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No. 1.—*Observations on the Egg-Capsules of Skates of the Family Rajidae, found in Japan and its adjacent waters*[1]

By Reizo Ishiyama[2]

INTRODUCTION

Elasmobranchs, as a group, are viviparous, ovoviviparous or oviparous but the batoids reproduce by the latter two processes only. Among the batoids all of the members of the family Rajidae are known to be oviparous, the eggs, fertilized internally, being deposited on the bottom there to develop and hatch. As between the ovoviviparous and oviparous types of breeding the reproductive organs do not differ fundamentally for in both cases the egg is enclosed in a capsule made by either a thin or a thick membrane, the tertiary egg envelope (Wilson, 1928, after Ludwig 1874) formed by the shell gland of the oviduct. In the ovoviviparous type, the capsule is made of the very thin beautiful membrane which serves the young fish only through its early development, and the young developed from the egg undergoes its development to adult form in the uterus. But in the oviparous species the egg when spawned is covered with a thick leathery membrane, the egg-capsule or shell. Thus two forms of the egg-capsule are recognized, the temporary and the permanent, which are, so to speak, superficially coincident with these two types of breeding habit. The type of viviparity for some batoids is not yet known but the skates belonging to the family Rajidae are typically oviparous and the egg, covered with a thick capsule, is laid in the early stage of development.

As regards the egg-capsules of Japanese rajid fishes the present writer gave a brief account, in which he pointed out that the features of the capsule seem to throw light upon the taxonomic status of the parent (Ishiyama, 1950). Subsequently, the features of the capsules of several species were annotated to assist in the identification of the species, as based on the above mentioned opinion (Ishiyama, 1952, 1955).

Prior to these works, a good deal of detailed and concise description of capsules of many species of elasmobranchs had already been given by a number of authorities. Of these, Clark

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(1922) attempted to incubate the eggs, and followed this with a description of the young of various European rajids. Dean (1904, 1906, 1912), Vladykov (1936), and Bigelow and Schroeder (1953) also made some observations in more or less detail on the features of the capsules of certain species. The conclusions made from the present investigation have been based in part on these works, as well as on various reports given by other authors.

In the present study, it has been found that the egg-capsules of Japanese rajid fishes have certain features that aid in their identification besides establishing possible relationships between genera and even between species; also these features may throw some light on adaptive differentiation of various species.

It is a pleasure to record here a debt of gratitude to Dr. K. Matsubara, Professor of the Kyoto University, for his kindness in giving valuable suggestions and in contributing a number of specimens for study. I am especially indebted to Dr. Henry B. Bigelow and to Mr. William C. Schroeder of the Harvard Museum of Comparative Zoology and the Woods Hole Oceanographic Institution for much assistance in the preparation of the manuscript. Further, many colleagues working on fisheries biology at various stations in Japan helped me with collections of specimens and with important literature. To them I am grateful.

MATERIALS AND METHODS

The specimens used in the present study were collected at various localities (Table 1 and Fig. 1), where the egg-capsules were obtained directly from parent females of three genera, involving twenty-one species and two subspecies, which represent almost all those members that are known in the seas around Japan. In addition to these, some capsules were removed from both oviparous and ovoviviparous adults, and the rest were gathered in the field. All the specimens are preserved in a formalin solution (10%) in our college.

The examinations were first made on the external features and followed by histological study, the specimens being cut in sections, 20-50 micra thick, with the aid of a cylinder microtome.

Table 1

The number of egg-capsules examined of 21 species and 2 subspecies of Japanese skates, together with localities, depths, and temperatures where parent females were captured. The six species and two subspecies which are abbreviated by the letters C, J, N, P, Q, Q′, S and W, respectively, are thought to be new to science. Abbreviations within brackets represent the seas where the specimens were collected: [C], East China Sea; [J], Sea of Japan; [O], Okhotsk Sea; [P], Pacific Ocean.

	Scientific name and its letter symbol			No. of egg-capsules examined and localities	Depth (m) followed by temperature (°C) where the parent females were captured*	
Northern form	Breviraja	tobitukai	A	5 [P]	300-400	9-10
	B.	isotrachys	B	4 [J;O]	90-230	3-4
	B.	sp.	C	5 [P]	500-700	3
	B.	diplotaenia	E	5 [P]	300-500	2-3
	B.	matsubarai	F	2 [P]	800-1000	2
	B.	aleutica	G	12 [P]	300-700	2
	B.	parmifera	H	2 [P]	?	?
	B.	smirnovi	I	4 [O]	100-200	5
	Rhinoraja	sp.	J	2 [P]	230-400	9-10
	Rh.	kujiensis	K	6 [P]	600-800	2
	Rh.	longicauda	L	4 [P]	300-600	5
Southern form	Raja	kenojei	M	10 [J]	80-90	17
	R.	sp.	N	6 [J]	50-90	21
	R.	hollandi	O	32 [C;J]	70-90	14
	R.	sp.	P	4 [J]	80-90	17
	R.	subsp.	Q	5 [J]	80-150	8-10
	R.	subsp.	Q′	8 [P]	30-50	21
	R.	fusca	R	4 [P]	20-50	12
	R.	sp.	S	4 [P]	20-40	11
	R.	tengu	T	2 [P]	150-200	14
	R.	pulchra	U	25 [J;O]	50-100	8
	R.	macrocauda	V	7 [P]	300-400	10
	R.	sp.	W	2 [P]	300-400	10

DESCRIPTION AND COMPARISON OF THE EGG-CAPSULES

A. External features:

Shape. The egg-capsule in rajids is usually rectangular in shape with a horny process at each corner. The anterior end of

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* Data from the Annual Report on the Fish Resources in Oct. 1951-Sept. 1952, Section 4: Bottom Fishes, published by Tohoku Regional Fisheries Laboratory, 1954, and from the Semi-Annual Report on Oceanographical Investigation Nos. 70-74, compiled by the Tokai Regional Fisheries Laboratory and published by the Investigation of Research Division of Fisheries Agency, 1943, 1951 and 1953.

the capsule is tightly fused with a more or less flattened margin which is directed downwards towards the head of the parent fish, but posteriorly it is loosely closed with a thinner pellicle, from which the embryo emerges at hatching, in most cases. The sides are in general finely keeled lengthwise, to a greater or lesser degree, for almost the entire length excepting the capsule of species U[1] (Fig. 3, U).

On the basis of shape, the egg-capsules may be classified into six forms (Figs. 2, 3) which will be described in detail.

Both dorsal and ventral sides of the capsules are more or less convex, but the dorsal side is in general decidedly more domed than the ventral and forms the dorsal border which is oriented towards the dorsal side of the body.

Size. It should be particularly noticed that the egg-capsule in the rajids is relatively large in size, although rather considerable intraspecific variations are found to exist in some cases. As a matter of fact, the size of the capsule may serve as a means for grouping the species. Measurements showing the variations in two examples follow.

Table 2

Variations in the dimensions of the capsules of two species, P and U. The numbers in parentheses represent the number of species examined.

Species	Main portion		Horns	
	length, mm.	width, mm.	anterior, mm.	posterior, mm.
P (32)	53.2-65.9	31.5-39.2	15.0-22.0	11.0-22.0
U (25)	140-185	70-94	——	——

The sizes of the egg-capsules were found, in general, to bear a relationship to the sizes of the parents, as illustrated in Figure 4, which would seem to be different from that given for birds (Huxley, 1932, p. 225).

Horns. At each of the four corners of the capsule there is shown a projection, the horn, one pair of which is usually longer than the other. Both the length and shape of the horn are im-

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[1] For the sake of brevity in the description, the specific names of all the rajids treated here are abbreviated by letters as shown in Table 1.

portant as a means of specific identification. Usually, the horn on the capsule of the northern form is long, whip-like in shape, and pointed distally, whereas it is reduced into a very short or rudimentary tube-like process on that of the southern form.

The length of the horn shows rather large intraspecific variations, as is shown in Table 2, so that it is possible to give only approximate dimensions for a given species. This difficulty is caused partly by the incomplete elongation of the distal portion and partly by the curling in that portion. As a rule, the length of the posterior horns tends to appear a trifle longer than that of the anterior ones.

As regards the features of the horn, the fissure, i.e., the slit, opening, or pore, which is the respiratory perforation located on the border of each horn, should be noticed (Figs. 2, 3). The perforation is tightly closed by an albumen-like substance, or soft tissue, when the capsule is deposited, but the substance closing the perforation vanishes gradually as development goes on. In the capsule referable to the northern form, the longitudinal fissure is present on the outside border near the tip of, or at the halfway point of, the horn (Fig. 2). In the southern one, however, the opening occurs either at the distal part of the horn or at each corner of the capsule (Fig. 3). With the features of the horn thus explained, the following six groups, H^1 to H^6, may be distinguished.

Group H^1 (Fig. 2, A) includes the capsule of but one species (species A), in which the horn is roundish in cross section, whip-like in shape, and is furnished with a longitudinal narrow slit located near the tip of the horn. The posterior horn is much longer than the anterior one. Group H^2 (Fig. 2, I) is found in the capsules of species H and I, where the horn is rather short, tape-like in shape and pointed at the distal end. The slit occurs near the halfway point of the horn, and moreover, its location differs between the anterior and posterior horns. Namely, the slits of the anterior ones are developed on the opposite side to those of the posterior horns. Group H^3 (Fig. 2, G) is represented by eight species: B, C, E, F, G, J, K and L. The horn of this group is intermediate between those of the preceding groups, but it is polygonal in cross section, and the slit is located far from the tips of both the anterior and posterior whip-like horns, the posterior usually being the longer. Group II^4 (Fig. 3, T) involves the horns found in the capsules of nine species (M, N, O, P, Q, R, S, T and V), all of which are southern members. The horn of this group is much shorter than that of most of the other members, tube-like in shape, and its opening is located at the distal end. Group II^5 (Fig. 3, U) is found only in species U, in which the horn is reduced to a short, flat projection connected with the broad lateral wing of the capsule. The slit opens near the tip of the projection. Group II^6 (Fig. 3, W) is represented by one species (species W), where the projection is rudimentary, caused by a broad expansion of both the lateral and the anterior-posterior margins of the capsule, and the opening is formed at each corner of the rectangle.

Configuration of the surface. There is a marked difference in the configuration of the surface of the main portion of the capsule between the northern and the southern forms. The capsule is more or less roughened with minute prickles or tubercles developing over the entire surface in that of the northern form, but it is, in general, very smooth in the southern one.

It may be convenient to compare the features of the northern and southern forms with the structural evidence of the capsules examined histologically as will be mentioned later on.

Fibroid tendril. The egg-capsule in the rajids is usually covered with a tight-fitting felty mass of fibres immediately after it is extruded from the parent female, but the fibres are gradually reduced after it is deposited in the sea. The lateral margin of the capsule is also provided with a mass of loose fibres, well developed in the species belonging to the northern form, especially in those found in deep water (Fig. 2, F, I), although the fibres are found to occur in greater or lesser degrees in all examples dealt with here. The degree of development of the felty mass of fibres in some cases is a character of value in distinguishing one species from another.

B. Histological structure of the egg-capsule:

The main portion of the capsule in the rajids is made of two or more kinds of tissue, which are referred to as an inner, pulpy, layer and an outer layer (Ishiyama, 1950). In general, the inner layer forming the lining of the capsule-wall is relatively soft and colorless, but the tissue becomes hard and the color changes from yellow to brown in the outer layer which covers the surface of the capsule. Generally the capsule in the northern form is characterized by having a much thickened outer layer which reveals, in different species, various features on the surface by the development of either tubercles or prickles of a hard, horny, brown substance. But the inner layer is rather thin, and without a noticeable difference in histological structure in the different species. In the southern members, on the other hand, a specialization is found to exist not only in the outer layer but in the inner one as well. Based on certain characteristics the writer classifies the capsules of the Japanese rajids into seven groups, abbreviated herein as Group Eg^1 to Eg^7.

Group Eg^1 (Fig. 5, A) is represented only by species A. The capsule-wall is made of two layers, the inner one being relatively thick with parenchymatous structure, whereas the outer one is very thin and faintly colored. A capsule of this type is smooth externally, translucent, and the yolk mass is visible *in situ*. This type may be the most primitive with respect to its histological structure. Group Eg^2 (Fig. 5, I) may be exemplified by the capsules of two species, H and I, in which the tissue of the wall consists of two layers, the outer one being very thick and bearing many dark-colored tubercles so that the surface of the capsule is rather rough. With regard to the degree of development and the shape of the tubercles two forms may be recognized, referred to here as Subgroups Eg^{2A} and Eg^{2B}. In Subgroup Eg^{2A} the character of the wall is as described above and shown in Figure 5, I in which the tubercles are sparsely developed in lengthwise series, and bear domed apexes when cut in cross section. Subgroup Eg^{2B} (Fig. 6, H), which corresponds to the Parmifera-type in my previous report (Ishiyama, 1950), is exemplified by that of species H; the tubercles occur more densely than in the preceding, and reveal a rather rough surface because of the many minute ridges running in lengthwise series. Group Eg^3 (Fig. 5, L) is exemplified by the capsule of two species (J and L), which corresponds to the Isotrachys-subtype in a previous paper (Ishiyama, 1952). The wall of this type also consists of the two layers, the outer being provided with some stalks and prickles as well, both of which are in a lengthwise series forming many obscure, minute longitudinal ridges. Group Eg^4 (Fig. 5, B) includes capsules belonging to six species (B, C, E, F, G and K), these capsules having in common a thorny, very rough surface. The tissue consists of the two layers, of which the outer one is very thick and characteristic. The surface is densely armed with numerous series of minute velvety prickles. Here, the fact should be mentioned that there exist three different forms of the spination which are referred to as Subgroup Eg^{4A} to Eg^{4C} Subgroup Eg^{4A} (Fig. 5, B; Fig. 6, C, E) includes the capsules of three species (B, C and E) and corresponds exactly to the Isotrachys-type in my previous report (Ishiyama, 1950). In this subgroup, the minute prickles covering the capsule are perpendicular to the surface, so that it feels very thorny when touched. The degree of development of the prickles, however, has progressed more in the capsule of species E than in that of species B and C (Fig. 7, B, E). Subgroup Eg^{4B} (Fig. 6, G, K) is represented by species G and K, whose capsules are characterized by having numerous, elongated prickles bent nearly horizontally forward on the surface of the capsule (Fig. 7, G). The length of the prickles is somewhat greater in species G than in K. Subgroup Eg^{4C} (Fig. 6, F) involves only the capsule of species F, and is quite peculiar in the manner of its armature, being referred to as the Isotrachys-supertype in my previous report (Ishiyama, 1952). The general features of the proper capsule and its histological structure are rather similar to Subgroup Eg^{4A}, but Subgroup Eg^{4C} differs from the latter in having many prickles which form a velvety texture on the surface densely beset with small stiff rods serrated at the tip, over which many strong fibroid masses of hair entirely cover the surface. Such being the case, the capsule has a rather smooth surface *in situ*, owing to its fibrous covering. It is believed, therefore, that this type of capsule might have evolved from the related forms, for it seems to be the most specialized.

Capsules of the southern species may be separated into three groups although they fall into but two groups as regards their features *in situ*. Group Eg^{5} (Fig. 5, R) is characteristic of the capsules of species R and subspecies Q and Q′, which have a smooth surface and a wall composed of two layers, a condition commonly found among the northern members. The inner layer is relatively thick instead of being thin, while the outer one has no differentiation on the outermost tissue. A capsule of this group seems to have the most generalized character, somewhat approaching that of Group Eg^1 aforementioned. Group Eg^6 (Fig. 5, T) includes the capsules of seven species: M, N, O, P, S, T and V. The capsules referred to this group appear much the same in external appearance as the preceding, but the two are sharply defined in histological structure. The tissue of the inner layer of Group Eg^6 is characterized by having a pulpy layer inserted in greater or lesser degree. Therefore, the wall is made of three layers, of which the outer one is usually very thin and furnished with minute granules which correspond to the basal portion of the fibroid hairs, covering the surface of the capsule. It must be pointed out here that both Groups Eg^5 and Eg^6 were included in the Kenojei-type, which was divided into two groups, as mentioned above in a foregoing report (Ishiyama, 1950), being based on histological evidence. Further, it is of considerable importance to record here that the relative thickness of both the inner and the pulpy layers differs among species (Fig. 5, T; Fig. 8, M, N, O, P, S, V). Thus the pulpy layer in species T is very thin as compared with the relatively thicker inner one, but both layers have moderate thickness in species M, S, and V, and the pulpy layer is quite remarkable in thickness as revealed in species N, O and P.

Based on these facts it may be possible to use the above characteristics in identifying those capsules which are quite similar in external appearance and thus difficult to distinguish one from another.

Group Eg^7 (Fig. 5, W) is represented by the capsule of species U and W. The wall referable to this group is also composed of three layers, as is the case with the preceding, but these are greatly different in respect to their histological structure and surface configuration as well. The pulpy layer of this group is reticulated to form a porous structure which is backed internally by a very thin inner layer; and besides, the outer layer becomes very thick, containing externally several zones of fibrous frame, transformed from the outermost tissue of the layer, and the surface is roughened by having longitudinal tubular fibres which can easily fall out by themselves without any strong friction. This group was referred to previously as the Pulchra-type in marking the characteristics observed on the capsule of species U, but the fibres which form the outermost tissue are different in the capsules of species U and W, the tissue in that of species U having very thickened fibres (Fig. 8, U) rather than fine thread-like ones as in species W (Fig. 5, W).

On the basis of these facts it may be said that this group (Eg^7) seems to be the most highly specialized among those found in the southern forms, and further, the structure revealed in the capsule-wall in species U may be more advanced than that in species W. On account of the evidence mentioned above, it will be assumed that the two extremes in the course of specialization in capsules of the southern form may be represented by Groups Eg^5 (Fig. 8, Q) and Eg^7 (Fig. 8, U).

Thus, the examination of the features of the capsules reveals much diversification in both the external and histological characteristics in the Japanese rajids.

