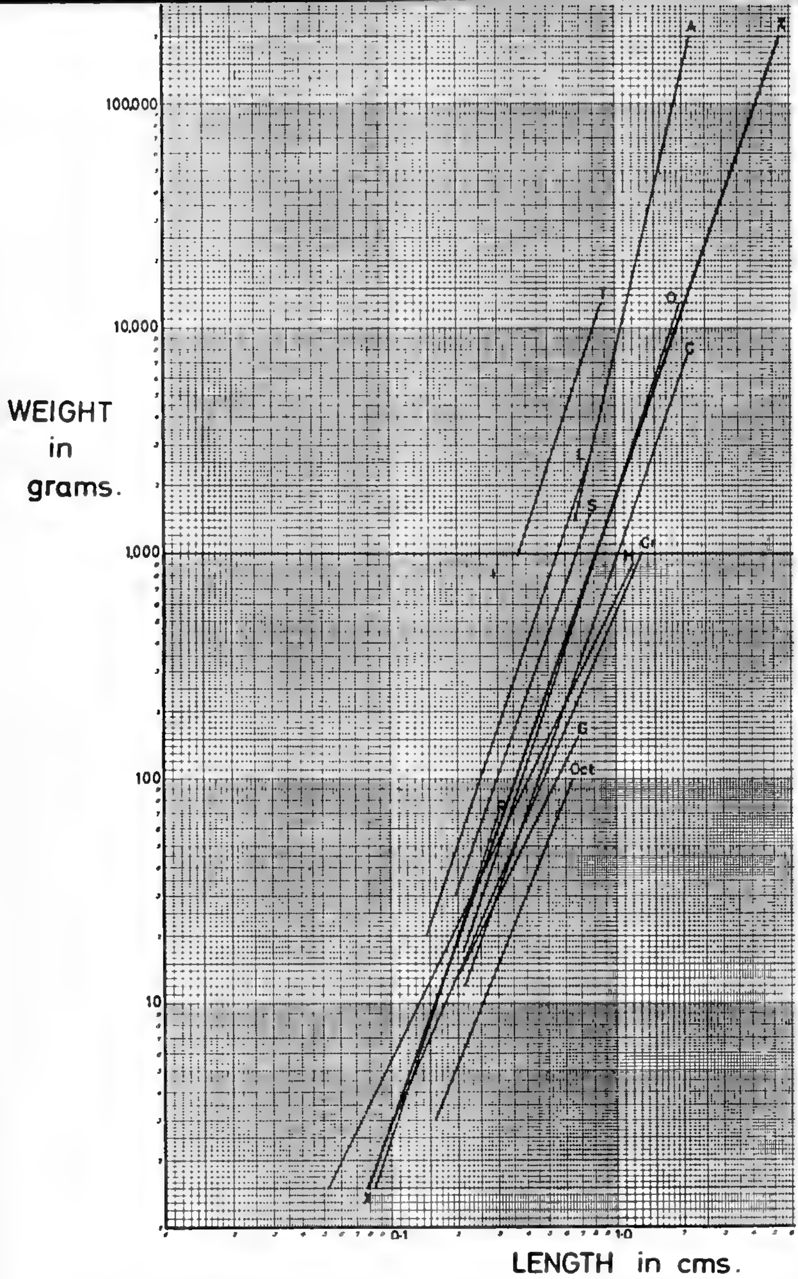

FIG. 24. A composite graph to show the calculated lines of the Oegopsid and Myopsid families dealt with here (with the exception of the Ommastrephidae which lies very close to the line labelled × and the Enoploteuthidae). The thick line labelled × was calculated by using points on the fitted lines for each family (three points were used for each family regardless of the number of specimens from which the family lines were derived). Thus this line is a very approximate mean line for oegopsids and myopsids as a whole.

T = Thysanoteuthidae ; A = Architeuthidae ; G = Gonatidae ; O = Onychoteuthidae ; C = Chiroteuthidae ; Cr = Cranchiidae ; Oct = Octopodoteuthidae ; H = Histioteuthidae ; L = Loliginidae ; R = Sepiolidae ; S = Sepiidae.

TABLE III.—*Table to show Relationship between a Beak Dimension and the Total Body Weight*

Family	Genus	Species	Dimension of beak used	Number of terms	*m*	*c*	Standard Deviation
Ommastrephidae	—	—	Lower rostral	156	2·93	3·24	0·145
	Sthenoteuthis	*caroli*	length	55	3·15	3·36	0·071
			,,				
	Todarodes	*sagittatus*	,,	39	2·83	3·17	0·123
	Todaropsis	*eblanae*	,,	14	2·45	3·01	0·086
	Illex	*illecebrosus*	,,	9	2·40	3·17	0·066
	Illex	*coindeti*	,,	14	2·47	2·98	0·076
Cranchiidae	—	—	,,	5	2·28	2·74	0·221
Chiroteuthidae	—	—	,,	4	2·83	2·98	0·129
Gonatidae	—	—	,,	2	1·99	2·52	—
Thysanoteuthidae	—	—	,,	3	3·06	4·30	0·181
Architeuthidae	—	—	,,	3	4·23	3·91	0·131
Octopodoteuthidae	—	—	,,	7	2·51	2·49	0·098
Onychoteuthidae	—	—	,,	24	3·00	3·25	0·105
Histioteuthidae	—	—	,,	32	2·04	2·79	0·121
Sepiolidae	—	—	,,	5	3·01	3·41	0·155
Sepiidae	—	—	Upper rostral length	13	2·83	3·50	0·090
Loliginidae	—	—	Lower rostral length	30	2·87	3·76	0·103
Octopodidae	—	—	Lower crest length	12	2·48	2·51	0·204
* All squids.	This equation was derived from points on the fitted lines (3 points for each family regardless of the number of specimens). This did not include the Octopodidae and Argonautidae		Lower rostral length (except in case of Sepiidae)	36	2·80	3·24	0·707

lines indicates that such an approximation will possibly be very inaccurate and should only be used as a last resort.