DISCUSSION

1. SYSTEMATIC SIGNIFICANCE OF THE EGG-CAPSULE

Based on the facts found in the external as well as in the histological characteristics of the egg-capsules of Japanese rajids, the present writer gives an analytical key to species and groups of species. From this key we may be able to recognize that the characteristics of the capsules are not only of much importance as a means for their identification but also that they seem to be of taxonomic importance.

1a. Very large in size, measuring more than 100 mm. in length exclusive of horns.

2a. Surface very rough being velvety in texture, Group Eg^4.

3a. Without strong fibroid hairs entirely covering the surface; prickles devoid of small stiff rods at their tips.

4a. Prickles rather long being perpendicular to surface, Subgroup Eg^{4A}.

5a. Posterior horns longer than width of capsule; capsules 106 mm. to 132 mm. in length and 76 mm. to 86 mm. in width . . . . *Breviraja isotrachys* (B, in Figs.); *Breviraja* sp. C (C, in Figs.).

5b. Posterior horns shorter than width of capsule; capsules 106 mm. to 120 mm. in length and 76 mm. to 78 mm. in width . . . . *Breviraja diplotaenia* (E, in Figs.).

4b. Prickles very long, bending anteriorly, Subgroup Eg^{4B}.

6a. Capsules much larger than those of other northern forms, about 120 mm. to 136 mm. in length and 73 mm. to 90 mm. in width; posterior horns longer than width of capsule; capsule-wall, exclusive of prickles, rather thin, being about 0.3 mm. in thickness
Breviraja aleutica (G, in Figs.).

6b. Capsules smaller than those of the preceding, about 104 mm. to 115 mm. in length and 69 mm. to 80 mm. in width; posterior horns almost equal to width of capsule; capsule-wall rather thick, measuring about 0.5 mm. to 0.6 mm. in thickness exclusive of prickles.
Rhinoraja kujiensis (K, in Figs.).

3b. Strong fibroid hairs entirely covering prickles, which are densely furnished with small stiff rods at their tips, Subgroup Eg^{4C}; length and width of capsules about 109 mm., to 113 mm., and 65 mm. to 67 mm., respectively; posterior horns longer than width of capsule; capsule-wall relatively thin, measuring about 0.2 mm. in thickness exclusive of prickles *Breviraja matsubarai* (F, in Figs.).

2b. Surface smooth or somewhat rough, without any velvety texture, Groups Eg^{2}, Eg^{6}, and Eg^{7}.

7a. Surface somewhat rough; horns tape-like in shape or reduced to rudiments, Groups H^{2}, H^{5}, and H^{6}.

8a. Horns rather long, growing slenderer toward tips, pointed at their tips, with a longitudinal slit located at their basal parts, Group H^{2}; capsule-wall composed of two layers, the outer one furnished with many tubercles over the surface, Group Eg^{2}.

9a. Length and width of capsule about 150 mm. and 90 mm., respectively; tubercles covering outermost layer sparsely developed with domed apexes, Subgroup Eg^{2A} *Breviraja smirnovi* (I, in Figs.).

9b. Length and width of capsule about 120 mm. and 90 mm., respectively; the tubercles densely developed with ridged apexes, Subgroup Eg^{2B}
Breviraja parmifera (H, in Figs.).

8b. Horns very short or rudimentary, with a round opening located at their tips or at each of the four corners, Groups H^{5} and H^{6}; capsule-wall composed of three layers, the outermost composed of many fibres running lengthwise in series, Group Eg^{7}.

10a. Horns very short, with the opening at their tips, Group H^{5}; broad notches present on sides; length and width of capsules from 140 mm. to 185 mm. and from 70 mm. to 94 mm., respectively
Raja pulchra (U, in Figs.).

10b. Horns reduced to rudiments, with an opening at each of the four corners, Group H^{6}; notches absent on sides; fibres composing outermost tissue less in diameter than those in 10a; greatest in size of all capsules examined, measuring about 235 mm. in length and 145 mm. in width. *Raja* sp. W (W, in Figs.).

7b. Surface smooth; horns short, tube-like in shape, Group H^{4}.

11a. Length of capsule about 100 mm.; capsule-wall very thick, measuring more than 1.0 mm., with a very thin pulpy layer which comprises about 13% of the total thickness of the wall.
Raja tengu (T, in Figs.).

11b. Length of capsules about 130 mm. to 140 mm.; capsule-wall relatively thin, measuring about 0.4 mm., with a pulpy layer which comprises about 42% of the total thickness of the wall
Raja macrocauda (V, in Figs.).

1b. Usually small in size, measuring less than 70 mm. in length exclusive of horns.

12a. Horns long, whip-like in shape, bearing a longitudinal fissure; surface either rather rough or very smooth, Groups H^1 and H^3.

13a. Surface rather rough, bearing minute prickles with ridged apexes: capsule-wall divisible into two thickened layers, being compact in structure, Group Eg^3; moderate in size, measuring about 57 mm. to 68 mm. long, and 33 mm. to 46 mm. wide
Rhinoraja sp. J (J, in Figs.); *Rh. longicauda* (L, in Figs.).

13b. Surface smooth, without any sculpture; capsule-wall translucent, composed of two layers, the outer one very thin, instead of being relatively thick, the inner one parenchymatous in structure, Group Eg^1; very small in size, measuring about 38 mm. long, and 22 mm. wide
Breviraja tobitukai (A, in Figs.).

12b. Horns short, tube-like in shape, bearing a round opening at the tip, Group H^4.

14a. Capsule-wall composed of two layers, Group Eg^5.

15a. Capsule-wall about 0.25 mm. thick; length and width of capsule about 51 mm. to 57 mm. and 33 mm. to 37 mm., respectively
Raja fusca (R, in Figs.).

15b. Capsule-wall thin, about 0.15 mm. thick; length and width of capsules about 43 mm. to 59 mm. and 29 mm. to 37 mm., respectively
Raja subsp. Q (Q, in Figs.); *R.* subsp. Q′ (Q′, in Figs.).

14b. Capsule wall composed of three layers, Group Eg^6.

16a. Capsule-wall 0.25 mm. to 0.4 mm. thick, with a pulpy layer which is thinner than 50% of the total thickness.

17a. Pulpy layer comprises about 20% to 30% of the total thickness of the wall; length and width of capsules 56 mm. to 66 mm. and 34 mm. to 37 mm., respectively; fibroid hair exceedingly well developed over the surface *Raja kenojei* (M, in Figs.).

17b. Pulpy layer comprises up to 50% of the total thickness of the wall; length and width of capsules 53 mm. to 65 mm. and 27 mm. to 39 mm., respectively; fibroid hair less developed than in 17a
Raja hollandi (O, in Figs.); *Raja* sp. S (S, in Figs.).

16a. Capsule-wall less than 0.2 mm. in thickness, with a pulpy layer comprising as much as 60% of the total thickness of the wall.

18a. Capsules measure from 49 mm. to 54 mm. in length; surface densely covered with fine fibres *Raja* sp. N (N, in Figs.).

18b. Capsules the smallest in size, measuring only from 39 mm. to 42 mm. in length; fine fibres covering the surface less developed than in 18a
Raja sp. P (P, in Figs.).

2. ADAPTIVE DIFFERENTIATION OF THE EGG-CAPSULES

As regards the present item the writer directs attention to the following points:

a.) The characteristics of the capsules differ between the northern and southern members: As already mentioned, the horns of the capsules of the northern members are as a whole much longer than those of the southern ones, and moreover the location of the respiratory perforation on the horn also differs between the two forms. Another remarkable difference between them is found to exist in the surface configuration and in the histological character as well. In the northern form, the outer layer is in general clad in an armour of either tubercles or prickles, which is useful as a means for identifying the capsule of this group of rajids. In the southern form, however, it is the internal tissue of the capsule-wall, remarkably modified in most cases and especially recognizable within the inner layer, that serves as a useful means of identifying the capsules of this group. Wherefore, it may be said that a modification of the outer layer is the more usual condition in the northern form, while it is the inner layer that has become modified in the southern one. This difference in characteristics may have resulted, in part at least, from differences in their breeding habits inasmuch as the capsules of the northern form, with their long horns or fibrous tendrils, are laid so as to be entwined around some object above the sea floor; but it is supposed, according to Clark (1922, p. 582), that the capsules of the southern form are attached to the bottom using the fibroid hair as an anchor.

b.) The differentiation in the characteristics of the capsule bears a close relationship to the geographical distribution of the adult skates: Generally speaking, there is a tendency in the Japanese rajids that the more northward the fish ranges, the greater the differentiation of the capsules. The capsule of species A, which is found in the southernmost part of the geographical distribution occupied by the northern forms, has the least degree of specialization in its characters as a whole. The capsules of species J and L, which are found farther northward next to the preceding species, have characteristics which seem to show greater progress in differentiation than that of the former. The same view may be expressed by the capsules of species I, which has a range of distribution from the deep sea in the southern region of the Sea of Japan to the far north and has the character of the capsule-wall of Group Eg^2. Further, the capsule-wall of Group Eg^4 is possessed exclusively by skates which reach still farther northward in distribution or inhabit deeper waters than those having the capsules of Groups Eg^1 and Eg^2. A case which exactly confirms this opinion may be given by the most specialized Group Eg^{4C} represented by the capsule of species F, which lives in waters of great depth (Ishiyama, 1952).

Among the southern forms, on the other hand, though there are some examples which do not fit the above conditions, it may be pointed out that in general the degree of development of the pulpy layer within the inner one seems to be correlated in the main with the distribution of the fish. For example, species Q and R were obtained in the coastal waters ranging from the extreme north to the southerly region of the main island of Japan, and the capsule-wall in these species is characterized by having only two layers (Group Eg^5), whereas species N and S, which are thought to be closely related to the preceding species, were found to inhabit the waters ranging from the middle region of the main island to farther south, and their capsule-wall is composed of three layers as in Group Eg^6. Another example of this is to be found in the capsules of species U and W. These two species not only have many specialized features in the capsule-wall (Group Eg^7), but also cover either an extremely wide horizontal distribution or the deepest region of the range. It should be mentioned here that the capsules of these two species are believed to be laid on the sea floor. Such being the case their capsules are often gathered by the trawl net.

Taking the above into consideration, we conclude that there seems to be a close relationship between the differentiation of the capsule and the geographical distribution as well as the breeding habits of the adult skates, though there are some examples that do not fit this conclusion.

3. CONSIDERATION OF THE DIFFERENTIATION OF THE CAPSULE

The egg capsule, of course, serves essentially for the protection of the egg, which is destined to form the young fish, during its period of development (Wilson, 1928, p. 274). Thus the capsules might have undergone successive changes in their characteristics in order to adapt to their environment. On this basis the writer has endeavored to classify the capsules of the Japanese rajids into eight types (Table 3).

Table 3

Characters of the egg-capsules in Japanese rajid fishes classified into 8 types. For abbreviations, see text.

Type	Horn. Group	Capsule-wall				Species
		Configuration of surface	Tissue	Group Eg and its Subgroup		
1	H^1	smooth	2 layers	Eg	——	A
2	H^2	rather rough	2 layers	Eg^2	Eg^{2A}	I
					Eg^{2B}	H
3	H^3	rather rough	2 layers	Eg^3	——	J; L
4	H^3	rough	2 layers	Eg^4	Eg^{4A}	B; C; E
					Eg^{4B}	G; K
					Eg^{4C}	F
5	H^4	smooth	2 layers	Eg^5	——	Q; Q′; R
6	H^4	smooth	3 layers	Eg^6	——	M; N; O; P; S; T; V
7	H^5	rather rough	3 layers	Eg^7	——	U
8	H^6	rather smooth	3 layers	Eg^7	——	W

Questions arise as to the possible causes of these differentiations in the capsules. Differential roles of the capsule which serve in the development of the embryos would seem to be present. This hypothesis, however, is based principally upon morphological evidence.

Although various opinions have been given in regard to the aeration of the capsule, they should agree with the view of Clark (1922, p. 586) in that the respiration of the embryo enclosed in the capsule takes place by means of general osmosis through the capsule-wall and by the circulation of water through the openings of the horns as well. Such being the case, it may be assumed that the capsules have a role divided into two main functions, mechanical and physiological.

According to Clark (1922) the period of incubation of the embryo rajid is very long, ranging from four to about fifteen months, even under artificial conditions. Therefore, it can readily be inferred that a similarly long period would be needed for the development of the embryo of the deep-sea forms inhabiting low temperatures (cf. Table 1). This is probably what might have caused the capsule to be clad in the armour which protects the egg mechanically from natural dangers during the long period of incubation. This hypothesis seems to justify the differentiation, at least, of the outer layer in the capsule-wall observed in the northern members, in which the successive changes of the layer, to some extent, bear a relation to their geographical distribution from the south to the northward. Thus the trend of differentiation in the capsules of the northern form may be easily traced, if we adopt the hypothesis mentioned above. It seems reasonable to believe, therefore, that the much smoother surface and undifferentiated structure of the capsule of Type 1 (Table 3) has resulted from its adaptation to the environment of the extreme southern area where the temperature is relatively high (cf. Table 1).

In the capsules in the southern form, the histological structure differs so much from that of the northern one, that the mechanical theory alone cannot be accepted for this case, but another hypothesis must be developed. The existence of tissue composed of such a delicate structure as the pulpy layer which develops in the wall in many of the forms would seem to offer but small resistance toward mechanical shock. On the other hand, the pulpy layer should assist the osmosis of the wall thus providing for the needs of a fast-growing embryo developing under a relatively high temperature. Thus, is it reasonable to assume that the differentiation in the structure of the capsule of the southern form might have been caused by the physiological needs of the embyro? Hypothetical as this may seem, it is logical to trace the trend of differentiation of the capsules in the southern form in this way. For example, the capsule of Type 5 has only two layers, and its representatives are found to inhabit even the shallow waters towards the extreme northern regions of our main island, whereas the skates of Type 6, having a capsule-wall composed of a somewhat more specialized structure than the preceding, inhabit areas mostly limited to the southern waters of the land.

Since Types 7 and 8 are rather aberrant in the structure of their capsules, it is difficult to develop a plausible hypothesis based either on the mechanical or on the physiological function of the capsule. The likelihood is that both of these processes take place. It may not be unreasonable to assume that the highly specialized features of these capsules might be linked to the special breeding habits of these species (U and W), the capsules of which usually contain more than one egg (ranging up to five in number) and are laid on the sea floor, as mentioned above.

White (1937, pp. 96-97) stated that "the raja-like forms have been reported from the Jurassic, so it is possible that this group branched from the squaloid line before the viviparous habit had been established. In all the oviparous groups there is shown some tendency toward ovoviviparity. . ." Thus, oviparous reproduction is thought to have occurred independently within groups of the sharks. However, there exist some tendencies in common among the elasmobranchs regarding the structure of the capsules of the oviparous forms.

Upon examination and comparison of specimens and of descriptions of various kinds of egg-capsules of oviparous sharks, the characters which are shared in common are as follows:

1. The capsules with smooth surface and devoid of any sculpture on the surface appear to be reminiscent of the temporary capsule of the viviparous fish.
2. The tendrils or the horns are often elongated in a varied manner in both groups.
3. The capsule-wall consists of two layers.

Considering these common characteristics in the capsules, it is credible to assume that the features in a capsule like that of species A may be expected to display the most primitive condition among the Japanese specimens, and this type of capsule appears to have been differentiated in two divergent directions as the specialization of the rajids progressed (Fig. 9), in contradiction to White's suggestion.

At any rate, judging from the features of the capsules thus considered, Types 4 and 8 may be considered the most specialized, and Types 1 and 5 the most primitive, in those of the northern and southern forms, respectively, in so far as the capsule is concerned. The differential patterns between these two pairs of extremes may be traced in Figures 9 and 10.

It is of special interest to note here that the trend of differentiation thus inferred from the features of the egg-capsules is closely related to that obtained in the structural evidence of the claspers which will be reported elsewhere. From this it may be emphasized that the character of the capsule bears a significance of fundamental phylogenetic importance, though in some cases extreme accommodation to the conditions of the environment precludes an exact parallel between the two trends. This fact may make clear the general idea that the organ concerned with reproduction is usually quite useful as a means of systematic classification.

As a result, the writer has arrived at the conclusion that the features of the egg-capsule are not only one of the contributing characters as a means for classification but also of basic importance for distinguishing the phylogeny so far as the Japanese rajid fishes are concerned. Furthermore, it can be assumed that these same conditions obtain for the capsules of rajids inhabiting other parts of the world for their capsules to some extent have features similar to our own species.

SUMMARY AND CONCLUSIONS

The egg-capsules of twenty-one species and two subspecies of rajids, which include almost all those heretofore collected by the writer in the waters around Japan, were examined in the present investigation.

Noteworthy features of the capsule were found in both the external and the histological structure. These characteristics include the shape, horns, fibroid tendrils and configuration of the external surface, and the structure of the capsule-wall.

In the so-called northern form, the capsule is characterized by having a long horn at each corner with a longitudinal respiratory fissure located midway near the tip of the horn, and having a rather simple structure of capsule-wall (the tertiary egg-envelope) composed of two layers. The outer horny layer, however, assumes a highly specialized appearance, characteristic among different groups and species, having developed a definite form of armour on the surface that may serve as a mechanical protection for the developing embryo in the low temperatures of its environment.

In the southern form, on the other hand, the capsule has a smooth surface and short horns which are usually perforated at the tip, and the wall shows a great variation not only in the inner layer but also, in some cases, in the outer one as well. Some capsules are formed of only two layers, as is also true of the northern form, but the majority are characterized by having three layers, a pulpy layer being inserted between the other two. A remarkable example of this is provided by two species of *Raja* which produce an egg-capsule (Fig. 3, U, W) highly specialized both in histological structure and in external form. From all this evidence it seems conclusive that the external form and histological structure of the capsule case are of importance either mechanically or physiologically, or both, for the development of the embryo under relatively high temperatures.

This concept, based chiefly on the geographical distribution and the manner of breeding of the adult in relation to the features of the egg-capsules, of different groups and species, suggests that the divergence in pattern of these features might have been due to environmental adaptation, in conformity with the two functional roles of the capsule. Should this hypothesis be justifiable, successive changes in the features of the egg-capsules of Japanese rajids (Figs. 9 and 10) may be classified ino eight types (Table 3).

These phenomena, an interesting instance of promorphological adaptive differentiation, foreshadow the general characteristics of the future embryo. This trend in the manner of differentiation within the capsules is related in the main to the phylogeny deduced from the claspers of this group of fish.

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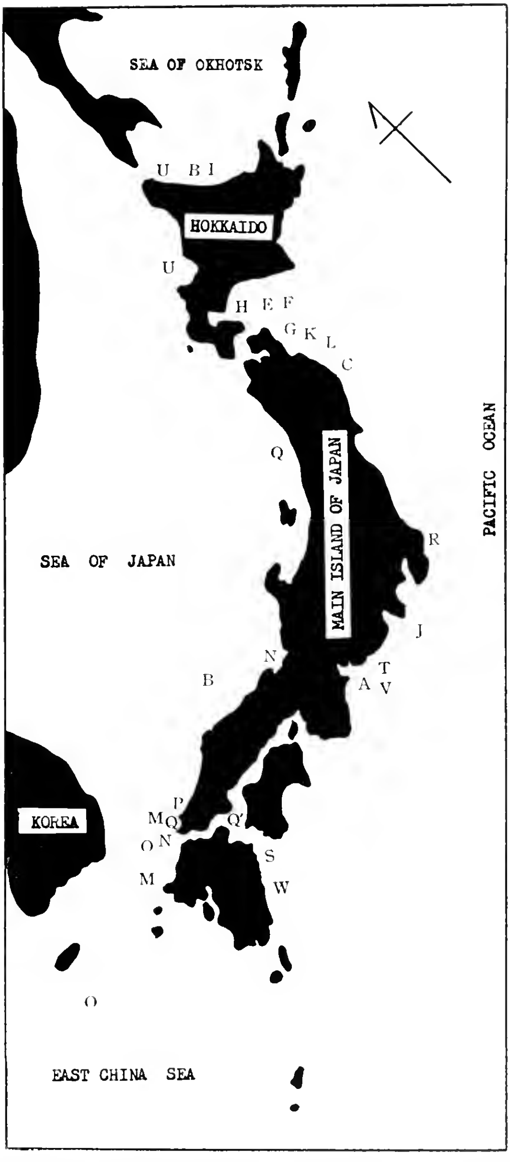

Fig. 1. Map showing localities where the specimens (egg-capsules) examined were taken. For abbreviations, see Table 1.

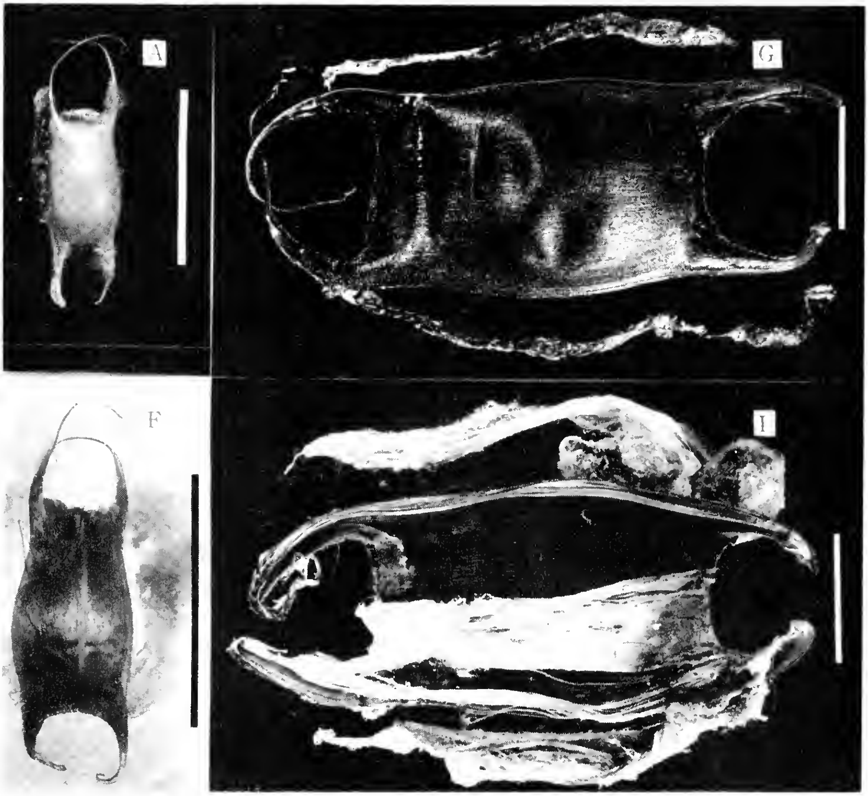

Fig. 2. Dorsal aspects of the egg-capsules of the northern forms, A, F, G and I. Abbreviations as in Table 1. White and black bars represent 5 and 2.5 cm., respectively.

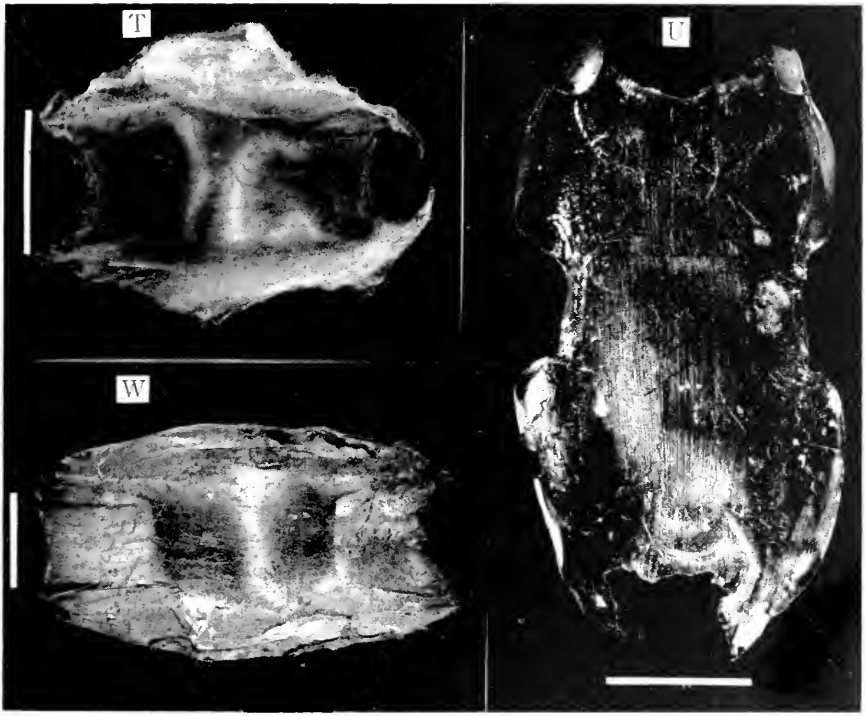

Fig. 3. Dorsal aspects of the egg-capsules of the southern forms, T, U, and W. Abbreviations as in Table 1. White bars indicate 5 cm.

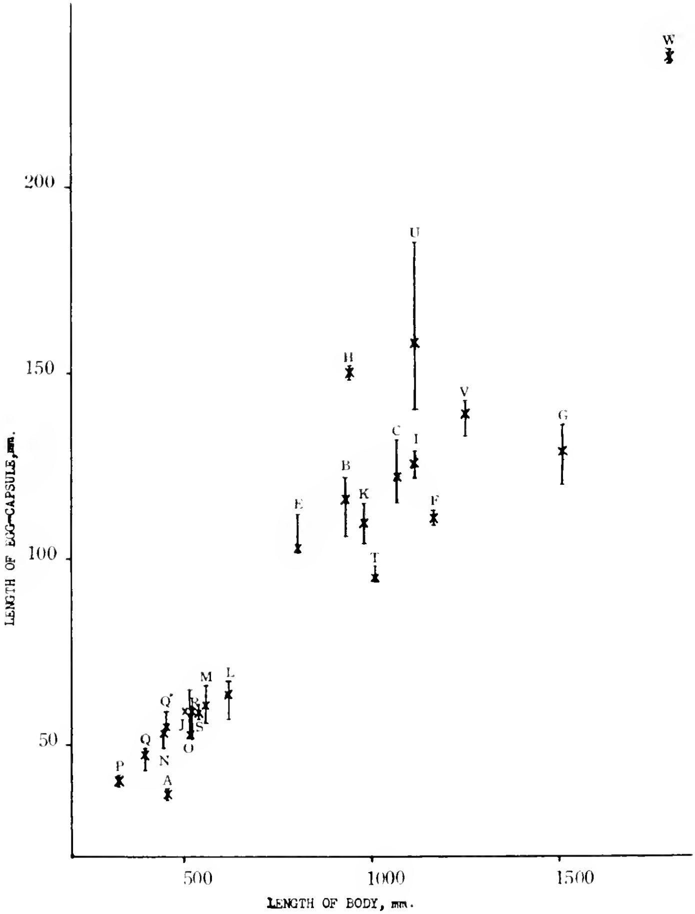

Fig. 4. Size-relation between lengths of the body of parent species and of the egg-capsules exclusive of horns, excepting W. Bar shows range in dimensions, and cross shows the arithmetic mean. Abbreviations as in Table 1.

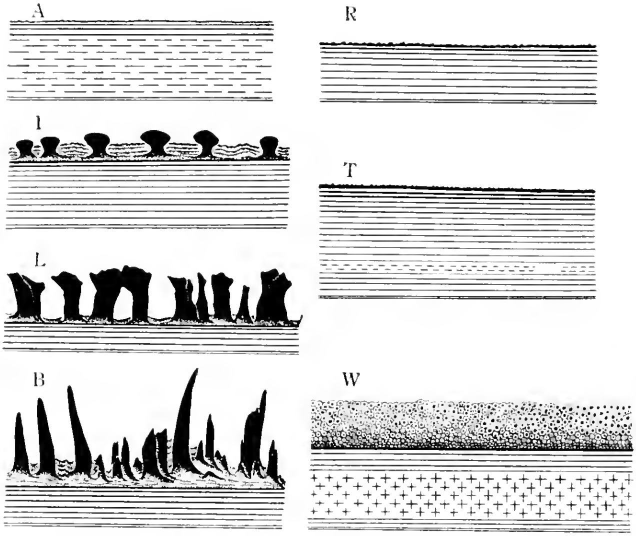

Fig. 5. Semidiagrammatic representation of the cross sections of capsule-walls in seven groups Eg^1-Eg^7. In these, solid lines represent inner layer; dashes, parenchymatous inner layer; broken ones, pulpy layer; crosses, reticulated pulpy layer; black covering upper border of each section with or without projections (protuberances or prickles) and dots, outer horny layer. A, group Eg^1; I, Group Eg^2; L, Group Eg^3; B, Group Eg^4; R, Group Eg^5; T, Group Eg^6; W, Group Eg^7. Magnification, A, x 100; B, I and L, x 24; R, T and W, x 15.

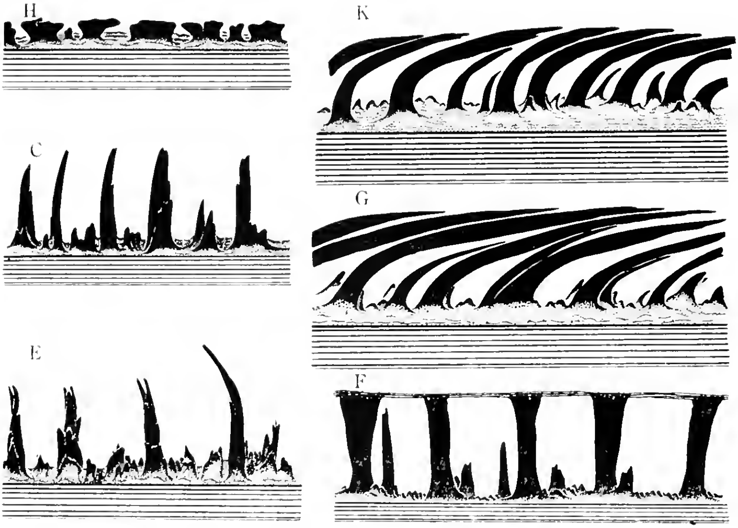

Fig. 6. Semidiagrammatic representation of the cross sections of capsule-walls showing varieties as in Figure 5. Magnification, C, E, F, G and K, x 15; H, x 24.

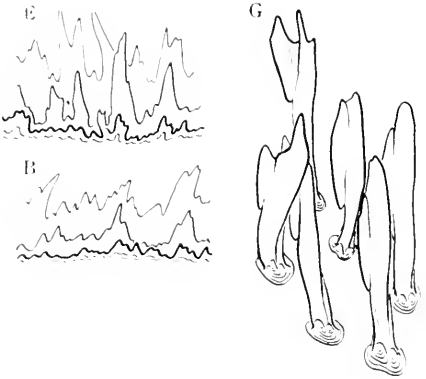

Fig. 7. Comparison of the arrangement of prickles developing over the surface of the egg-capsule in three species, B, E and G. B and E, longitudinal sections; G, dorsal aspect. Magnification, x 15.

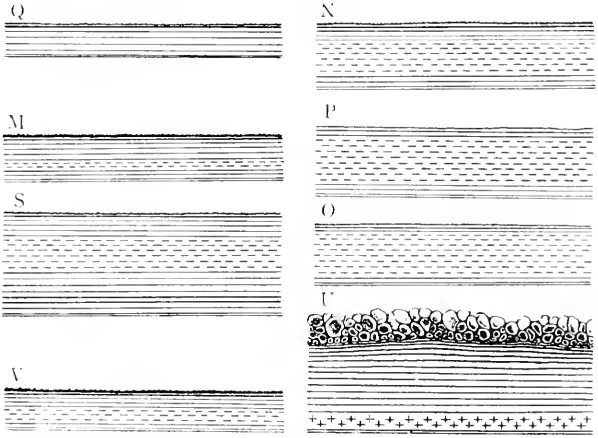

Fig. 8. Semidiagrammatic representation of the cross sections of capsule walls, showing varieties as in Figure 5. Groups represented are Eg^4, Eg^5 and Eg^7. M, Q, U and V, x 15; N, O, P and S, x 66.

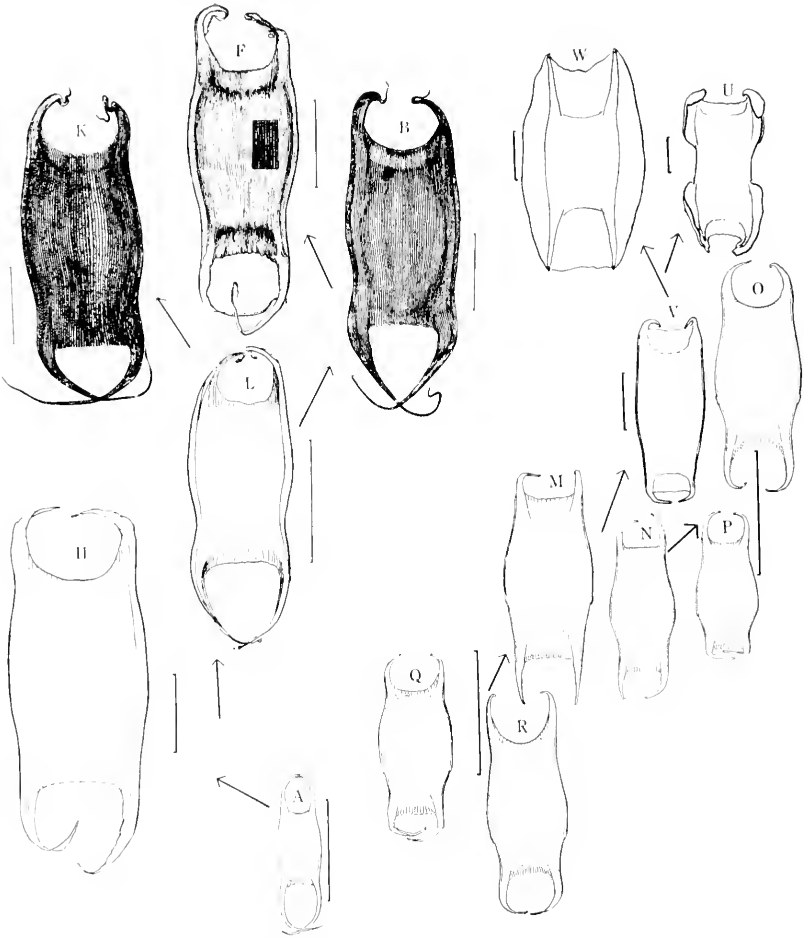

Fig. 9. Dorsal aspects of the egg-capsules, showing the probable phyletic relationship. The fibroid hairs covering the capsule in species F are partly removed so as to show the prickles underlying them. Scales accompanied, 5 cm.

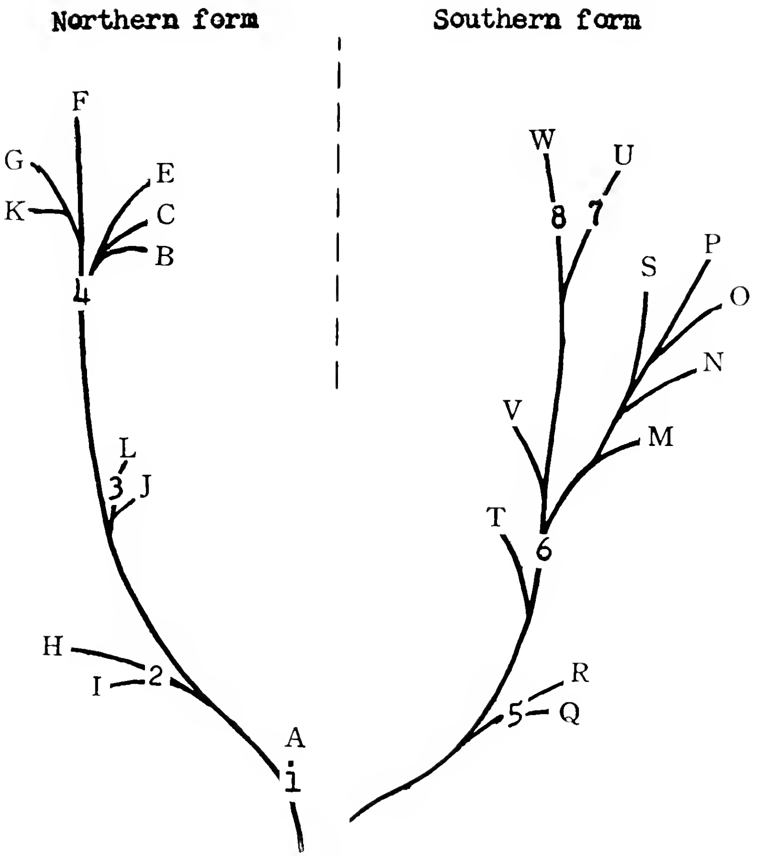

Fig. 10. Suggested phylogeny based on the egg-capsules of Japanese rajid fishes. Each number found in the figure represents the type of the capsule.