VII. DISCUSSION

Identification of a beak lies between the one extreme of recognizing it as a cephalopod beak and the other extreme of recognizing the race or population to which the cephalopod belonged. Here, I have been able to provide criteria which will distinguish between family groups and, in a few specific instances, between inferior groups. The present work shows that identification of beaks to the level of family is of great potential value. First, it will give much information regarding relative abundance of families in different geographic regions, details of maximum size and relative importance of the various families in the economics of the sea. Secondly, from the point of view of workers studying predators of squids, recognition of families present in stomachs may provide useful information concerning depth and areas of feeding and dietary requirements. Thirdly, if beaks can be grouped into families, a link may be established between loose beaks in a stomach or on a region of the ocean floor and the species of that family which are known to occur in the same region. For example, many species in the Ommastrephidae have fairly distinct geographical distributions which only partly overlap so that if a number of ommastrephid beaks are found in an area they are *more likely* to belong to perhaps one or two species commonly found in that area than to other species of the family. Thus, the *species* may be inferred by the use of criteria presented here, together with some knowledge of distribution. Similarly, beaks from stomachs may be tentatively identified to species when identifiable squids are found with the beaks in the same stomach. By examining the beaks of the complete squids and by using the stable criteria given here, it is possible to group loose beaks into probable species. This means of identification is obviously not infallible but it should prove useful in many instances (Clarke 1962b). Finally, when the relationship between rostral length and total body weight is examined, one finds that there are differences between families so that identification to family makes any calculation of body weight from rostral length more accurate than if all families are grouped together.

There are several reasons for wishing to calculate the total body weight from rostral length. Such a calculation gives an idea of the size and weight of squid represented by beaks in a predator's stomach or on a region of the ocean floor. The calculation, however, is rather inaccurate owing to several factors. Because of individual variability, estimates of the total weight from the rostral length are likely to be only very approximate. If one beak were used to calculate the probable weight of the squid which possessed it, the proportional error could be large. The proportional error would be less if an average weight of, say, a thousand beaks were calculated. This would be so, even if the curves for the various families were accurate. Some of the curves presented here are based on very few specimens so that they may not be very accurate and this introduces another serious error into weight computations. Another source of error accrues from the fact that the several species within a family may have different rostral length to body weight relationships (Text-fig. 14). This is found in the Ommastrephidae but inadequacy of material prevents an assessment being made for other families. Such intrafamily variation means that if only one species of a family is represented any calculation of the average body weight will be misleading if it is based upon the family curve instead of the species curve of body weight to rostral length relationship. This introduces a rather interesting theoretical point. There seems to be some relationship between the slope of the curve and the maximum weight of a species (in the Ommastrephidae) so that the deviation of a species from the mean curve of the family is limited in some way. This fact helps us because it limits the error which may result from the consideration of a single species. Although such an error should always be remembered, the fact that it *is* limited, means that the consideration of the family unit is still useful in cases where the species cannot be identified or their body weight to rostrum relationship is not known. Whether such a variation and limitation upon the variation exists in other families will only be found by the examination of further material. It is clear that

TABLE IV.—*A List of Authors who have Published Drawings of the Beaks of Some Cephalopods which have not been Available for Study Here*

This list is by no means exhaustive but does support the identification data given in this paper. The drawings vary in their detail but none of them disagree with the identification criteria presented here. The names given are those used by the authors.

Author	Date	Species
W. Adam	1941	*Lolliguncula mercatoris.*
	1954	*Grimpoteuthis* sp., *Meleagroteuthis hoylei*, *Stigmatoteuthis* sp.
S. S. Berry	1912	*Polypus bimaculatus.*
	1918	*Calliteuthis miranda*, *Loligo etheridgei*, *Sepia chirotrema Opistoteuthis persephone.*
C. Chun	1910	*Spirula australis.*
R. K. Dell	1951	*Histioteuthis cookiana.*
	1952	*Nototodarus sloanii*, *Sepioteuthis bilineata*, *Sepioloidea pacifica*, *Octopus maorum*, *Robsonella australis*, *Argonauta nodosa.*
W. E. Hoyle	1886	*Cirroteuthis magna*, *Octopus punctatus*, *O. marmoratus.*
C. Ishikawa	1914	*Enoploteuthis chunii.*
G. Jatta	1896	*Eledone moschata*, *Ocythoe tuberculata*, several other rather poor drawings.
L. Joubin	1924	*Vitreledonella richardi.*
A. Naef	1923	*Chiroteuthis veranyi*, *Alloteuthis media*, *Loligo vulgaris*, *Sepietta oweniana*, *Octopus salutii*, *O. unicirrus*, *Eledone moschata*, *Ocythoë tuberculata*, *Argonauta argo.*
R. Owen	1880	*Enoploteuthis cookii.*
G. Pickford	1949*a*	*Vampyroteuthis infernalis.*
	1949*b*	*Octopus bimaculatus.*
G. C. Robson	1932	*Grimpoteuthis meangensis*, *Haploclaena lunulata*, *Graneledone setobos.*
J. Steenstrup	1898	*Architeuthis* sp., *Gonatus fabricii*, *Ommastrephes pteropus ; Loligo forbesi.*
S. Thore	1949	*Dorsopsis taningi*, *Eledonella pygmaea*, *Amphitretus pelagicus*, *Vitreledonella richardi*, *Alloposus mollis.*
A. E. Verrill	1879–82	*Architeuthis* (5 species), *Histioteuthis collinsii*, *Loligo pealei*, *Heteroteuthis tenera*, *Octopus bairdii*, *Stauroteuthis syrtensis.*
G. Voss	1951	*Octopus burryi.*
	1953	*Pickfordiateuthis pulchella.*
	1956	*Architeuthis physeteris.*

the limitations discussed here, together with the limits of the accuracy of the weight measurements which have been mentioned above (p. 459) mean that an estimate of total body weight from the rostral length may possibly be very inaccurate. However, it will be a reasoned estimate based upon measurement and not a wild guess. As more squids are weighed and more beaks illustrated and measured the weight to rostral length curves can be improved.