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A GENERIC REVIEW OF THE PLOVERS (CHARADRIINAE, AVES)

By Walter J. Bock

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March, 1958

No. 2 — *A Generic Review of the Plovers (Charadriinae, Aves)*

By Walter J. Bock

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For many years the relationships between the grey and golden plovers have been argued about with little agreement between the opposing schools of opinoin. While there has been much discussion of the problem, a critical evaluation of the evidence supporting the maintenance of the genus "*Squatarola*" as distinct from *Pluvialis* has never been presented. With this in mind, Dr. Ernst Mayr sugested that I undertake a study of the skull morphology of the large plovers (*Pluvialis*) so that the earlier works of Lowe could be better evaluated and so that our understanding of the relationships of these species could be further clarified. Preliminary examination of some specimens and study of Lowe's papers on the anatomy and classification of the shorebirds revealed that the variations in the skull morphology and the plumage color and pattern as outlined by Lowe were not limited to *Pluvialis,* but were common to the entire subfamily. Further study of Lowe's and Peters' classification of the Charadriinae *sensu stricto* focused attention on the need for a revision of the existing generic arrangement. This need has already been pointed out by Steinbacher (1932) in his review of Lowe's major paper (1931b), and is reflected by the dissatisfaction of many workers with Peters' classification as indicated by the various, but conflicting proposals to modify his system.

Plovers have always held the interest of ornithologists from which it can be said almost *ipso facto* that many different classifications have been advanced for them. Before 1800 the species of plovers were placed in one of two large inclusive genera, *Charadrius* or *Vanellus.* The next century was characterized by the proposal of many new genera, almost to the extreme of having only one species to each genus. Seebohm, in his monumental work on the classification and distribution of the shorebirds (1888), objected to this trend toward what he considered a monotypic and impractical generic concept. In his classification, the plovers were placed in three genera, *Charadrius* (= the Charadriinae of Peters), *Vanellus* and *Lobivanellus* (= the Vanellinae of Peters).

This arrangement, although it is conservative, and the genera *Vanellus* and *Lobivanellus* are artificial, is far more acceptable than the classification in use today. With the publication of volume 24 of the "Catalogue of the Birds in the British Museum" (Sharpe, 1896), the plovers were once again divided into many genera. More importantly, Sharpe's arrangement of these genera is so unnatural that a clear idea of the generic relationships cannot be gained from study of his work. Lowe's papers on the anatomy, relationships and classification of the shorebirds, including the plovers, serve as the basis for much of the current classification of the Charadriidae *sensu lato*. Unfortunately, although Lowe did much work on the anatomy of plovers, most of his interpretations are, at best, questionable and have led to an unacceptable taxonomic arrangement. Rensch (1923), in his review of Lowe (1922), had suggested that the variation in the skull may well be modified by variations in the jaw muscles or some other factor and that there had been much parallel evolution of the skull within the plovers. The clue to a more reasonable interpretation of the skull variation has been subsequently pointed out by several German workers, but no one has yet done a complete job of checking Lowe's papers and aligning the skeletal and plumage variations with an acceptable classification of the Charadriinae *sensu lato*. Peters (1934) corrected some of Lowe's errors, mainly by shifting several misplaced genera from the Vanellinae to the Charadriinae *sensu stricto,* but in general used Lowe's conclusions as the basis for his classification, which thus still contains most of Lowe's misinterpretations. Peters' two subfamilies are natural (monophyletic) groups but they are subdivided into far too many genera. In recent years some genera, especially in the charadriine plovers, have been merged — a trend leading back to the classification of Seebohm. However, the merging has been erratic, with little agreement in the delimitation of genera, as most clearly shown in the case of *Charadrius* whose limits differ with almost every author. The merging of the charadriine genera reached its extreme limit with the recent action of the Nomenclature Committee of the British Ornithologists Union (Anonymous, 1949). This committee placed all British plovers, with the exception of *Vanellus vanellus,* into *Charadrius* without giving reasons for their action or taking the non-British species into consideration. Even if it were correct, this type of work is unsatisfactory, for only the opinion of the several workers is presented, without the supporting evidence. Lastly, there has been no recent attempt to understand the position of the more aberrant species found in the Southern Hemisphere or the course of evolution within the subfamily.

The aims of this paper are several. Firstly, Lowe's studies on the morphology of plovers are reviewed and a new interpretation is presented in the hope that it will be in agreement with the classification of plovers here presented. Secondly, a study of the relationships and a generic classification of the plovers is advanced. This classification is based mainly on a study of external characters, of habits, habitat, and some features of the internal anatomy, chiefly the osteology. Behavior will not be used in spite of the fine work that has been done on a few species, largely because the behavior of most species is still unknown. This, however, is not to be interpreted as an attitude of underevaluation of the usefulness of comparative ethology in understanding the relationships between species of plovers, for I believe that a comparative study of their behavior may prove to be the key to clarification of the phylogeny within the large genera.

Most of the characters used in this work are those that can be seen in study skins. The original survey was done in the Museum of Comparative Zoology and supplemented by study in the American Museum of Natural History. I was able to examine all known species of plovers and most of the major plumage variations. Skeletons of a number of species were available, and those studied are listed below:

Vanellus	*vanellus*	4 specimens
"	*coronatus*	2 specimens
"	*gregarius*	1 specimen
"	*chilensis*	3 specimens
"	*indicus*	2 specimens
"	*tricolor*	3 specimens
"	*miles*	2 specimens
Pluvialis	*apricaria*	1 specimen
"	*dominica*	13 specimens
"	*squatarola*	29 specimens
Charadrius	*hiaticula*	26 specimens
"	*wilsonia*	3 specimens
"	*vociferus*	16 specimens

Charadrius

"	*melodus*	10 specimens
"	*alexandrinus*	4 specimens
"	*montanus*	3 specimens

These specimens were examined in the collections of the American Museum of Natural History, Cornell University, and the Museum of Comparative Zoology, or borrowed from the United States National Museum, the Museum of Vertebrate Zoology at the University of California and the Museum of Natural History at the University of Kansas. In addition, a few alcoholic specimens were examined, some specimens of *Pluvialis dominica,* of *P. squatarola* and a few species of *Charadrius.* They were checked for the size and position of the nasal glands.

I am deeply indebted to Dr. Ernst Mayr who suggested the original problem, helped and guided the entire study. The officials of the Museum of Comparative Zoology and the American Museum of Natural History were most cooperative and helpful to me in the course of my work. Drs. Friedmann, Pitelka, Tordoff and Sibley kindly made available skeletons that were of great value in the study of the skull morphology. Drs. Ernst Mayr, Dean Amadon, Ernest Williams, Karl Koopmann, Daniel Marien, Robert Dressler, and Mr. Robert Risebrough have read the manuscript and offered many useful comments and suggestions for which I am most grateful. Mr. William Partridge must be thanked in particular for his help in providing information about South American plovers and for translating some important papers written in Spanish. Mr. Terrell Hamilton kindly translated von Boetticher's revision of the lapwings from the French. Miss Patricia Washer is to be credited with the fine drawings of the skull and palate.

In any taxonomic paper it is of the greatest importance to state the principles on which the proposed classification is based, but it is not necessary to outline these principles in every paper. The principles followed in this study are the same as those used in my revision of the herons (Bock, 1956). In brief, a broad concept of the genus and family is used for this is in closer agreement with the present-day species concept and results in a sounder, more easily comprehended classification.

Characters Used

Understanding of a taxonomic study depends almost entirely upon a clear presentation of the characters upon which the study is based. It is not enough to give complete and accurate diagnoses of the proposed groups because, unless he is a specialist in the group, the reader usually cannot separate the significant from the non-significant characters or understand how the characters vary. Futhermore, merely to discuss the variation of the characters is still not sufficient. To insure a full understanding of a character, it is necessary to describe and discuss its variation, its function, and how it is correlated with other structures to form character complexes. Character complexes must be treated as units, not as separate entities, for the same selection forces act on all and thus fuse them into a single evolutionary unit. When studied in this manner the selection forces acting on the character and its evolution can be more accurately examined. After the functional and phylogenetic aspects of a character have been separated and analyzed, its taxonomic value can be evaluated on a much sounder basis. The value of a systematic study is greatly increased if the taxonomic characters are evaluated in this way and, although I realize that I fall short of the goal, the characters used in classifying the plovers are presented with these ideas in mind.

The Skull

Of the several characters used by Lowe in his classification of the plovers, the skull and the color of the back were considered by him to be the most important. Eight skull characters were listed; however, only the first two were of any importance. These two characters show the most striking variation, which was "correlated" with the color of the back and upon which the classification of plovers was largely based. Since the skull characters played so large a role in Lowe's writing, I shall cite them in full and then give a brief summary of his interpretations.

In separating the genera *Pluvialis* and "*Squatarola*," Lowe lists the following skeletal characters (Lowe, 1922, pp. 478-482):

"Turning to the skull we find:

"(a) That the lacrymals in *Squatarola* are strikingly different, being prominent out-jutting processes, almost Larine or Tringine in appearance; while in *Pluvialis* their outer margin is rounded and merged into the line of the orbital rim, being continued forwards and inwards in a smooth and somewhat noticeable convexity in a manner somewhat reminiscent of *Vanellus* (text-figs. 10b & 11b).

"(b) The interorbital space presents very distinct differences in the two forms. In *Squatarola* it is narrower both actually and relatively, while the raised corniced and everted orbital rim so characteristic of *Pluvialis* is not present; moreover, the grooves for the supra-orbital glands are not nearly so deep or defined as in *Pluvialis,* and the general arrangement here is Larine or Tringine (Text-figs. 10b & 11b). In *Squatarola* there are no anterior foramina caudad of the lacrymals. They are well marked in *Pluvialis,* and this seems to be a Charadriine character. In *Squatarola* the inner margins of the grooves for the supra-orbital glands meet in the middle line of the vertex, forming a prominent sagittal ridge down the centre. In *Pluvialis* there is a fairly broad and clearly-marked smooth medial depression down the centre of the interorbital space, which is not encroached by the supra-orbital grooves.

"(c) Turning to the palatal plates, we find in *Squatarola* that the postero-external angle is rounded off (in some specimens much cut away). In *Pluvialis* the angle is squarer.

"(d) In *Squatarola* the ectethmoid or antorbital plate is somewhat triangular in form, the extero-inferior angle representing the apex. In *Pluvialis* the antorbital plate has a quadrilateral form." Adding in a footnote, "This, at any rate, is evident in perfectly ossified examples."

"(e) In *Squatarola* the descending process of the lacrymal falls perpendicularly to just touch the apex of the antorbital plate. In *Pluvialis* it runs along the outer margin but does not fuse with it.

"(f) Turning to a comparison of the maxillo-palatines, we find that in the two forms under discussion these are not identical. In *Squatarola* they appear to be more closely applied to the pre-palatines, their posterior of free points being little separated from the palatal plate. In *Pluvialis* the free ends converge towards the middle line and underline the vomer, so that that part of the vomerine process is hidden when these structures are viewed from the palatal aspect. The maxillo-palatines in *Pluvialis* are also more shell-like concavo-convex structures (or more scroll-like). The attachment to the palatal process of the premaxilla is less than is *Squatarola.*

"(g) In *Squatarola* I have noticed that the dentary margin of the premaxilla is not completely fused with the corresponding portion of the maxillo-palatine as it is in *Pluvialis.* This is a Larine as opposed to Pluvialine character.

"(h) In *Squatarola* the postero-external angles of the basitemporal plate end in two fairly conspicuous downwardly projecting processes of bone. These processes are but little evident in *Pluvialis,* but are quite characteristic of the Laridae and Sternidae. If well-prepared skeletons of the skulls of the two genera under discussion are compared, these differences are generally apparent. A similar distinction is noted between *Larus* and *Stercorarius.*''

Later in the same paper (p. 483), the species of *Charadrius* were divided, on the basis of the same characteristics, into two groups, ''*Leucopolius*'' (resembling ''*Squatarola*'') and *Charadrius* (resembling *Pluvialis*). It should be noted that not all of the species of *Charadrius* as recognized in this paper or by Peters were included by Lowe in ''*Leucopolius*'' or *Charadrius;* some were placed in other genera.

The color pattern and color of the back of these genera were given (*op. cit.*, pp. 483-485) and the latter ''correlated'' with the skull. The light versus dark back color was said to be correlated with the degree of ossification of the supra-orbital rims (= characters ''a'' and ''b''). Lowe considered the less ossified skull and light dorsal color primitive (''adumbrated'') and the more ossified skull and dark dorsal color advanced. As he put it, the former condition was the initial attempt by nature to produce these characters and the latter was the more complete (finished) product. Thus, relationship on the horizontal level (in the same taxonomic group) is shown by skull type and back color. On the vertical axis (between ancestral and derived groups) relationship is indicated by color pattern. ''*Squatarola*'' and ''*Leucopolius,*'' in addition to a number of other forms, were combined as the ''Pre-Charadriinae,'' a primitive group that was considered a subfamily, but never given formal status by Lowe or any subsequent author. In a later paper, Lowe (1933a) again discussed the problem of color and color pattern and here presented a list of eight ''pairs'' of species, set ''A'' being pale colored dorsally and having the skull type of ''*Squatarola,*'' and set ''B'' resembling *Pluvialis* in these characters. The relationship between the 16 species is as outlined above. That is, each species or genus in set ''A'' (= primitive subfamily) gave rise to the corresponding species or genus in set ''B'' (= advanced subfamily), which assumes parallel evolution on a grand scale. Lowe speaks of some forms (his ''Pre-Charadriinae'') as ''living fossils'' (1922, p. 488; 1933a, p. 120), and believes that various groups of birds are maintained as they were in past geological ages thus allowing ornithologists to establish phylogenetic series based on living forms. He states further (1933a, p. 114) that in the ontogenetic development of the skull of the advanced group there is a stage in the immature bird when the skull resembles that of the adult "pre-charadriine" plover. He is quite correct in his observations and indeed for a time I believed, misled by an incorrectly identified skull, that the differences between the two skull types were mainly age variations, the "pre-charadriine" condition representing the immature and the

Table 1

Character complex 1	*Character complex 2*
Least ossified skull Light dorsal color	More ossified skull Dark dorsal color
Ancestral (primitive)	Descendant (advanced)
"Pre-Charadriinae"	Charadriinae
"*Squatarola*"	*Pluvialis*
"*Leucopolius*"	*Charadrius*
Set "A" (1933a) Each species or genus of the eight groups listed	Set "B" (1933a) Corresponding species or genus

The vertical columns represent the two charadriine subfamilies as delimited by Lowe. They are characterized by having a similar skull and back color. The horizontal levels show ancestral and descendant groups which are bound together by a common color pattern, the pattern being different for each group.

"charadriine" condition representing the fully ossified adult skull. This is not the case, as I discovered later. Lowe, in stating that the skull of the advanced type passed through the "primitive" stage in its ontogeny, claimed that (1933a, p. 114): "This would appear to support my conclusion that the Grey Plover and Kentish Plover are members of a group which may be regarded as antecedent in origin to, or at least more generalized than the more specialized group of which the Golden and Ringed Plovers are representatives." This is a direct application of the theory of recapitulation and as in so many other cases has led to an erroneous conclusion. Lowe always argued very strongly that these characters were not directly affected by the present day environment, but represent the condition inherited unchanged from an ancestral form. Finally, he never stated whether he considered color pattern or back color and skull type as the more important in showing relationships between genera of plovers. Table 1 summarizes Lowe's interpretations of the relationships within the plovers.

The subfamilies Vanellinae and Lobivanellinae were established by Lowe in 1922, only to be merged by him in a later paper (1931b). The main difference cited by Lowe between the Vanellinae and the Charadriinae (including the "Pre-Charadriinae") is the condition of the supraorbital rims, which in the Vanellinae are simply more ossified than in *Pluvialis*. The use of the more completely ossified nature of the supraorbital rims as the major distinguishing feature of the Vanellinae necessitated placing many obvious charadriine plovers, such as *Charadrius vociferus*, in the Vanellinae, a move to which many workers objected.

The main object in briefly summarizing Lowe's interpretations of the variations in the skull and back color in the plovers is to show that any classification based on them would be artificial. Unfortunately space does not permit a clear explanation of all the disputed points which has made the above discussion somewhat confusing. Lowe may well be right in some of his conclusions (for example, placing the turnstones in the Scolopacinae), but as so much of his work on classification and phylogeny is unsound, all of it must be reviewed before being accepted. In regard to the plovers, I was unable to accept any of Lowe's conclusions after a careful consideration of both the evidence and other possible interpretations. The results of the present study force me to suggest that Lowe's conclusions dealing with the anatomy and phylogeny of plovers be ignored in future considerations of the relationships within the Charadriinae *sensu lato*.

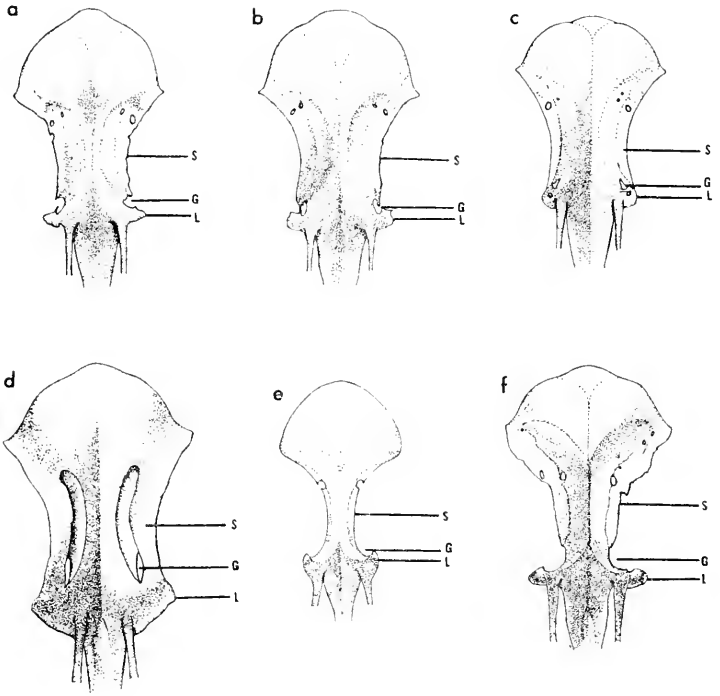

Figure 1. Dorsal view of the skull of a) immature golden plover (*Pluvialis dominica*), b) intermediate stage golden plover, c) adult golden plover, d) adult lapwing (*Vanellus vanellus*), e) adult turnstone (*Arenaria interpres*), and f) adult grey plover (*Pluvialis squatarola*) to illustrate the variation in the degree of ossification of the supraorbital rims. The labels are, from posterior to anterior, the supraorbital rims (S), the groove or foramen for the duct of the nasal gland (G), and the lacrimal bone (L). Figures are approximately life size.

Characters "a" and "b." Lowe did not describe these characters with sufficient clarity. Therefore the nature of the variation and correlation of these characters will have to be more clearly outlined before an alternative interpretation can be offered.

Examination of the differences between "*Squatarola*" and *Pluvialis* in these characters reveals that the degree of ossification of the supraorbital rims is the most important factor. In "*Squatarola*," the rims are only slightly ossified, hence the interorbital space is narrower, there is a groove, not a foramen, for the duct of the nasal gland at the anterior end of the groove in which the gland lies, and the lacrimals jut out to the sides. In the adult skull of *Pluvialis dominica,* the supraorbital rims are more fully ossified, hence the interorbital space is wider, there is a foramen, not a groove, for the duct of the nasal gland at the anterior end of the groove in which the gland lies, and the lacrimals do not jut out to the sides, but merge with the edge of the supraorbital rims in an even curve. In the lapwings, the supraorbital rims are still more ossified with small, but definite grooves for the nasal glands. Thus the interorbital space is very wide, a foramen is present for the duct of the nasal glands, and the edge of the supraorbital rims and the lacrimals merge with one another in a very smooth curve. See Figures 1f, 1c, and 1d which illustrate these structures in *Pluvialis squatarola, P. dominica,* and *Vanellus vanellus* respectively.

Lowe (1933a, p. 114) reported that the skull of the immature *Pluvialis dominica* ("the advanced type") passes through a stage that resembles the adult skull of the "pre-charadriine" group. My series of *dominica* fully supports this observation. The skulls of a very immature, an intermediate, and an adult golden plover are illustrated in Figures 1a, 1b, and 1c. These show an increase in the ossification of the supraorbital rims and with this, a change from the "pre-charadriine" to the "advanced" condition. Determination of the age of these skeletons is based on the total degree of ossification of the skeleton including the supraorbital rims; no skulls of known age were available. (I have only one specimen of known age, a piping plover [*Charadrius melodus*] W.B. 432 deposited at Cornell University, a bird banded as a chick and collected seven years later. The bones of this specimen, including the supraorbital rims (see Figure 2c), were completely ossified.)

When this ontogenetic change became apparent it was necessary to determine the exact nature of the fully adult (=ossified) skull of *P. squatarola.* In my series of *P. squatarola* which contained both immature and adult birds, the skulls of all specimens resembled that of the immature golden plover. It is doubtful that a series of almost thirty birds collected at random over all of North America would be composed entirely of immature birds, and indeed, some specimens are certainly adults as shown by the total degree of ossification of the skeleton. It can be concluded that the adult skull of *squatarola* is similar to the very immature skull of *dominica* (see Figures 1a and 1f). The rims of the im-

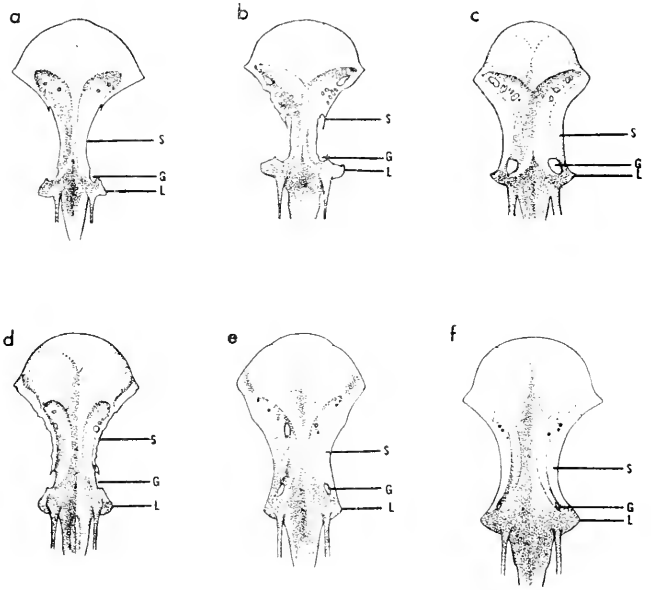

Figure 2. Dorsal view of the skull of a) adult snowy plover (*Charadrius alexandrinus*), b) adult Wilson's plover (*Charadrius wilsonia*), c) adult piping plover (*Charadrius melodus*), d) immature killdeer (*Charadrius vociferus*), e) adult killdeer, and f) adult mountain plover (*Charadrius montanus*) to illustrate the variation in the degree of ossification of the supraorbital rims. Abbreviations as in Figure 1. Figures are approximately life size.

mature killdeer (*Charadrius vociferus*) are less ossified than those of the adult and resemble those of the adult snowy plover (*C. alexandrinus*) or Wilson's plover (*C. wilsonia*) (see Figures 2a, 2b, 2d, and 2e). However there is no basis, as we will see more clearly later, to conclude that the skull of *squatarola* represents an ancestral type; it merely has less ossified supraorbital rims and if a species such as *P. dominica* has more fully ossified rims, it has had to pass through a *squatarola*-like stage sometime in its ontogeny — there is no alternative.

The elimination of the possibility that the differences observed are the result of comparing an immature with an adult bird necessitated an investigation of other possible factors that could influence the degree of ossification of the supraorbital rims. Since the roof of the skull is so intimately associated with the nasal (or supraorbital) glands, it would seem reasonable to try and determine whether there is a correlation between the size of these glands and the degree of ossification of the supraorbital rims. This suggestion is not new, but has been previously advanced by several German workers, who in fact have given the best possible answer to the problem of the variation in size of the nasal glands and the correlation between the size of the gland and the degree of ossification of the supraorbital rims, but the value of their work has never been fully recognized.

Schildmacher (1932), on the earlier suggestion of Heinroth, showed that in *Anas platyrhynchus* the salt content of the environment directly affected the size of the nasal glands during the life of the individual and hence the morphology of the roof of the skull. In general, the saltier the water, the larger are the nasal glands and the less ossified are the supraorbital rims and the lacrimal bones. The reason for this correlation is of no importance to us at this time, but will be discussed later; the important thing is that an inverse correlation between the size of the nasal glands and the ossification of the supraorbital rims does exist. To show this, Schildmacher conducted a simple, but conclusive experiment. He took ducklings from the same brood and reared half of them with fresh water for drinking, while the other half had salt water. At the end of a year he killed half of each group and prepared the skulls. The birds reared on fresh water had well ossified supraorbital rims and small nasal glands while the salt-water birds had poorly ossified supraorbital rims and well developed glands. These changes are clearly shown in Stresemann (1927-34, p. 52) who illustrates, after

Schiöler (1925, Danmarks Fugle, Bd. 1), the differences in the skull of the Continental European race and the Greenland race of the mallard. The remaining ducks were placed together on fresh water and at the end of the second year they were killed and their skulls prepared. This time all of the skulls were alike and resembled the skulls of the birds raised on fresh water. The changes found by Schildmacher are phenotypic and can be brought about by simply changing the salt content of the water. Schildmacher's experiments were carefully conducted with all of the necessary controls and there is no reason to doubt his results or interpretations. He points out that the supraorbital rims of the salt-water-dwelling race *Anas platyrhynchus conbosaes* of Greenland are less ossified than those of the fresh-water European race *platyrhynchus*, the differences being comparable to those he obtained in his experiment. Lastly, Schildmacher reported on several eiders (*Somateria mollissima*) and a marine merganser (*Mergus serrator*) which were held on fresh water for several years. While the nasal glands did not change as much as in the case of the mallard, they did degenerate slowly in both species. It is not surprising to have a smaller change in the gland of a salt-water bird, for the nasal glands are more important to salt-water species and hence it would be advantageous to have the size of the organ more completely determined genetically and less susceptible to changes in the environment.

Technau (1936a, 1936b) studied the nasal gland in the entire class of birds. He showed that one of the functions of the secretion of the nasal glands is to protect the mucous membrane of the nasal cavity against the action of salt water.[1] With this he concluded that if, of two races of the same species or of two closely

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[1] While this paper was in press, I learned of the studies of Schmidt-Nielsen and his collaborators on the function of the nasal glands of marine birds (Federation Proc., vol. 16 (1): 113-114, 1957; Amer. Journ. Physiology, April, 1958). They have shown that the nasal glands secrete (excrete) salt thereby enabling marine birds to be independent of fresh water. Schmidt-Nielsen told me (personal communication) that they have not discovered any other function of the nasal glands so that my statement of its function would be incorrect. However, the following argument of the evolution and taxonomic value of the nasal gland and associated structures is still perfectly correct with this newly discovered function of the nasal gland. Indeed, it is easier to see how the size of the gland will alter with changes in the salinity of the environment for as the amount of salt increases, the glands will have to increase in order to remove the excess salt from the body and vice versa.

related species, one were found on salt and the other on fresh water, the size of the nasal gland would differ between the two. Several cases were cited to support this conclusion, as for instance the salt-water species *Charadrius hiaticula* and the fresh-water *C. dubius* (1936b, pp. 601-603). The difference in size of the nasal glands in this species agrees with his conclusion though not as clearly as would an extreme salt-water species such as *C. alexandrinus* compared to *C. dubius*. However, the special problem of variation in the size of the nasal gland in any family was outside the scope of his study, and while Technau presented all the necessary evidence, it remained for another worker to utilize his results to solve the problem of the variation in the ossification of the supraorbital rims in the plovers.

Stegmann (1937) in a short note discussed the relationship between "*Eupoda*" (=*Charadrius*) *a. asiatica* and "*E.*" *a. veredus* which he points out are conspecific, as concluded earlier by Hartert. Yet Lowe had placed these forms in the "Pre-Charadriinae" and the Vanellinae, respectively, on the basis of skull morphology. These forms, I should add, constitute one of the pairs of species listed by Lowe in his 1933a paper. *Charadrius a. asiaticus* breeds in areas of salt deserts, *veredus* in areas of fresh water, and both winter in the interior of Africa. On the basis of this and the results of Technau's study, Stegmann concluded that the dissimilarity in the degree of ossification of the supraorbital rims was caused by a difference in the size of the nasal glands resulting from the difference in the salinity of the environment of the two species.

Lowe knew of the earlier papers on the nasal glands including Marples' (1932) discussion, but discounted the nasal glands as a possible explanation in favor of his earlier interpretation. However, Lowe's interpretation (1933a, pp. 119-129) has no factual basis and is best rejected in favor of the interpretation outlined by Technau and Stegmann.

If our hypothesis is correct, then a tabulation of the habitat and the degree of ossification of the supraorbital rims (or the shape of the skull) should show a definite correlation. What is actually being compared is the salinity of the habitat and the size of the nasal glands. The glands and the supraorbital rims change together (see below). Unfortunately a complete survey of all species cannot be made at this time for the skulls of many species are lacking in our collections as well as the much needed data on the habitat. I shall, however, outline several cases for which the necessary evidence is available.

Since this study originally started with a consideration of the grey and golden plovers, it would seem fitting to discuss them first. The golden plovers, *dominica* and *apricaria*, are predominantly fresh-water birds and have well developed supraorbital rims (Figure 1c). On the other hand, the grey plover (*squatarola*) which is predominantly a salt-water bird, has very poorly ossified rims (Figure 1f). This agrees with our hypothesis.

Of the North American species of *Charadrius*, *montanus* and *vociferus* are fresh-water birds, *wilsonia* and *alexandrinus* are the most extreme salt-water forms, and *melodus* and *hiaticula* are intermediate, but are found more on salt water than on fresh water. If the skulls of these species are compared (Figures 2a, 2b, 2c, 2e, and 2f) the close correlation between the degree of ossification of the supraorbital rims and habitat is readily apparent. The skull of *hiaticula*, which is not figured, is almost identical with that of *melodus*.

The lapwings are all strictly fresh-water birds and are even found on dry grasslands. They have the smallest nasal glands and the most ossified supraorbital rims (see Figure 1d). The close resemblance between the lapwings and some of the charadriine species such as *Charadrius vociferus, C. montanus, C. asiaticus veredus, Eudromias morinellus* and *E. ruficollis* (see Figures 2e and 2f), which were placed in the Vanellinae by Lowe, is due to the fact that these species are also strictly fresh-water forms and not because of any close relationship between these species and the lapwings.

The relative difference in size of the nasal glands in a fresh-water species (*Charadrius vociferus*) and a moderately salt-water species (*Charadrius hiaticula*) is shown in Figure 3.

It is thus safe to conclude that, in general, there is a strong correlation between the habitat and the shape of the skull. The species listed by Lowe in his "Pre-Charadriinae" (those with a *squatarola*-like skull) are generally salt-water birds while the species included in his "Charadriinae" (those with a *dominica*-like skull) are mainly fresh-water birds. All marine (or salt desert) species do not have one type of skull and all fresh-water-dwelling species a second type, but rather within a group, the coastal (or salt desert) species have less ossified rims than the fresh-water-living species of that group. This point must be made because some marine species, such as *Charadrius melodus* or *C. hiaticula,* have more ossified supraorbital rims than some other marine forms such as *Pluvialis squatarola* or *Charadrius alexandrinus.*

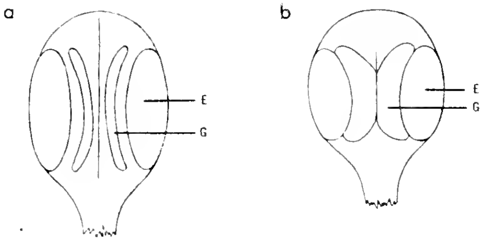

Figure 3. Diagrammatic sketch of the head of a) fresh-water plover, the killdeer, (*Charadrius vociferus*) and b) salt-water plover, ringed plover, (*Charadrius hiaticula*) to show the difference in the size of the nasal glands (G) and their relationship to the eyes (E).

One problem remains. What is the basis of the correlation between the size of the nasal glands and the degree of ossification of the supraorbital rims? Support for the glands is easily provided for by the heavy membranes present in this region in those species with poorly ossified rims — a support of bone is not needed. A number of experiments that have a direct bearing on this problem have been reported by Murray (1936) in his general treatise on bone. In the treatment of the functional changes in bone, he discusses (p. 78) the yet unexplained fact that "other pressures can cause either atrophy or at any rate limitation of growth of bone in the direction of the pressure." Blood vessels, tendons and muscles can press against the surface of a bone and restrict growth of the bone at that point. Several experiments were cited in which the bone grew after the overlying muscle had been removed. A large nasal gland would exert a similar pressure on the bone of the supraorbital rim and in this way prevent development of bone in this region. This could be experimentally verified by a unilateral removal of the gland and examination of the skull for changes after an appropriate period of time. This has not yet been undertaken and the basis for the correlation is still an open question.

In summary, the hypothesis is offered that the characters "a" and "b" of Lowe are affected by the size of the nasal glands and hence by the saltiness of the environment. There is a considerable mass of supporting data for this hypothesis, but it is by no means absolutely proven. A complete survey of all species to determine how well the correlation holds remains to be done. As mentioned above, this is impossible at this time because of a great lack of both skulls and habitat information for each species. A listing of the breeding and wintering grounds as well as the migration routes of each species is needed. It is also necessary to know what percentage of each species or subspecies lives on fresh or salt water, as well as whether the species breeds on fresh water and winters on the coast. An excellent example of the kind of data needed is shown by the map of the breeding and wintering grounds of the European races of *Charadrius hiaticula* in Salomonsen (1955, p. 45), who stresses the importance of the wintering area as well as the breeding grounds in understanding the selection forces that are acting on a species. Habits are important, for a bird may be strictly coastal, yet seldom go near the water, as for example *Charadrius melodus*. Knowledge of the age of the specimen is absolutely necessary because only fully adult skulls may be compared. Needless to say, a mixture of adult and immature skulls could completely obscure the picture as it did in the early stages of this investigation. It is impossible at this time to determine exactly how easily a change in the environment could change the size of the nasal gland (and also how closely the size of the nasal gland and degree of ossification of the rims are correlated), but the available evidence indicates that the selection pressure of the environment is quite strong, and if altered, it could readily change the size of the gland. This change may be genetic, nongenetic, or very likely a combination of both. It would be interesting and of the greatest value to perform the simple experiment of Schildmacher on several species of plovers. This would at least show whether the nasal glands and supraorbital rims can be phenotypically modified by the environment. Other yet unknown factors may act on this region of the skull, and must not be discounted at this time.

The variation in the amount of ossification of the supraorbital rims has provided an excellent example of an osteological feature that exhibits a very marked change as the result of a relatively minor change in the environment. The character is so readily modified that the variation in the rims has little or no value in showing generic relationships and cannot and will not be used at all in establishing the classification of plovers to be presented later in this paper. It certainly does not have the phylogenetic importance that has been ascribed to it by Lowe.

Characters "c" to "h." The remaining skull characters described above do not seem to be correlated with characters "a" and "b" or with each other and therefore will be discussed separately. A careful comparison was made only between *Pluvialis dominica* and *squatarola* which serves as the basis of the following discussions.