A number of workers on cephalopods have included figures of squid beaks in their description of species. Such figures are widely scattered throughout the literature

TABLE V.—*Table of Nomenclature. A Comparison between Terms Used Here and Previous Terms*

Terms used here	Verrill	Steenstrup	Naef	Comment
1. Rostrum	Rostrum	Naeb	Beisefortsatz	The new term distinguishes between the edge and the inner sides.
2. Inner side of rostrum	Cutting edge		Beisskante	
3. Inner edge of rostrum				
4. Hood	Frontal lamina (in upper beak) Mentum or chin (in lower beak)	Pandedelen (in upper beak) Hagedelen (in lower beak)	Aussenplatte + part of Beisefortsatz	The new term is equally applicable to both beaks and its limits are clearly defined. —
5. Lateral walls and the crest	Palatine lamina (in upper beak) Gular lamina (in lower beak)	Ganepladen or Ganedelen (in upper beak). Strubedelen (in lower beak)	Innenplatte	The new term makes the two beaks comparable and it is more convenient to regard the two sides as separate.
6. Wings	Alae	Vinger	Seitenflugel	This term has been used before and explains the structures rather better than the alternative "alae".
7. Shoulder	Anterior or cutting edge of ala (in upper beak). Part of anterior edge of ala (lower beak)	Skjaerand	—	This term is a little more explanatory and is defined more exactly here.
8. Medial side or surface of the wing	—	—	—	—
9. Jaw angle	Notch	—	—	Notch implies a "recessed angle" and has been avoided for this reason.
10. Medial	—	—	—	Facing the sagittal plane of the beak.
11. Lateral	—	—	—	Facing away from the sagittal plane of the beak.
12. Outer	—	—	—	The side towards the outside of the animal.
13. Inner	—	—	—	The side towards the inside of the animal.

and I have made no attempt to make a comprehensive list of them. However, I have examined very many figures of beaks contained in such papers and have been unable to find any non-variable features which conflict with the diagnostic characteristics for each family which I have given above. A list of some of the authors who have published figures of beaks is given in Table IV (p. 474).

I have already (1962a) drawn attention to the possibilities presented by the identification of cephalopod beaks. Such an identification may be used in the study of stomach contents of cetaceans, seals, fish and birds.

In addition, beaks should help in assessing the distribution and relative numbers of the different families by a study of their occurrence in gut contents and in bottom deposits (Belyaev, 1959). The specimens from geological strata may facilitate the construction of an evolutionary tree of modern cephalopoda.

The closer study of beaks may prove useful in the study of specific and subspecific categories. As mentioned above (p. 436) *Todarodes sagittatus* from Madeira has a beak which darkens at a smaller size than specimens of the same species from Icelandic and Norwegian waters. Whether this difference is really subspecific or specific is not known at present but the beaks indicate a difference which should be investigated. Similar variations may help in resolving problems of identification in many difficult groups such as the family Histioteuthidae and the genus *Octopus*.

The fact that the older squids all have beaks which are extensively darkened, will be helpful in determining whether specimens represent the later stages of life or only the larval stages of a species. This should be very useful in the study of the Chiroteuthidae and the Cranchiidae in which the larval stages of some species have been given different specific and generic names from the adult (e.g., see Muus, 1956).

The larger species (e.g., *Architeuthis* spp. and *Dosidicus gigas*) have beaks in which extension of the dark region takes place at a large size when compared with all the species believed to be smaller which are considered here. This suggests a means of forecasting the presence of large specimens in a species. Thus for example, on these grounds, one would not expect to find very much larger specimens of *Histioteuthis bonelliana* and *Illex illecebrosus* than are known at present.

This preliminary work cannot pretend to be complete in itself but I hope that it will provide a foundation for future work and encourage closer study of beaks in relation to weight in cephalopods.

VIII. A KEY FOR THE PARTIAL IDENTIFICATION OF THE LOWER SQUID BEAKS CONSIDERED IN THIS PAPER

Text-fig. 25 should aid in the use of this key which is only intended as an aid in preliminary sorting. For further details the relevant sections of the text and the plates should be consulted. The lower beaks are usually more easily identifiable and are therefore considered in relation to the weight data.

1.	No clearly defined jaw angle	2
	There is a distinct jaw angle ; tip of rostrum is pointed	3

2. A ridge on the medial side of the lateral wall runs from near the jaw angle to the posterior corner of the lateral wall and this often has an undarkened region below it ; the shoulder is continuous with the rostrum ; the lateral walls are shallow *OCTOPODA*
There is no ridge at the bottom of the lateral wall ; there is a deep, semicircular recess in a position where the jaw angle is found in the squids . . . . SEPIIDAE
3. There is a clearly-defined, narrow ridge on the lateral wall 4
If a ridge is present at all, it is not narrow 5

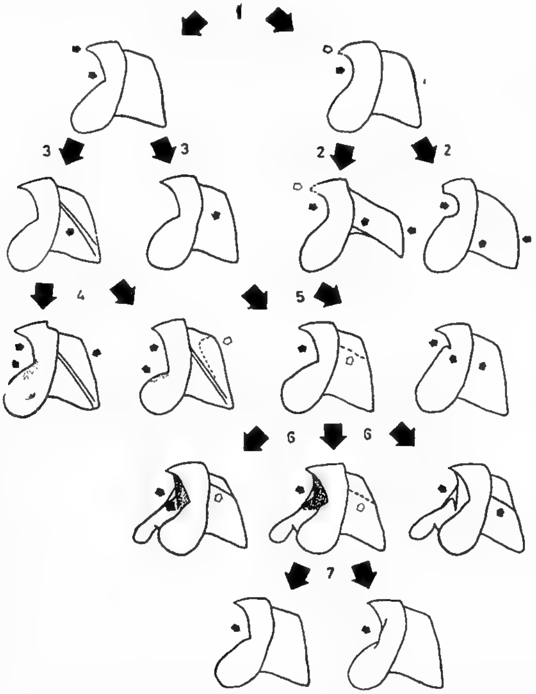

FIG. 25. Scheme for the preliminary identification of lower beaks. This should be used in conjunction with the key. Large arrows and numbers show the numbered operations of the key. Small arrows indicate the feature used at each stage. The light arrows indicate features which are useful but may or may not be present.

4. The area between the crest and the ridge of the lateral wall is darkened ; exposed cartilage does not cover the leading edge of the wing and lateral wall ; the rostrum is not noticeably longer than the wing . HISTIOTEUTHIDAE and ENOPLOTEUTHIDAE
The area between the crest and the ridge of the lateral wall may or may not be darkened ; exposed cartilage covers the leading edges of the wing and lateral wall (i.e., shoulder) ; the rostrum often has the appearance of being long in comparison with the wing length . . . . OCTOPODOTEUTHIDAE and CHIROTEUTHIDAE
5. The rostrum is short relative to the wing length ; there is no indication of a ridge on the lateral wall ; the jaw angle is clearly recessed.
ARCHITEUTHIDAE and THYSANOTEUTHIDAE

The rostrum is only slightly, if at all, shorter than the wing ; there may or may not be a ridge on the lateral wall ; the jaw angle may be slightly recessed, obtuse or acute . . . 6
6. There is a clear strip between the medial surface of the wing and the anterior of the lateral wall ; no ridge across the lateral wall but there may be a poorly-defined fold of the wall . . . Ommastrephidae
There is a "step" between the medial surface of the wing and the anterior lateral wall ; a distinct ridge runs across the lateral wall to the posterior edge Onychoteuthidae
Neither of the conditions found in the Ommastrephidae and the Onychoteuthidae are found in the region near the jaw angle ; there may or may not be a ridge running across the lateral wall . . . 7
7. There is no indication of a ridge running across the lateral wall ; the jaw angle can be seen when the beak is viewed in profile . . . Loliginidae and Sepiolidae
There may or may not be a ridge across the lateral wall ; the jaw angle cannot be seen when the beak is seen in profile because of a prominent fold of the hood-wing complex . . . Cranchiidae and Gonatidae

KEY FOR THE PARTIAL IDENTIFICATION OF THE UPPER BEAKS CONSIDERED IN THIS PAPER

Upper beaks are often very difficult to distinguish but some of them can be easily recognized and if they are found joined to the lower beaks by muscle their identification may be useful. This key is likely to prove most helpful when the larger beaks are being considered. For further details the text and the plates should be consulted.

1 Very short hood (see Pl. 22A) . . . Octopodidae
Hood not noticeably short . . . 2
2. Shoulder covered by cartilage . . . Chiroteuthidae and Octopodoteuthidae
Shoulder not covered by cartilage . . . 3
3. Jaw angle very obviously curved ; rostrum normal size ; shoulder does not form sharp cutting edge . . . Gonatidae
Jaw angle very obviously curved ; rostrum minute (Pl. 22E) ; shoulder forms a sharp cutting edge . . . Argonautidae
Jaw angle not clearly curved . . . 4
4. False angle present (in large specimens) . . . 5
No false angle . . . 6
5. The shoulder is rounded near the jaw angle to form a small false angle Enoploteuthidae
The broken edge of the wing forms the back of the false angle . . . 7
6. The inner end of the wing is transparent and the outer edge of the transparent region is straight . . . Ommastrephidae
If the inner edge of the wing is transparent the outer edge is not straight . . . 8
7. The lateral wall and the wing components of the shoulder extend forward to the same level or the wing extends further forwards than the lateral wall Onychoteuthidae (*Moroteuthis*)
The lateral wall extends further forwards than the wing Histioteuthidae and Cranchiidae (*Mesonychoteuthis*)
8 Jaw angle is obtuse . . . Sepiolidae
Acute or recessed jaw angle . . . 9
9. Very pronounced indentation in the periphery of the lateral wall . . . Sepiidae
Indentation not very pronounced Loliginidae, Architeuthidae and Thysanoteuthidae

SUMMARY

1. Cephalopod beaks have been described and precise terms have been defined which are applicable to both upper and lower beaks.

2. Changes in the relative dimensions and the darkening of beaks during growth have been described in a wide range of cephalopod families. Particular attention has been paid to the oegopsid families but details of myopsids and octopods are included for comparison.

3. Beak shape changes with increase in beak size and the dimensions bear a simple allometric relationship to one another. These relationships are different in the different families and were calculated by using the formula $\log y = m \log x + \log c$. The standard deviations of points from these " average " regressions was also found.

4. The variation of beak form has been studied and stable criteria have been found which may be used to identify beaks to family.

5. Features have been found which can be used to distinguish between some species within the same family.

6. A key for the preliminary grouping of beaks into families has been constructed.

7. The relationship between beak size and the total body weight has been found for all the families studied. Limitations in the use of beak size to estimate total weight are discussed.

8. Possible applications of this work have been discussed. Identification of beaks should aid the study of stomach contents and the study of the distribution, biology, systematics and evolution of squids.

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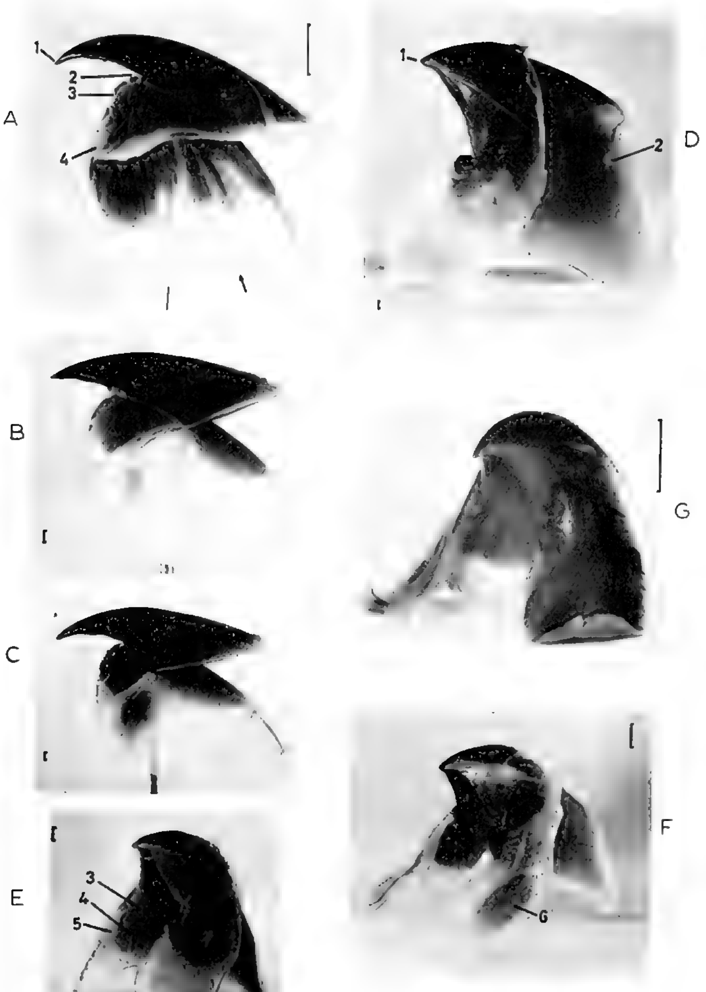
PLATE 13