The "postero-external" angle of the palatines is highly variable in both species, this variation being in part natural and in part artificial, as the result of preparation. The range of variation appears, however, to overlap completely in the two species.

The ectethmoid of *squatarola* is, in general, triangular, while that of fully ossified skulls of *dominica* is quadrilateral in shape. If in *squatarola* there were a slight increase in ossification in the space between the apex of the ectethmoid and the descending process of the lacrimal, then the difference between the two species would disappear. This difference is so slight, and so well within the range of variation of the ectethmoid in *Charadrius* that it is doubtless of no generic importance.

I was unable to see any difference in the descending process of the lacrimal. In each species this process reaches the apex of the ectethmoid to touch or fuse with that bone in a similar way.

There is much variation, both individual and artificial (due to preparation), in the structure of the maxillo-palatines, but I was unable to see any constant difference between the two species.

The dentary process of the premaxillary is completely fused with the maxillo-palatine in both species. However it is entirely possible that a suture may be present in very young individuals. Any difference that may exist is most likely due strictly to variation in age.

The small process found at the "postero-external" angle of the basitemporal plate is present in both species and may be somewhat larger in *squatarola*. There is, however, a cap of tissue, probably cartilage or collagenous fibers, covering the process, which if lacking in a specimen would produce a large difference in the size of the process. The interesting feature of this process is that the internal process of the articular (medial process) of the lower jaw "articulates" on it. As the lower jaw opens, it apparently rotates on the basitemporal process as well as on the articular surfaces of the condyles of the quadrate. A full discussion of this "articulation" will be presented in a separate paper.

I have carefully checked these characters in *Pluvialis* but only briefly in *Charadrius*. However, there is no evidence to indicate that the differences as given by Lowe hold up in the latter genus. To conclude, these characters show very little difference between groups of species in *Pluvialis* or *Charadrius* and do not appear to be of value in showing relationships in those genera. Hence they will not be used in this study.

Hind Toe

The presence or absence of the hind toe has been considered by some authors to be one of the important characteristics in delimiting genera of plovers. The best example is the use of the presence of the hind toe in "*Squatarola*" as one of the major reasons for separating that genus from *Pluvialis*. It is commonly believed that, with few exceptions, all species of plovers lack the hind toe, and hence the presence of the hallux in *P. squatarola* was regarded as a very important feature. However, about half of the species of lapwings and a few charadriine plovers also have a hind toe, which fact reduces its value as a taxonomic character.

When present, the hind toe is usually very short and somewhat elevated above the plane of the remaining toes and is clearly functionless. The metatarsal for the hallux of *squatarola* is very small and free floating in the fascia of the rear of the tarsus and thus is usually lost during preparation of the skeleton. In addition, the musculature for this toe appears to have degenerated. I have dissected one specimen of this species and found what seem to be the tendons leading to the hallux. They were much reduced but because the region was somewhat damaged, I could not determine with certainty if or how they inserted on the hallux. One specimen of *squatarola* has been reported (Brooks, 1919) to be lacking the hind toe and an extensive check of all species may well reveal more cases of a similar nature.

The reduction and eventual disappearance of a vestigial structure would be favored, as it is advantageous to inhibit the ontogenetic development of a functionless character. This simply conserves energy during embryonic development when there is rapid growth and the available energy (in terms of food) is limited. Thus if an inherited structure is not necessary to the individual during its life, its degeneration and final disappearance will be selected for, provided the proper mutations occur. The peculiar pattern of variation so characteristic of a vestigial structure results from the random occurrence of the mutations that inhibit its development. The presence or absence of a functionless structure or, when present, the variation in size or development merely demonstrates that the proper mutations have occurred in some lines and not in others.

Hence the hind toe is of no value in showing relationships in the plovers. The presence of the hallux in *Pluvialis squatarola* and its absence in its congeners probably means that the proper mutations have not yet appeared in this species and have in the others and is thus of no taxonomic value. Delacour and Mayr (1945) reached the same conclusion when they placed the grey and golden plovers in the same genus. In doing so, they say (p. 106): "Genera that are based on this loss of a morphological character are rarely valid." This conclusion has been further supported and expressed by von Boetticher (1951) for plovers and other groups, by Delacour (1951a) for woodpeckers and kingfishers, and by Mayr, Linsley and Usinger (1953, p. 122) as a general taxonomic rule. The presence or absence of the hallux has been determined and the date recorded here only to show an example of the type of variation exhibited by a vestigial structure (see Tables 2 and 3).

Wattles

Wattles are found in some species of lapwings and when present vary greatly in size, shape, and color. In general, they are found in the space between the bill and eye and vary in size from a small disk a few millimeters in diameter to a large double wattle two centimeters long. Both sexes have wattles which are approximately the same size in each. They are usually yellow or red in color.

It has proven impossible to detect any trends in the variation of the wattles or indications that the species possessing wattles (see Table 2) are related. It is more likely that wattles have evolved and regressed independently several times in the lapwings. Thus Seebohm's arrangement of the lapwings into two groups on the básis of the presence or absence of a wattle is artificial.

At present I know of no published discussion of the functional significance of wattles in plovers. Admittedly, most of the species possessing wattles are found far from civilization, but at least one species, *Vanellus miles novaehollandiae,* occurs close to large cities in Australia and several other species can be observed in zoos. A study of the behavior of these species to determine whether wattles play a role in displays might contribute considerably to understanding their variation in the lapwings.

From their position and variation in size and color, it seems reasonable to suggest that the wattles serve as releasers associated with "courtship" or other displays or perhaps serve as species-specific recognition marks. Wattles are found in many other groups of birds, including the pheasants. The wattles in the male of *Lophura bulweri,* one of the pheasants, are used in the "courtship" displays (Delacour, 1951b, pp. 181-182). Structures used in "courtship" are peculiar in that the differences between species are generally very striking and usually do not fit into a regular pattern of variation. A more complete discussion of the problems associated with this type of character is given in the section on the plumes of herons (Bock, 1956, pp. 7-10). Delacour (1951b, p. 123) discusses the problem of wattles in the pheasants and Sibley (1957) summarizes the problem for birds in general. In brief, it should be remembered that the differences in species recognition marks are generally only of specific value, not generic.

Wing Spur

Many species of lapwings possess a spur at the bend of the wing. Where a distinct spur is lacking there is a bony knob which lies under the skin and can be felt on a study skin. The spur or knob is a bony projection on the proximal end of the carpometacarpus and varies in length from a blut projection that does not extend beyond the feathers of the wing to a sharp spur reaching a length of two centimeters (see Rand, 1954, p. 128, for more precise figures). The spur is equally well developed in both sexes although that of the male may be a few millimeters longer. Spurs are not found in the charadriine plovers; however, there is an enlargement at the proximal end of the carpometacarpus. More precisely this process is located at the base of the alula digit and is no doubt homologous with the bony knob and spur of the lapwings. This process which in its original and also present function serves as the point of insertion of the muscle extensor metacarpi radialis provides a bony mass (knob) at the bend of the wing. As shall be shown below, this bony mass is a pre-adaptation which increases the efficiency of the wing as a weapon. The new selection force concerned with increasing the efficiency of the wing as a weapon seizes this process and developed it into a sharp spur in several species of lapwings.

The lapwing plovers are very aggressive birds especially in the breeding season. Countless reports of various species "defending" the nest or territory by flying at the intruder can be found in the literature. A picture of *Vanellus miles novaehollandiae* (Oliver, 1955, p. 270) shows the bird in a "defensive" position — crouched low with the wings half spread. The bend of the wing is one of the best weapons in birds, as so well shown by the geese and pigeons. The adult lapwing may fly at the intruder and strike it in the face or other soft part, with the wings. Nethersole-Thompson (1940) reports lapwings (*Vanellus vanellus*) attacking sheep that have strayed too close to their nest. The birds flew over the back of the sheep and struck at them with their wings. A knob or, even better, a sharp spur at the bend of the wing would increase the effectiveness of the blow that may be strong enough to startle the intruder and cause it to retreat. Lucas (1893) and Rand (1954) favor the idea that wing spurs are used for fighting (including "courtship"), citing many groups that have spurs on the wings or that use the wing as a weapon.

Another suggestion is that the spur may have a function in the "courtship" or other displays. There are many displays in which the bird faces another individual and half raises its wings. If this additional function were demonstrated, it would in no way invalidate the first hypothesis; the spur can have both functions at the same time.

Why there is so great a variation in the development of the spur in different species of *Vanellus* is a mystery. There may well be some correlation between the habits and the length of the spur, but the habits of lapwings are unknown to such an extent that we are unable to formulate any hypothesis. Lucas suggested that the size of the spur was directly correlated with the size of the wattles; however, data presented in Table 2 shows little evidence of this correlation. The best conclusion based on the available evidence is that the presence or absence of a spur in some species of *Vanellus* is almost definitely not an indication of relationship. Most likely the spur evolved or regressed independently several times in this genus and cannot be used to group species together.

Color and Color Pattern

Color itself is usually of little importance in showing relationships between species and genera of birds. On the other hand, color pattern is often of considerable value, although generally not above the generic level. This appears to be true for the plovers.

It is well known that the back color of many (all?) species of plovers agrees with the color of the ground and serves as protective coloration. An excellent example is the piping plover (*Charadrius melodus*) which is found only on sand beaches and in color is light grey dorsally. It is usually impossible for the human observer to see the birds even though they may be calling just 100 feet away; only when they run are they easily seen. In a series of thorough studies it was shown that in the larks the color of the back is correlated with the color of the soil on which the larks live (Niethammer, 1940; Vaurie, 1951, pp. 442-446). It would be desirable to correlate in a similar manner for the plovers the color of the soil and color of the back, but too often the color of the soil could not be determined from the literature, and to present such a table would be more guesswork than fact. However, a survey of the literature reveals numerous statements on the concealing nature of the back color. Some examples are *Vanellus coronatus* (van Someren, 1956, p. 124), *V. tricolor* (Favaloro, 1944, p. 151), *V. miles novaehollandiae* (Favaloro, 1944, p. 146), *Charadrius venustus* (van Someren, 1956, p. 123), *C. tricollaris* (Haagner, 1910, p. 503), *C. modestus* (Goodall *et al.*, 1951, p. 221), *Anarhynchus frontalis* (Stead, 1932, p. 92: Oliver, 1937, p. 3), *Pluvianellus socialis* (Goodall *et al.*, 1951, p. 216), and *Eudromias ruficollis* (Goodall *et al.*, 1951, p. 208). This list could be greatly expanded, with at most a few or no cases in which the color of the back does not harmonize with the substrate. From this, we can conclude that the plovers have protectively colored backs which are under the influence of a strong and easily changed selection force (color of the ground) — a force which could alter several times during the evolution of a species or of a higher category of plovers.

In contrast to this ecotypic interpretation of back colors, Lowe (1922, p. 487; 1933a) considered the difference of a light versus dark dorsal color in the various species of *Pluvialis* and *Charadrius* to be important phylogenetically. Pale back color was thought to be primitive and to have given rise to the darker color. Furthermore, he tried to correlate the color of the back with the skull type (see above, p. 33) and asserted that the color of the back is not primarily affected by the selection forces of the present day environment. However these conclusions cannot be accepted because they were based on factual inaccuracies, as for example, the color of the back of *C. melodus* is given as darker than that of *C. alexandrinus* and the same as that of *C. hiaticula*, a statement which is quite incorrect.

The shape of the skull and the color of the back are selected for by two entirely different forces, salinity as against the color of the soil, which although they are often associated, are independent of one another. Therefore these two characters cannot be considered as correlated. If a plover lives on sandy beaches along the ocean, it will most likely have a pale colored back and a skull as illustrated for *Charadrius alexandrinus*. There is no reason to believe, on the basis of these characters, that this species is closely related to other plovers living in the same environment and therefore having these same characteristics. Indeed, if the closest relative of the plover living on sandy coastal beaches is a species dwelling inland on muddy fields, then this species would most likely have a dark colored back and a skull as illustrated for *Charadrius vociferus*. These two sets of characters are as different as they could possibly be, yet do not invalidate the conclusion based on other characteristics that these species may be closely related. It need not be pointed out that it is a rather simple matter during the evolution of the plovers for species to shift from fresh water to salt water or from mud flats to sand beaches. Because the selection force (i.e. the environment) could easily change several times during the differentiation of two species or groups of species and because these selection forces are so powerful, I feel that certain characters, as for example the shape of the top of the skull or the color of the back, are too easily affected by the action of the environment (selected for) to be of any value in a generic revision. To say this in another way, related species may (but not necessarily) be similar in certain readily modified characters (back color and skull morphology), but those species that are similar in these characters are not necessarily related. This is in general true for any character that is under the influence of a strong selection force (= environment) which can easily change during the evolution of a group.

Pattern of coloration is usually more stable than color, for while color may change in response to a selection force, it can do so on the existing pattern. To be sure, convergence is still an important consideration because a particular selection force can select for the same pattern in unrelated birds. Usually, however, the more complex a color pattern is, the less chance there is for convergence to occur, but if a certain pattern is highly adaptive in a certain environment, it can occur in unrelated forms found in the same habitat, as shown by Friedmann (1946, p. 395).

In plovers, several color patterns are of uniform expression over large numbers of species and appear to be important in showing relationships. The head and breast markings are very constant in *Charadrius*. In *Vanellus*, the pattern of the wing and tail is almost completely uniform in the entire genus. Here the words of Seebohm are as true today as they were in 1888 (p. vi): "I have found that in many cases the colour of such parts of the plumage as are unaffected by age, sex, or season, and which is therefore presumably of ancient origin, is apparently of much greater value in ascertaining the relationships of many birds than the so-called structural characters, which are compelled by the laws of evolution to change with the changing habits or environment of the species."

In *Charadrius* the breast bands and head markings act as disruptive marks especially when the bird is sitting on the nest. They probably also serve as species-specific releasers and this may well be the reason for their peculiar variation. Smith and Hosking in their study of *Charadrius hiaticula* point out (1955, p. 82): "It will be evident from a study of the photographs, that the Ringed Plover makes full use of the black and white patterning on its breast, chin and head, and also on its tail to produce a maximum effect of threat." Stead (1932) describes the same postures for *Charadrius bicinctus* and *Anarhynchus frontalis*. The color and color pattern of the head and breast in *Vanellus* probably also serve as releasers and species-specific recognition marks which may account for the complex and seemingly haphazard pattern of variation of these characteristics in this genus. Until more is known of the "courtship" displays of most species of plovers, especially of the lapwings, we can only assume that the differences in color pattern are important in the behavior of plovers. The forces that select for differences in these characters are so strong and varied (depending greatly upon which species are sympatric) that the resulting variation of color pattern has largely obscured the relationships between species. Thus while color pattern is very valuable in allying large groups of species, the variation within each pattern can be used only with the greatest caution to show relationships in *Charadrius*, and even less in *Vanellus*.

Osteology

The skeletons of some species of plovers (see above, p. 29) were compared primarily to see if there were any characters that separated the lapwings from the charadriine plovers, and secondly to see if there were any differences between *Charadrius* and *Pluvialis*. A complete study was not done as the skeletons of relatively few species were readily available and an examination of these specimens indicated that it would not be practical to borrow the necessary material for a thorough investigation at this time.

In brief, the plovers seem to be a very homogeneous group osteologically. In the skull the most striking difference is the contour of the roof which has already been discussed in detail (see p. 31). The size and shape of the ectethmoid varies, especially in *Charadrius,* and may well be correlated with the size of of the bill, but it is not known what possible taxonomic implications it may have. Rensch (1923, p. 69) suggested that the outline of the foramen magnum differs between *Charadrius* and *Pluvialis,* that of *Charadrius* being more oblong, that of *Pluvialis* rounder. I have examined skulls of *P. dominica* and *P. squatarola* and the North American species of *Charadrius* for this character. In general, Rensch's observations were confirmed, but some variation exists in *Charadrius* and until this is more fully investigated, the value of the foramen magnum as a diagnostic character cannot be determined.

The limb bones as well as the trunk skeleton were compared with equally negative results. The proximal end of the tarsometatarsus may differ between *Pluvialis* and *Charadrius.* In *Charadrius* there appear to be more canals in the hypotarsus for the passage of tendons than in *Pluvialis*, but not enough species have been studied to be sure that this is a constant difference.

To conclude, I have been unable, after a brief survey, to discover any osteological characters that proved to be useful in understanding the relationships within the plovers. However, some of the characteristics such as the shape of the foramen magnum or the configuration of the canals of the hypotarsus may prove to be valuable with further study. Because the plovers are a very homogeneous group, if a comparative study of their osteology is done in hopes of finding additional clues to relationships, large series of skeletons will be needed in addition to a good representation of species to be certain that individual and age variations are distinguished from the true differences between genera.

No other anatomical systems were studied.

The Position of the Charadriinae

A study of the status and taxonomic ranking of the plovers as a group is beyond the scope of this paper. However, because opinions on the relationships and status of the plovers differ so greatly, a brief summary of the problem should be given. The plovers were considered as a subfamily of the Charadriidae (which included most of the birds known as the "shorebirds") in the important works of Seebohm, Fürbringer, Gadow, Beddard and more recently by Stresemann and by Mayr and Amadon. On the other hand, Sharpe, Ridgway, Lowe, Peters and Wetmore separated the plovers as a distinct family (perhaps including such genera as *Haematopus*), which is currently the more widely accepted view.

The present trend toward a broad concept of taxonomic categories has more promise for a sounder, more rational classification of birds than the existing one which is based on the theory that morphological differences, no matter what they are, require taxonomic separation. In the proposed classification, most of the formerly recognized genera are merged and the close relationship between the remaining genera is emphasized. Hence there is no longer any need for maintaining family status for the plovers or the two subfamilies as currently used. The most consistent classification is to include the plovers as a subfamily of an enlarged family of shorebirds. The classification of Mayr and Amadon (1951) will be accepted for the purposes of this paper and the usage of family and subfamily names will follow their terminology.