The Ommastrephidae. A, B and C show the three stages of darkening of the upper beak. D, E, F and G show four stages in the darkening of the lower beak. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm. in B-F and 1 cm. in A and G.

A and G. N10D. 43 *Sthenoteuthis caroli.*
B. N10D. 74 *S. caroli.*
C. N10D. 72 *S. caroli.*
D. *Dosidicus gigas* B.M. 83.11.3.6.
E. *Todarodes sagittatus* Madeira 1959.7.
F. *Illex illecebrosus* Bidder, 1960.

Although several species are illustrated here all the stages of darkening occur during the development of the beak within each species.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D
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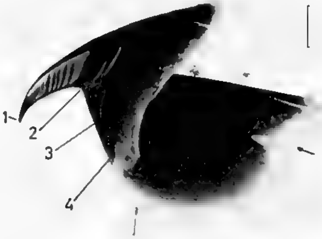
B
G
C
E
3
4
5
6
F
6

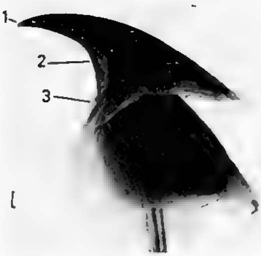
PLATE 14

The Onychoteuthidae (A–D) and the Gonatidae (E–G). A and E are upper beaks; B, C, D, F, G are lower beaks. A and B are *Moroteuthis* Antarctic, 1959–60. 1.; C and D are *Onychoteuthis banksi* Canada, 1957. 13.; E–G are *Gonatus antarcticus* "Discovery" Cephalopod catalogue No. 265. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm. in C–G and 1 cm. in A–B.

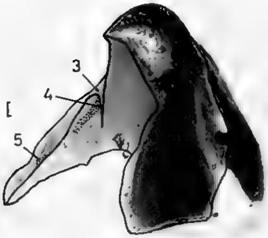
A



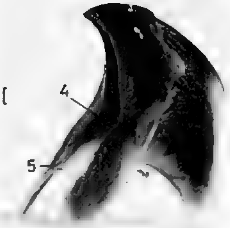
E



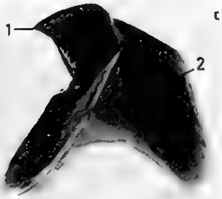
C



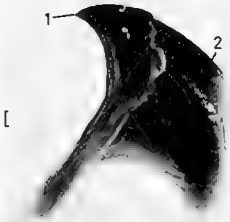
F



D



G

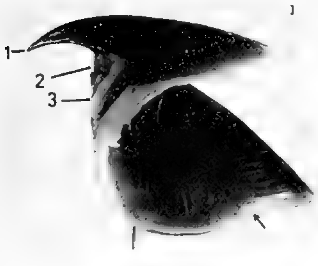


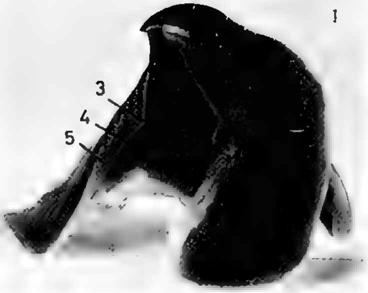
B

PLATE 15

The Histioteuthidae. A–C *Histioteuthis bonelliana* Madeira, 1959; D. *Calliteuthis dofleini* Canada, 1957.8; E–F *Calliteuthis* sp. Madeira, 1959.8. A upper beak; B–F lower beaks. D is at an earlier stage of development than E and F. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm.

A





C

B

D

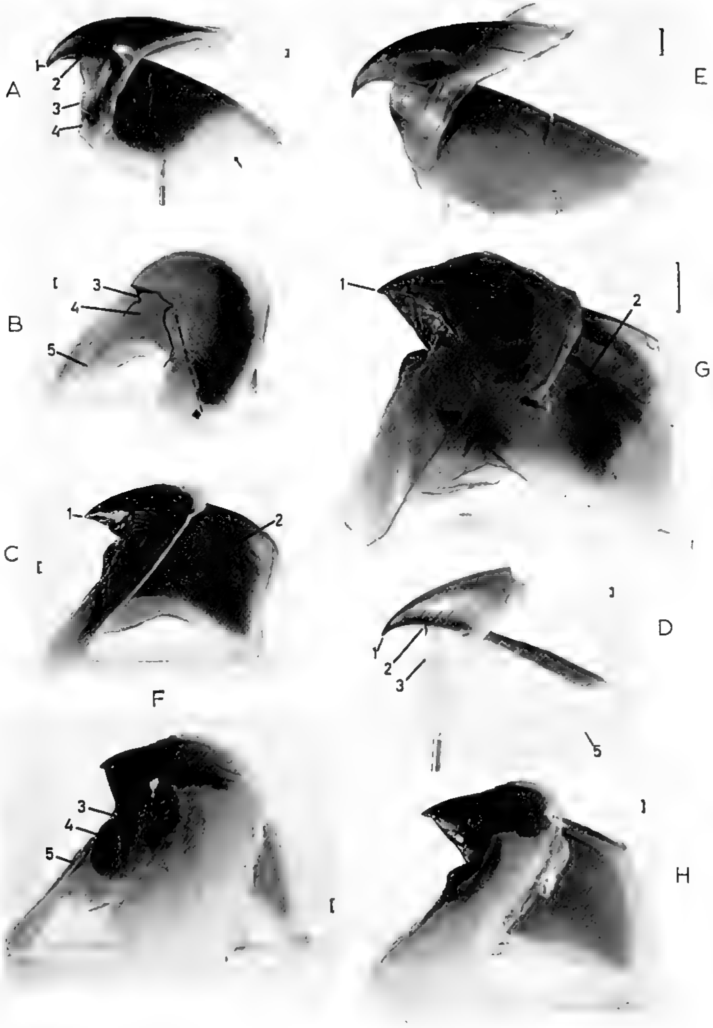
E

F

PLATE 16

The Thysanoteuthidae (A–C) and the Architeuthidae (D–H). A, D and E upper beak; B, C, F, G, and H the lower beak. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm. in A, B, C, D, F, H and 1 cm. in E and G.

A–C *Thysanoteuthis rhombus*, Madeira, 1959.
E and G *Architeuthis* sp. Azores. Robert Clark.
D, F, H *Architeuthis* sp. Madeira, 1959.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D
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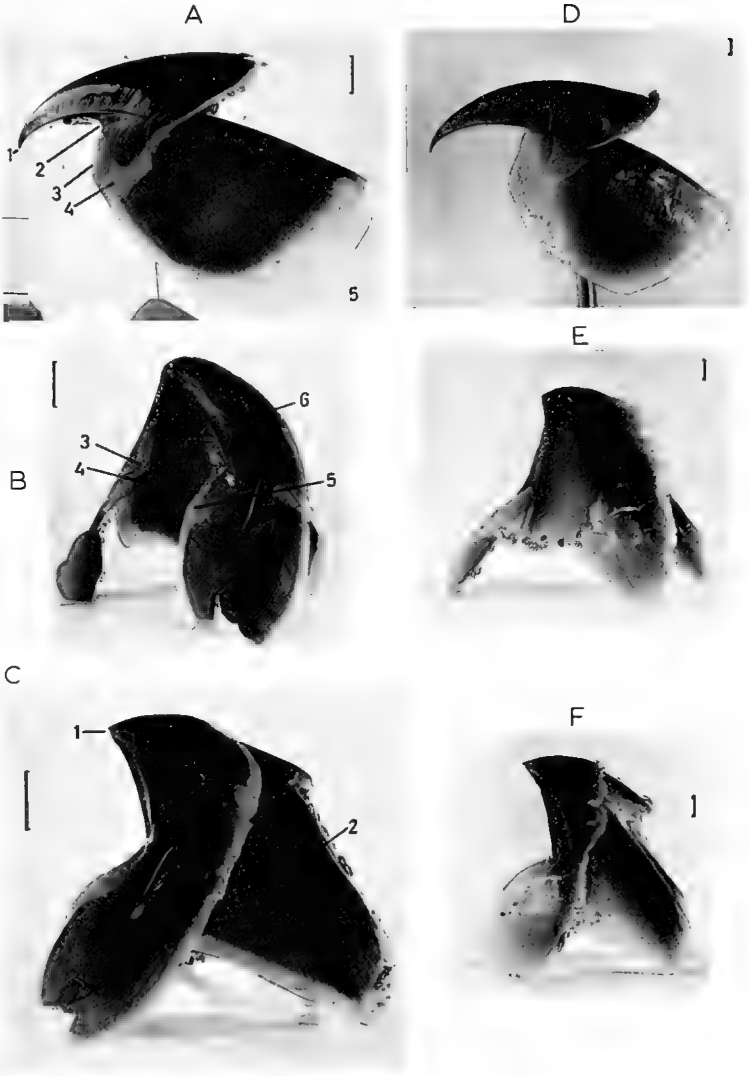
F
3
4
5
H

PLATE 17

The Octopodoteuthidae. A–C *Cucioteuthis* Madeira, 1959; D–F *Octopodoteuthis* "Discovery" Cephalopod catalogue No. 230.

A and D upper beaks; B, C, E and F lower beaks. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm. in D–F and 1 cm. in A–C.


A
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C
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2
F

PLATE 18

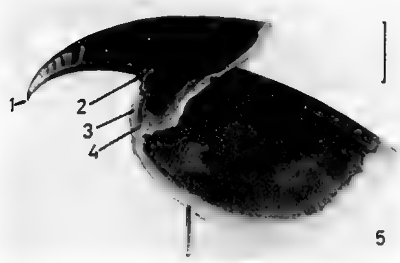
The Chiroteuthidae (A–E) and the Enoploteuthidae (F–G).

A–C *Lepidoteuthis grimaldi* Madeira, 1959. C.
D–E *Mastigoteuthis* sp. " Discovery " Station 4259.
F–G *Enoploteuthis leptura* " Discovery " Station 4743.

A, D and F upper beaks; B, C, E and G lower beaks. The numbers indicate features useful for identification and are explained in the text.

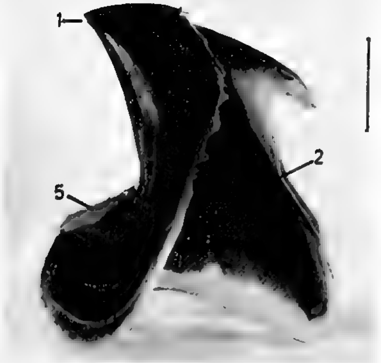
The scales represent 1 mm. in D, E, F and G, and 1 cm. in A–C.