Some difficulty may arise in the discussions over the exact meaning of the family and subfamily names. In the event of any possible confusion, the following convention will be adopted. When the names Charadriidae or Charadriinae are used in the sense of Mayr and Amadon they will not be qualified or they will be followed by *sensu lato*, and when they are used in the sense of Peters, they will be followed by *sensu stricto*.

The limits of the Charadriinae and a description of the subfamily are somewhat difficult to give largely because of the uncertain position of the genera *Arenaria* and *Aphriza* (the turnstones and surfbirds) and to a lesser extent, *Phegornis* and *Peltohyas*. A full discussion of each group will be presented below. Most important is that, with the possible exception of these four genera, all of the species included in the Charadriinae in this study are more closely related to each other than to any other genus of the Charadriidae. If future study should prove that any of these four problem genera are indeed to be included in the Charadriinae, they would almost certainly constitute a group(s) separate from the genera included in the Charadriinae in this study.

The plovers comprise a single subfamily of the Charadriidae with no formal groups recognized between the subfamily and generic levels. A good diagnostic description for the plovers has not been given in any of the standard works on the anatomy and classification of birds. However, within the plovers, the largest gap exists between the lapwings (*Vanellus*) and the genera of charadriine plovers (*Pluvialis*, *Charadrius*, *Anarhynchus*, *Eudromias* and *Pluvianellus*). The charadriine plovers form a very closely knit group with only slight gaps between the genera. While these gaps are small, they are larger than the gaps between the congeneric species which merge into one another in many characteristics. Essentially there is a large genus, *Charadrius*, with a very closely allied genus, *Anarhynchus*, and three small outlying genera, *Pluvialis*, *Eudromias* and *Pluvianellus*. If the proposal of the Nomenclature Committee of the British Ornithologists Union (Anonymous, 1949) is followed, then all of the charadriinae plovers must be placed in *Charadrius;* there is no other alternative. This is not an unreasonable course of action and may even be the best, but at present I feel that it would be too inconsistent with the current concepts of avian taxonomy and prefer to maintain the several genera of charadriine plovers as proposed in this paper.

The following arrangement of genera and species attempts to show relationships as based on a comparative study of the characters described above. It would be desirable to group the genera and species in some definite sequence, say from the most primitive to the most specialized form in each category. Unfortunately, however, I have been most unsuccessful in discovering what is primitive and what is specialized, so that the linear arrangement is mainly for convenience and is admittedly partly artificial. Superspecies (for definition, see Mayr, *et al.*, 1953.

p. 29) are bracketed. Whenever a species has been transferred to a new genus, the old generic name (Peters' classification of 1934 is used as the basis of comparison) follows in parenthesis.

Classification of the Charadriinae

Genus *Vanellus*
vanellus
crassirostris (Hemiparra
armatus (Hoplopterus)
spinosus (Hoplopterus)
duvaucelii (Hoplopterus)
tectus (Sarciophorus)
malabaricus (Lobipluvia)
albiceps (Xiphidiopterus)
lugubris (Stephanibyx)
melanopterus (Stephanibyx)
coronatus (Stephanibyx)
senegallus (Afribyx)
melanocephalus (Tylibyx)
superciliosus (Anomalophrys)
gregarius (Chettusia)
leucurus (Chettusia)
cayanus (Hoploxypterus)
chilensis (Belonopterus)
resplendens (Ptiloscelys)
cinereus (Microsarcops)
indicus (Lobivanellus)
macropterus (Rogibyx)
tricolor (Zonifer)
miles (Lobibyx) includes
novaehollandiae
Genus *Pluvialis*
apricaria
dominica
squatarola (Squatarola)
obscura (Pluviorhynchus)

Genus *Charadrius*
hiaticula
placidus
dubius
wilsonia
vociferus
melodus
thoracicus
pecuarius
tricollaris
alexandrinus
peronii
venustus
collaris
bicinctus
falklandicus
mongolus
leschenaultii
asiaticus (Eupoda)
modestus (Zonibyx)
montanus (Eupoda)
melanops (Elseyornis)
cinctus (Erythrogonys)
rubricollis
novaeseelandiae (Thinornis)
Genus *Anarhynchus*
frontalis
Genus *Eudromias*
morinellus
ruficollis (Oreopholus)
Genus *Pluvianellus*
socialis

Genera = 6
Species = 56

Incertae sedis

Genus *Phegornis*
(=Scolopacinae ?,
see p. 80)
mitchellii
Genus *Peltohyas*
(=Glareolidae ?,
see p. 84)
australis

Genus *Aphriza*
(=Scolopacinae ?,
see p. 85)
virgata
Genus *Arenaria*
(=Scolopacinae ?,
see p. 85)
interpres
melanocephala

Genera recognized by Peters and synonymized here are:

Afribyx = *Vanellus*
Anomalophrys = *Vanellus*
Belonopterus = *Vanellus*
Chettusia = *Vanellus*
Elseyornis = *Charadrius*
Erythrogonys = *Charadrius*
Eupoda = *Charadrius*
Hemiparra = *Vanellus*
Hoplopterus = *Vanellus*
Hoploxypterus = *Vanellus*
Lobibyx = *Vanellus*
Lobipluvia = *Vanellus*
Lobivanellus = *Vanellus*
Microsarcops = *Vanellus*
Oreopholus = *Eudromias*
Pluviorhynchus = *Pluvialis*
Ptiloscelys = *Vanellus*
Rogibyx = *Vanellus*
Sarciophorus = *Vanellus*
Squatarola = *Pluvialis*
Stephanibyx = *Vanellus*
Thinornis = *Charadrius*
Tylibyx = *Vanellus*
Xiphidiopterus = *Vanellus*
Zonibyx = *Charadrius*
Zonifer = *Vanellus*

The following species, accepted by Peters, have been reduced to subspecific status or synonymized (see under the respective genera):

Charadrius alticola = *C. falklandicus alticola*
Charadrius sanctaehelenae = *C. pecuarius sanctaehelenae*
Eupoda veredus = *Charadrius asiaticus veredus*
Lobibyx novaehollandiae = *Vanellus miles novaehollandiae*
Rogibyx tricolor = *Vanellus macropterus*

In the generic headings that follow, the generic name is followed by the describer's name, then the type species follows in parenthesis, and finally the year in which the genus was described. The included species are listed and a brief generic synonymy is given. For a more complete synonymy, the reader is referred to the standard works of Sharpe, Ridgway, Peters, and Hellmayr and Conover. The ranges are taken chiefly from Peters.

VANELLUS Brisson (VANELLUS) 1760

Synonymy: Hoplopterus Bonaparte, 1831 (*spinosus*); *Chettusia* Bonaparte, 1841 (*gregarius*); *Lobivanellus* Strickland, 1841 (*spinosus*); *Sarciopterus* Strickland, 1841 (*tectus*); *Cranellus* Tobias, 1844 (*spinosus*); *Vanellochettusia* Brandt, 1852 (*leucurus*); *Belonopterus* Reichenbach, 1852 (*chilensis*); *Tylibyx* Reichenbach, 1852 (*melanocephalus*); *Sarcogrammus* Reichenbach, 1852 (*indicus*); *Xiphidiopterus* Reichenbach, 1852 (*albiceps*); *Stephanibyx* Reichenbach, 1852 (*coronatus*); *Hoploxypterus* Bonaparte, 1856 (*cayanus*); *Ptiloscelys* Bonaparte, 1856 (*resplendens*); *Lobipluvia* Bonaparte, 1856 (*malabaricus*); *Difilippia* Salavadori, 1865 (*crassirostris*); *Hemiparra* Salavadori, 1865 (*crassirostris*); *Limmetes* deFilippi, 1870 (*crassirostris*); *Nomusia* Heuglin, 1877 (*crassirostris*); *Lobibyx* Heine, 1890 (*novachollandiae* = *miles*); *Microsarcops* Sharpe 1896 (*cinereus*); *Eurypterus* Sharpe, 1896 (*leucurus*); *Zonifer* Sharpe, 1896 (*tricolor*); *Anomalophrys* Sharpe, 1896 (*superciliosus*); *Euhyas* Sharpe, 1896 (*leucurus*); *Zapterus* Oberholser, 1899 (*leucurus*); *Rogibyx* Mathews, 1913 (*tricolor* = *macropterus*); *Afribyx* Mathews, 1913 (*sengallus*); *Titihoia* Roberts, 1924 (*melanopterus*).

Included Species: vanellus, crassirostris, armatus, spinosus, duvaucelii, tectus, malabaricus, albiceps, lugubris, melanopterus, coronatus, senegallus, melanocephalus, superciliosus, gregarius, leucurus, cayanus, chilensis, resplendens, cinereus, indicus, macropterus, tricolor, and *miles.*

Diagnosis: When the color and pattern of the body plumage are considered, the lapwings are a very diverse group, but there is a common tail and wing pattern that ties the species together. The tail (except for *leucurus*, which has an all-white tail) is white basally with a broad black band on the distal half and often with a narrow white terminal band. The primaries are always black and generally (except for *vanellus* and *miles* which have a unicolored wing) marked by a broad wing stripe that

Table 2

Species	Hind Toe	Wing spur	Wattles		Habitat
			size	color	
vanellus	+	—	—	—	marshes
crassirostris	+	—	—	—	streams, lakes
armatus	—	+ (9-12mm)	—	—	grasslands, flats near water
spinosus	—	+ (5-11mm)	—	—	fields near water
duvaucelii	—	+ (11-13mm)	—	—	marshes, rivers
tectus	—	—	1, large	crimson	dry grasslands
malabaricus	—	—	2, large	yellow	dry grasslands
albiceps	—	+ (18-23mm)	1, large	greenish yellow	marshes, streams
lugubris	—	—	—	—	dry grasslands
melanopterus	—	—	—	—	dry grasslands
coronatus	—	—	—	—	dry grasslands
senegallus	+	+ (3-11mm)	2, large	red and yellow	marshes, dry fields
melanocephalus	+	—	1, small	red	marshes
superciliosus	—	—	1, small	yellow	dry grasslands
gregarius	+	—	—	—	marshes
leucurus	+	—	—	—	grasslands, marshes
cayanus	—	+ (4-9mm)	—	—	marshes, streams
chilensis	+	+ (8-14mm)	—	—	marshes
resplendens	—		—	—	mountain streams
cinereus	+	—	1, small	yellow	marshes
indicus	+	—	1, small	red	marshes, dry fields
macropterus	+	+ (15mm)	2, large	pink and white	?
tricolor	—	—	1, small	red	fields
miles	+	+ (15-17mm)	2, large	yellow	marshes

Variation of several characters in *Vanellus*. If the characteristic is present in a species, it is symbolized by a +, if absent, by a —. Under wing spur the figures following the + are the lengths of the spur given by Rand; a — means that a knob rather than a fully developed spur is present.

begins on the greater coverts of the primaries and extends diagonally across the secondary coverts and the secondaries themselves so that in some species the innermost secondaries are completely white. Such features as the head and breast pattern, and presence and size of the wattles and wing spur vary from from species to species and probably serve as releasers in connection with species-specific behavior displays and hence are specific, not generic characters. In habitat, the lapwings are all inland birds, found on dry grasslands or barrens, marshes, swamps or the edges of streams and rivers. They are noisy birds, constantly flying around an intruder and calling loudly, much more so than the charadriine plovers.

Range: World-wide except for North America. The center of distribution is Africa and, to a lesser extent, southern Asia.

Remarks: Compared to Peters' treatment of the lapwings, the proposal to place the lapwings in a single genus seems at first to be very radical. Yet if we compare the merits of the two arrangements, the greater usefulness of the present proposal should become apparent. In Peters' classification, the 25 species of lapwings are placed in 19 genera of which only *Stephanibyx* and perhaps *Chettusia* contain more than a single superspecies — a classification in which almost every genus is monotypic. If, on the other hand, the lapwings are regarded as congeneric, the result will be a single genus of 24 (or 25) species. By the standards of avian taxonomy this is a large genus, but no more so than many others such as *Buteo* (27 species), *Corvus* (32), *Accipiter* (33), *Larus* (35), *Anas* (36), *Falco* (37), *Caprimulgus* (39), *Dicaeum* (41) and *Turdus* (63). These genera are characteristically highly successful groups which have undergone an extensive adaptive radiation to produce the large and complex groups we know today. A serious attempt has been made to discover divisions within the lapwings that could be considered as genera, but at best only poorly marked trends of certain characters could be determined — no clearly separated groups of species could be found. We are thus faced with accepting either Peters' arrangement or placing the lapwings in a single genus: at present there seems to be no other alternative. If the broad limits of *Charadrius* are accepted, and as the other alternative is a relatively useless monotypic generic classification, there should be little doubt that the most reasonable action is to place all of the species of lapwings in *Vanellus,* as proposed in this paper.

White (1952) and more recently von Boetticher (1954) have studied the relationships of the lapwings and attempted to synonymize some of the small genera. White quite correctly pointed out that the characters on which the old genera were based (presence or absence of the hallux and scutellation of the tarsus) were of little taxonomic value. He then based his relationships on the nature of the wattles and the wing spur. Von Boetticher used the presence (including the relative development) or absence of the hind toe, of the wattles and of the wing spur as the major characters in establishing his genera. As has already been shown in this paper, all of these characters do not appear to have any value in determining generic relationships. Thus, while these works have merit as attempts to understand the relationships within the lapwings, the genera proposed by these authors are with little doubt artificial and therefore cannot be accepted.

Merely to place the lapwings in a single genus is of no more help in understanding their relationships than to place each species in a separate genus. I have tried, but with little success, to sort out subgroups or trends within the lapwings. It is doubtful that the problem of relationships between the species of *Vanellus* can ever be solved by a study, no matter how intensive. of museum skins or of the internal anatomy because the characteristics seen on the the skins are subject to strong and variable selection forces while the internal anatomy is too uniform. Rather, solution of this problem will probably be through an investigation of comparative behavior or perhaps serology and similar studies. Several subgroups, however, do separate out and these will be presented as the best possible arrangement for the present. The characters supporting these groups are very vague and best serve to illustrate the extreme difficulty of the problem and the weakness of the suggested arrangement. The relationships and a rough indication of the distribution of the lapwings are illustrated in Figure 4.

Africa, the center of distribution for the genus, is the home of

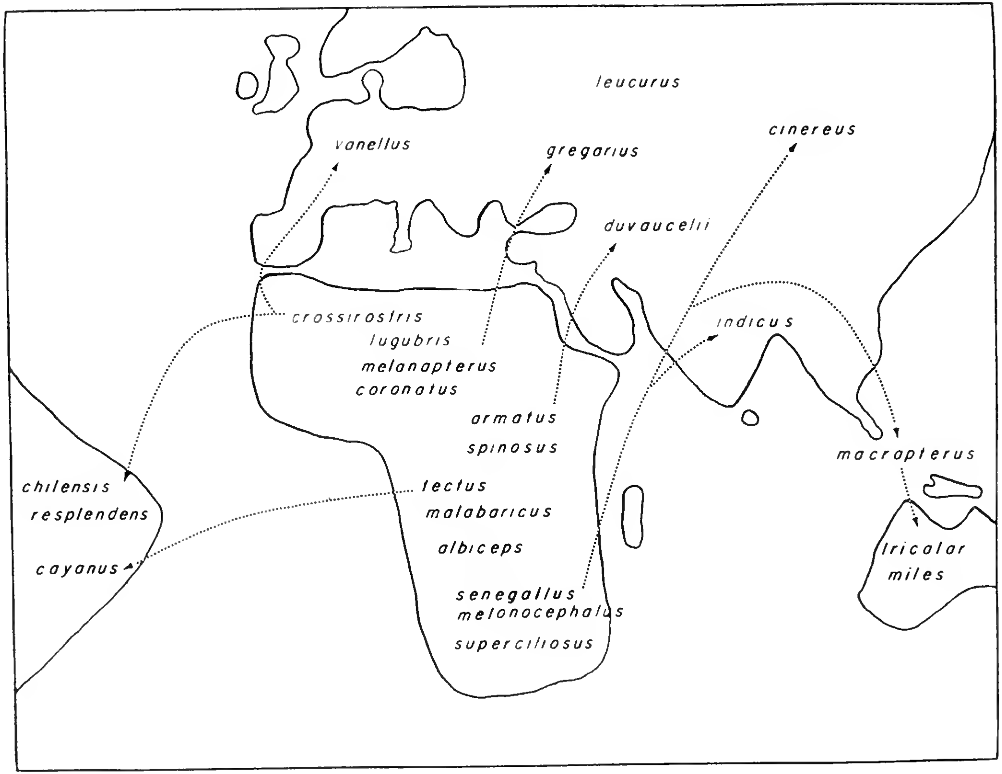

Figure 4. Diagram showing the relationships within *Vanellus.* The species are placed in the continent in which they breed. Relationships between groups and the probable routes of dispersal are shown by the dotted lines. See the text for a discussion of the relationships within the lapwings.

the largest species group, namely *crassirostris,* the *armatus-spinosus-duvaucelii* (Asiatic) complex, *tectus, malabaricus, albiceps* and the *lugubris-melanopterus-coronatus* complex. The characters shared by these species are hard to define, but the wing pattern is somewhat similar in all of them and there are some general similarities in the head and breast pattern. The European *vanellus* is probably an offshoot of this group.

The species *senegallus* and *melanocephalus* may well be related to one another as they are the only lapwings with streaking on the throat. They are similar to the first group in wing pattern and coloration of the throat and may be considered as a branch of that group.

The small *superciliosus* is quite different from the other lapwings in that the color of the breast is red (unique in this genus), and the fact that it lacks the head markings found in many of the other species. At present it is impossible to point to any species as its closest relative.

The two species found in central Asia, *gregarius* and *leucurus,* may be related to *coronatus* of Africa. The breast and head pattern of *gregarius* is similar to that of *coronatus.* The close similarity between *gregarius* and *leucurus* makes it reasonably clear that they diverged from a common ancestor after it had become established in Asia.

The South American *cayanus* appears to be derived from the large African group, but again it is impossible to point to any species as its closest relative. It has a breast band and head pattern like some of the African species, but the coloration of the back is quite unique. The brown of the center of the back is bordered by white while the scapulars are black, a pattern that is found nowhere else in the lapwings.