A



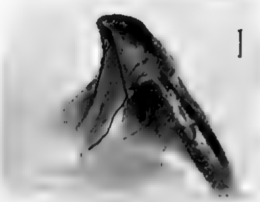
B

C



D

E



G

F

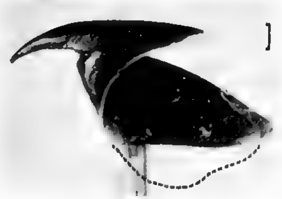


PLATE 19

The Cranchiidae. A–C *Phasmatopsis cymoctypus*, 1959
D *Taonius megalops* Canada, 1957.
E and F *Mesonychoteuthis hamiltoni* Antarctic, 1959–60, 11.

A the upper beak; B–F lower beaks. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm. in A–D and 1 cm. in E–F.

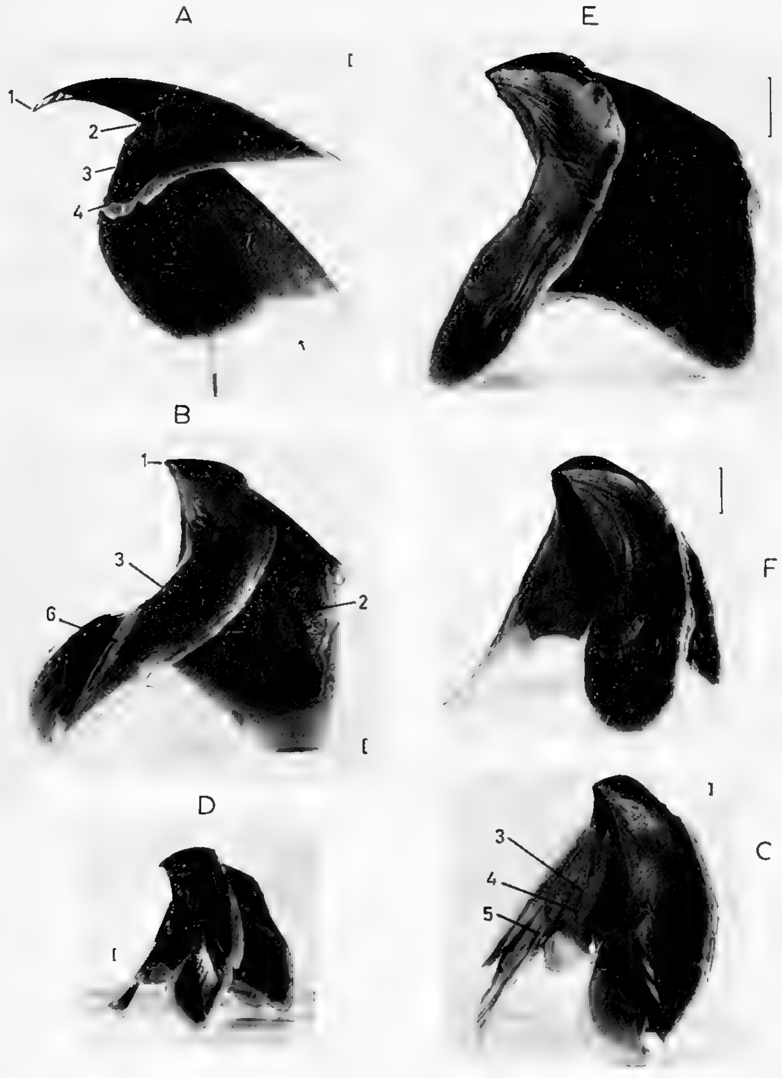

A
1
2
3
4
E
B
1
3
6
2
F
D
C
3
4
5

PLATE 20

The Loliginidae. A and B *Loligo forbesi* Plymouth 1950.6.
C *Loligo forbesi* N10D. 72.
D F *Sepioteuthis* B.M. No number.

A and D upper beaks; B, C, E and F lower beaks. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm.

PLATE 20

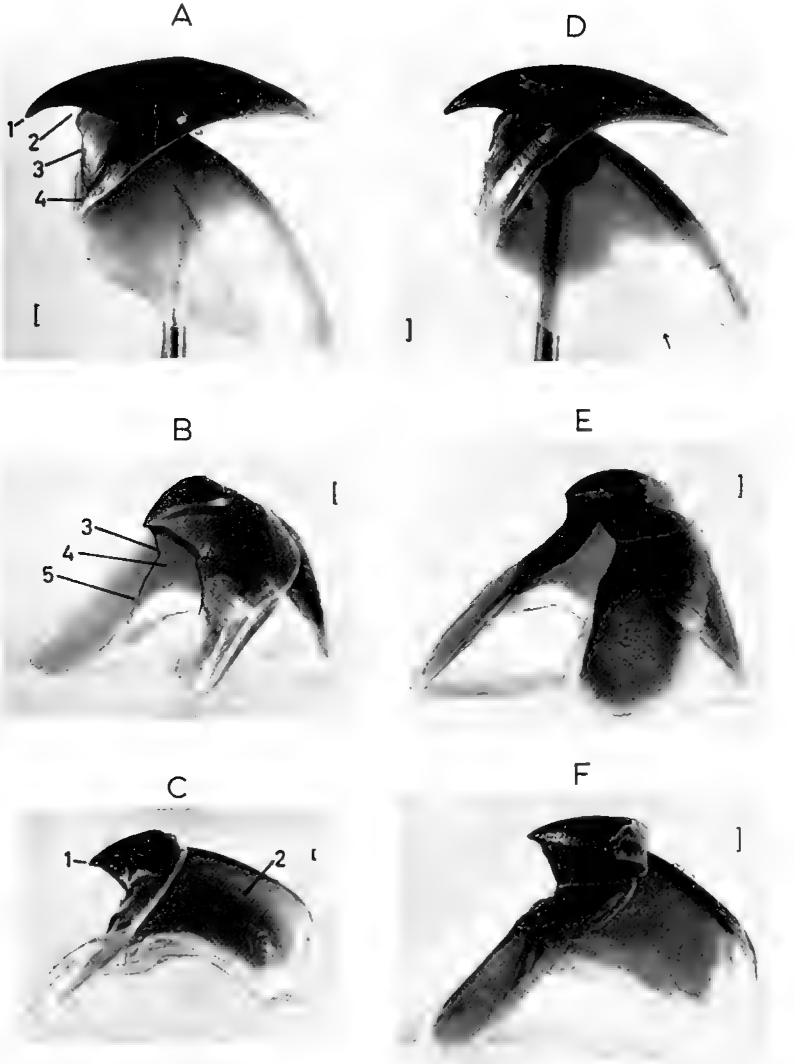


PLATE 21

The Sepiolidae (A C) and the Sepiidae (D G) A and D upper beaks; B, C, E, F and G lower beaks. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm.

A–C *Rossia macrosoma* var. (very large).
J. A. Stevenson 22.5.28. Scarborough.
D B.M. 1947.10.14.1 2.
E–G *Sepia officinalis* Madeira, 1959 1.

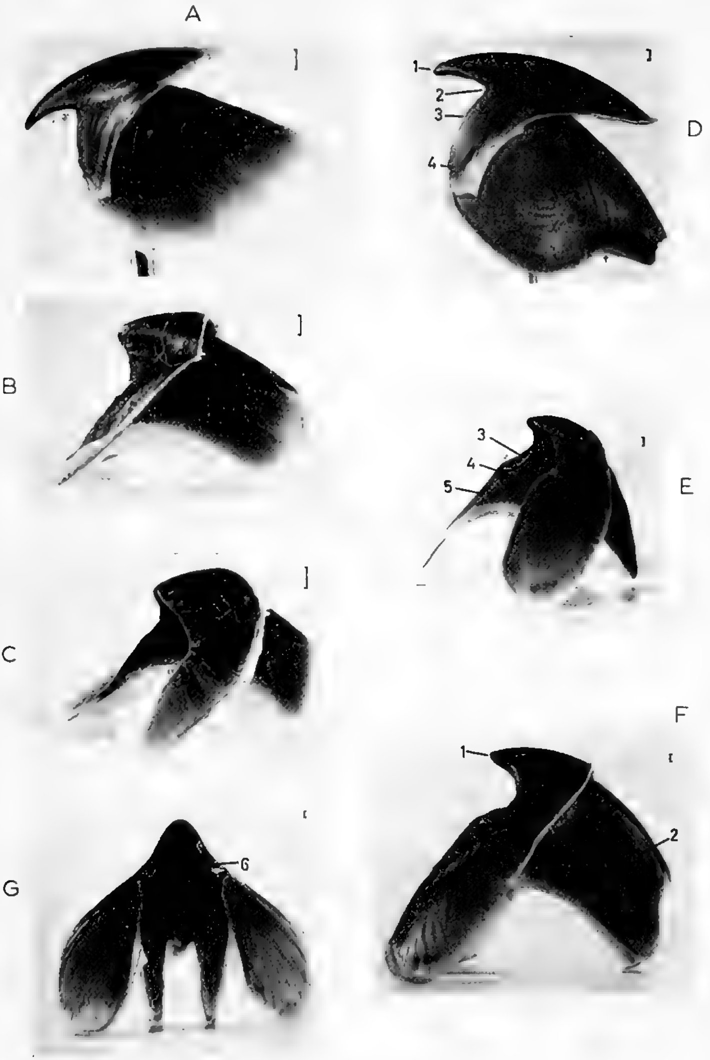
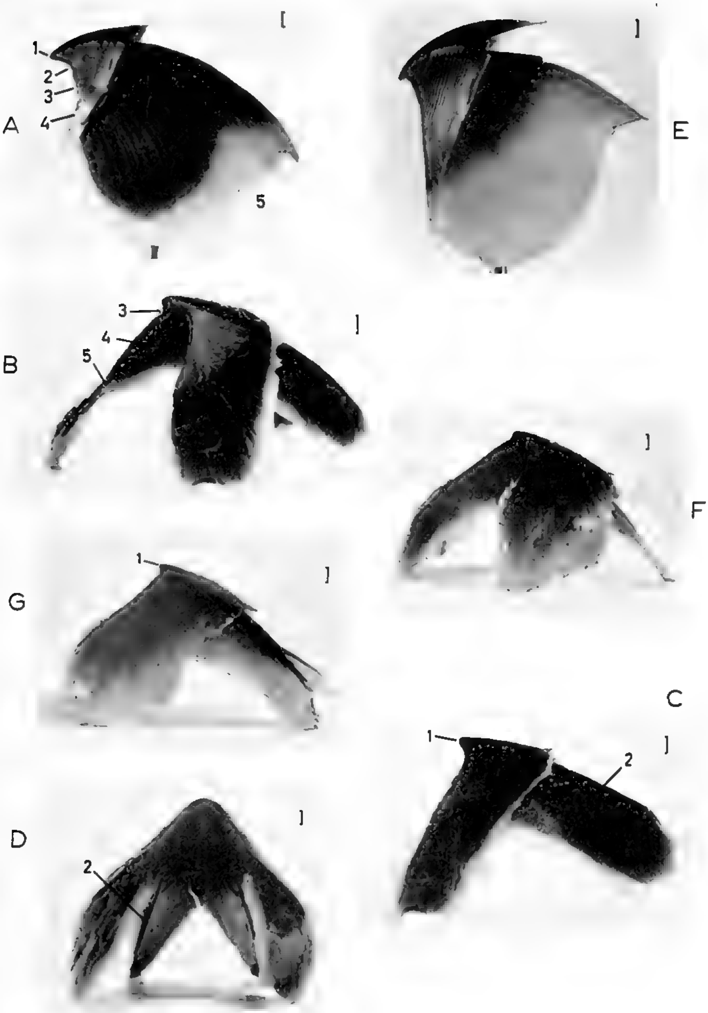

A
1
2
3
4
D
B
3
4
5
E
C
F
1
2
G
6

PLATE 22

The Octopodidae (A–D) and the Argonautidae (E–G). A and E upper beaks; B–D and F–G lower beaks. The numbers indicate features useful for identification and are explained in the text. The scales represent 1 mm.

A C *Eledone cirrhosa* B.M. 1929.11.13.1–2.
E G *Argonauta argo* B.M. 64.2.

PLATE 22



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The page numbers of the principal references and the new taxonomic names are printed in **bold** type.

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