The other two species of South American lapwings, *chilensis* and *resplendens* are closely related to one another and represent an invasion of South America separate from *cayanus.* The back of each species is a metallic greenish color similar to that of *vanellus.* In addition, *chilensis* possesses a head tuft and black breast band like those of *vanellus.* These species are certainly closest to *vanellus.*

The complex consisting of *cinereus, indicus, macropterus, tricolor,* and *miles* (including *novaehollandiae*) constitute the Far Eastern and Australian lapwings. Except for *cinereus,* all have a black crown and some black on the breast. The back of all species is brown, all have wattles and generally a fainter wing bar than their congeners. They seem to be closest to some of the species of the large African group, perhaps *melanopterus* or *albiceps*.

It can now be appreciated why I consider the evidence supporting the delimitation of these groups as very poor. The above arrangement has to a large extent divided the lapwings into groups according to their geographic occurrence. This may convey the impression that there has been a small radiation in each of these regions, which probably is not the case. What seems to be more likely is that Africa was the center of diversification and the species have spread from there. There is little doubt that there have been two separate invasions of South America. Asia and Europe were invaded from Africa by at least five different lines, *vanellus*, *gregarius*, *cinereus*, *indicus* (giving rise to the other Far East and Australian species?), and *duvaucelii*, and there may have been more (some of the other Far East and Australian species).

The ranges of *miles* and *novaehollandiae* as given in the literature appear to be allopatric. The major differences between these forms are an extension of the black crown down the hind neck and sides of the breast in *novaehollandiae* and a difference in the wattles and body size. They are similar in all other features and as their ranges seem to be allopatric, it is assumed in this paper that they are conspecific. However, there is still doubt as to whether or not the ranges of these forms overlap in Queensland and if they do, *miles* and *novaehollandiae* must be regarded as distinct species, and in that case would constitute a superspecies.

The three species of the former genus *Hoplopterus* — *spinosus*, *armatus* and *duvaucelii* — are all allopatric. The ranges of *armatus* and *spinosus* come close to one another and some authors (Mackworth-Pread and Grant, 1952, pp. 357-358) show their ranges overlapping in Kenya, but a careful survey of the literature indicates that there is no overlap in breeding range (Jackson, 1938, pp. 354-355). While the color pattern of the three species is similar, there are a number of plumage differences which make the species strikingly dissimilar so it is likely that if the ranges did overlap, individuals of the several species would avoid one another and thus prevent mixed pair formation and interbreeding. No intermediates between the species have ever been reported, nor is there any indication of trends in one species toward another. Hence they are best considered as distinct species, but as their ranges are allopatric, they form a superspecies.

Zonifer tricolor of Australia was described by Vieillot in 1818 several years before Horsefield described *Rogibyx tricolor* of Java in 1821. Since these two species are now placed in the same genus, a name must be substituted for *Rogibyx tricolor*. The next available name for the Java bird is *macropterus* Wagler, which was published in the combination *Charadrius macropterus* in Wagler's Systema Avium (1827, p. 77, species 54).

PLUVIALIS Brisson (APRICARIA) 1760

Synonymy: Squatarola Cuvier, 1817 (*squatarola*); *Pluviorhynchus* Bonaparte, 1856 (*obscura*).

Included species: apricaria, dominica, squatarola and *obscura.*

Diagnosis: The back of these large chunky plovers is mottled brown or grey (less so in *obscura*) while the underparts are uniformly black or reddish brown (*obscura*) in color. There may or may not be a wing stripe or white patch on the rump and tail. The conspicuous color of the underparts is lost in the post-nuptial molt and replaced by a greyish or tan color. The immature is similar in color to the adult in the non-breeding plumage.

Range: Breeds in the Arctic tundra south to Central Europe, migrates and winters south to southern Africa, South America and Australia. *Pluvialis obscura* is found only in New Zealand.

Remarks: I have shown in another part of this paper (see above, p. 31) that the characters used to separate *Squatarola* from *Pluvialis*, mainly the structure of the skull and the presence of a hind toe in *Squatarola*, are of no help in showing relationships or differences on the generic level. The two forms are so nearly identical in all respects that there should be no doubt that they are congeneric. There is a greater difference between *obscura* and is congeners. Its back is only faintly mottled in addition to its underparts being reddish, not black in color. Compared to the large number of similarities in color pattern and body size and shape, the differences in the color of the back

Table 3

Species	Hind Toe	Breast bands		Back color	Range
		number	color		
Pluvialis					
apricaria	—	—	black	brown	Holarctic
dominica	—	—	black	brown	
squatarola	+	—	black	light grey	Holarctic
obscura	—	—	reddish brown	brown	New Zealand
Charadrius					
hiaticula	—	1, complete	black	brown	Holarctic
placidus	—	1, complete	black	brown	Eastern Asia
dubius	—	1, complete	black	brown	Old World
wilsonia	—	1, complete	black	brown	New World
vociferus	—	2, complete	black	brown	New World
melodus	—	1, incom., or complete	black	light grey	North America
thoracicus	—	1, complete	black	brown	Madagascar
pecuarius	—	—	white	brown	Africa
tricollaris	—	2, complete	black	brown	Africa
alexandrinus	—	1, incom.	black	light brown to grey	World-wide
peronii	—	1, incom.	♂, black ♀, red	pale brown	East Indies
venustus	—	1, complete	red	light grey	Africa
collaris	—	1, complete	black	brown	South and Middle America
bicinctus	—	2, complete	upper black lower red	brown	New Zealand
falklandicus	—	2, complete	black	brown	South America
mongolus	—	1, complete	rufous	brown	Asia
leschenaultii	—	1, complete	rufous	brown	Asia
asiaticus	—	—	reddish	brown	Asia
modestus	+	—	reddish	brown	South America
montanus	—	—	tan	brown	North America
melanops	—	1, complete	black	brown	Australia
cinctus	+	1, complete	black	brown	Australia
rubricollis	—	1, incom.	black	pale brown	Australia
novaeseelandiae	—	—	white	brown	New Zealand

Table 3 (Continued)

Species	Hind Toe	Breast Bands		Back Color	Range
		Number	Color		
Anarhynchus					
frontalis	—	1, complete	black	grey	New Zealand
Eudromias					
morinellus	—	—	rufous	grey-brown	Palaearctic
ruficollis	—	—	grey	brown	South America
Pluvianellus					
socialis	+	1, diffuse	grey	grey	South America

Variation of several characters in the charadiine plovers. As in Table 2, a + indicates that the character is present; — indicates absence of the character. Under the heading of breast bands, incomplete means that the band is not continuous around the breast. If the breast band is absent, the color of the breast is given, otherwise the color of the band is given.

and reddish brown breast lose much of their importance. This is supported by the condition in *Charadrius* where the color of the breast bands may be black or rufous in closely allied species or even in the same species. The habits of *obscura* are much like those of *dominica* (Robson, 1884).

The two species of golden plovers (*dominica* and *apricaria*) are very similar to one another and their ranges are almost completely allopatric. All of the major works on Palearctic birds state that the ranges of the two overlap in the region of the Yenisei River in Western Siberia (Popham, 1897, p. 192, Dementiev and Gladkov, 1951, pp. 40, 47); hence the two forms must be considered as distinct species. As the amount of overlap is so slight and the two species are so similar, their relationship to one another is best shown if they are placed in the same superspecies, as has been concluded by Delacour and Mayr (1945, p. 106). The closeness of this relationship is further supported by the report of an apparent hybrid between the two species (Popham, 1900).

CHARADRIUS Linneaus (HIATICULA) 1758

Synonymy: Erythrogonys Gould, 1838 (*cinctus*); *Eupoda* J. F. Brandt, 1845 (*asiaticus*); *Thinornis* G. R. Gray, 1845 (*novaeseelandiae*); *Zonibyx* Reichenbach, 1852 (*modestus*); *Podasocys* Coues, 1866 (*monta-*

nus); *Eupodella* Mathews, 1913 (*veredus* = *asiaticus*); *Elseya* Mathews, 1913 (*melanops*); *Elseyornis* Mathews, 1914 (*melanops*); See Peters, 1934, pp. 245-246 for complete synonymy.

Included species: hiaticula, placidus, dubius, wilsonia, vociferus, melodus, thoracicus, pecuarius, tricollaris, alexandrinus, peronii, venustus, collaris, bicinctus, falklandicus, mongolus, leschenaultii, asiaticus, modestus, montanus, melanops, cinctus, rubicollis, and *novaeseelandiae.*

Diagnosis: Small to medium sized plovers, usually with a heavy breast band or a black forehead and black line connecting the bill and the eye, or both. This very characteristic breast and head pattern, so well illustrated in *hiaticula,* is found in a more or less developed state throughout the genus. In the superspecies *asiaticus-modestus* these markings have largely disappeared, but the last remnants can still be seen. The pectoral bands may be single or double; often they are incomplete around the breast and exist only as a vertical bar on the shoulder or may be completely absent. The breast band is usually black but may be reddish or rufous. In one species, *peronii,* the male has a complete black band while in the female the band is rufous and incomplete. In a few species the black breast band is complete around the back. More commonly, however, there is a complete white collar on the hind neck which separates the brown or grey crown from the back. The back is dark brown to pale grey in color. Underparts are usually white except for the breast bands, but in a few species, such as *modestus,* the breast may be reddish in color. A white wing stripe may be present or absent. The central tail feathers are dark brown or grey according to the color of the back while the lateral feathers are white. In a few species such as *vociferus* the tail pattern has become elaborate. Most species have little or no sexual or seasonal variation in plumage and the immature is similar to the adult.

Range: World-wide.

Remarks: Except for the addition of several somewhat aberrant species, Peters' delimitation of the genus *Charadrius* is followed in this paper. Like *Vanellus,* the genus is large and complex and the path to understanding the relationships between the species is full of pitfalls. My attempts to arrange the species in a natural order and to discover the relationships between them have met with only limited success because of the nature of the characters used. The color of the back is strongly selected for as concealing coloration and, contrary to Lowe's claims, is of little use in showing relationships. The number, development and color of the breast bands and head markings

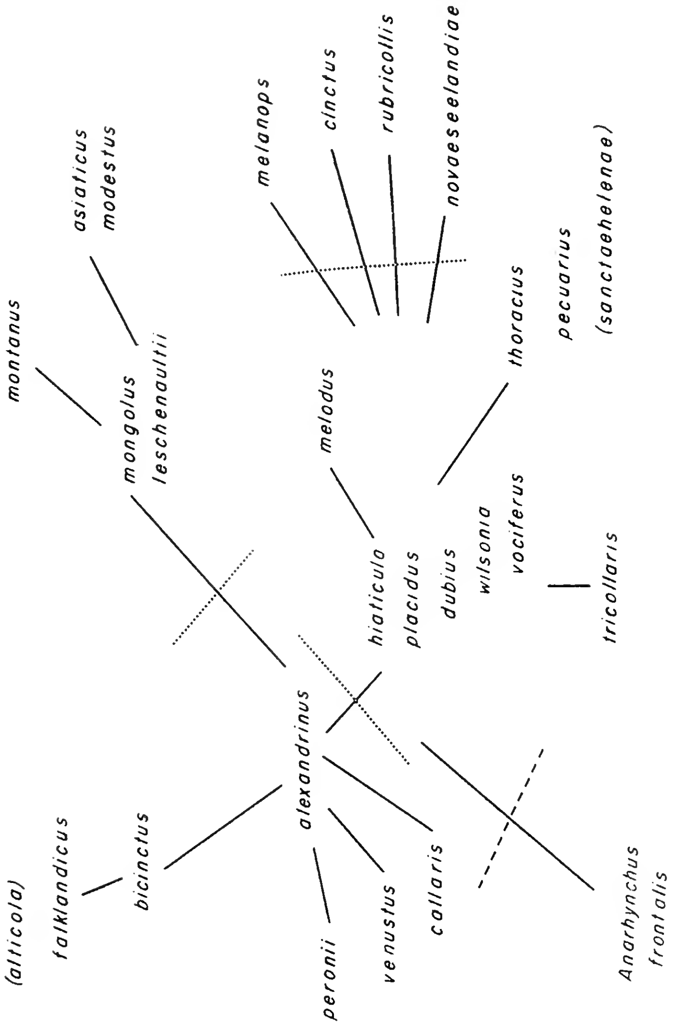

Figure 5. Dendrogram showing the relationships within *Charadrius* and the closely related *Anarhynchus*. The dotted lines separate the major sections within *Charadrius* and dashed line separates *Anarhynchus* from *Charadrius*. See text for a discussion of the relationships and evolution in *Charadrius*. (For *thoracius* read *thoracicus*.)

vary greatly and probably serve as releasers associated with both "courtship" displays and species recognition. In proposing the relationships outlined below, I have used mainly the pattern of the head and breast and to a slight extent the color of the back, but always mindful of the many dangers that exist. As in the lapwings, I doubt that it will be possible to discover the course of evolution in *Charadrius* by a study of museum skins. Nor is internal anatomy likely to provide the answer to the problem. Most probably, the solution will be supplied by a comparative study of their behavior and perhaps other techniques such as serology.

It has been impossible to determine which species or characteristics are primitive or specialized. However it is useful to designate one species as the basis for comparative purposes, and *hiaticula* has been selected for this mainly because it is so well known and not because it is considered primitive. The relationships within *Charadrius* are illustrated in Figure 5.

Group A. The typical species of the ringed plover group are *hiaticula*, *placidus*, *dubius*, *wilsonia*, *vociferus*, and *melodus*. Aberrant members are *pecuarius*, *thoracicus* and *tricollaris*.

These species are characterized by a rather well developed head and breast pattern. The African *pecuarius* and *thoracicus* have the head markings as in *hiaticula*, but a pectoral band is present only in *thoracicus*. The most aberrant member of the ringed plovers is *tricollaris* which has two breast bands but a grey throat and a somewhat different head pattern.

Charadrius pecuarius of Africa is very similar to the larger *sanctaehelenae* of St. Helena. The major differences between the two forms are the larger size and the lack of the tan color on the breast in *sanctaehelenae*. These two forms are similar in all other respects and there is no reason to consider them as distinct species. Thus it is proposed that they be regarded as conspecific as they generally were before Peters gave *sanctaehelenae* specific rank in his "Check-list."

The Madagascan *thoracicus* is also very close to *pecuarius* and may represent an earlier invasion of Madagascar by a pre-*pecuarius* stock. Later *pecuarius* invaded Madagascar for the second time so that today the two species are sympatric. The interesting fact is that *thoracicus* has a breast band which is a "primitive" trait in this genus; its loss in *pecuarius* represents a more advanced condition. If Africa is the original home of the species, then this is a case of a peripheral population of a species retaining a primitive characteristic. There is, however, an equally good alternative hypothesis, namely that Madagascar is the ancestral home of the species which invaded Africa and gave rise to *pecuarius* which in turn reinvaded Madagascar. If this were true, it would be the "central" population that retained the primitive character.

The ringed plovers *hiaticula* and *semipalmatus* are considered conspecific for the purposes of this paper. A fuller discussion of the status of these forms will be presented in a separate paper. To this complex belongs *placidus* which is perhaps best regarded for the present as a distinct species, but belonging to the same superspecies as *hiaticula.*

Group B. The sand plovers embrace the species *alexandrinus*, *peronii*, *venustus*, *collaris*, *bicinctus* and *falklandicus*. The sand plovers have in general a lighter colored back than that of the ringed plovers and commonly have rufous on the crown or breast. Considering *hiaticula* as our reference species, *alexandrinus* can be derived from it by a regression of the breast bands and a change from a dark to a light-brown back. *Charadrius alexandrinus*, in turn, became a world-wide species and seemed to have given rise to *peronii* in the East Indies, *venustus* in Africa and *collaris* in South America. These species are so similar to *alexandrinus* that were it not for the fact that each one is sympatric with some race of *alexandrinus*, they would be considered conspecific with it. The relationships between *alexandrinus*, *falklandicus* (including *alticola*) and *bicinctus* are more complex and will have to be discussed with some detail.

Charadrius falklandicus is found from the southern tip of South America north through Patagonia to northern Argentina. The closely related *alticola* ranges in the high Andes from northern Argentina to Peru. There is no overlap in the ranges of these two forms as given in the latest catalogues (Steullet and Deautier, 1939, pp. 565-566, 567; Hellmayr and Conover, 1948, pp. 61-64). They are very similar in size and plumage except that there are two very heavy breast bands in *falklandicus* as compared to the very faint ones of *alticola*, and that *falklandicus* loses its reddish crown and head and breast pattern in the winter while the winter plumage of *alticola* is similar to its breeding plumage. These differences are slight compared to the overall similarities between the two birds and as there is no overlap in their ranges, there is no reason why they should not be placed in the same species. Mr. William Partridge of Buenos Aires tells me the distribution pattern of *falklandicus* and *alticola* (that is, ranging from the lowlands of Patagonia north into the Andes as far as Peru) is a common pattern of many Patagonian birds.

The mountain *alticola* is similar to *collaris* which is found in the lowlands of South America and north to Mexico. Except for a difference in size (*alticola* is larger), and the presence of a single heavy breast band in *collaris*, the two species are similar. It is possible that *alticola* is a highland representative of *collaris* that gave rise to *falklandicus*, but this is highly unlikely.

The closest relative of the subspecies *falklandicus* is *bicinctus* of New Zealand. They are almost identical except for the color of the lower breast band which is red in *bicinctus* and black in *falklandicus*. The color of the breast bands varies greatly in this group of *Charadrius* so that the contrast of a black versus a reddish band is not a very important difference. Both species lose the breast bands and head markings in the fall molt. In order to express their great similarity and as they have with little doubt descended from the same common ancestor, *falklandicus* and *bicinctus* will be considered as members of the same superspecies. The problem of dispersal over the water gap between South America and New Zealand will be discussed later.

Charadrius bicinctus has probably evolved from an *alexandrinus*-like form as shown by its similarity to that species in plumage color and pattern and by the fact that it has recently been reported to have hybridized with the Australian subspecies *alexandrinus ruficapillus*. A full discussion of the hybrid and its history can be found in Oliver (1955, p. 263). The following account has been abstracted from his discussion. Firstly, it must be mentioned that *bicinctus* breeds only in New Zealand and that part of the population migrates to Australia each winter. This could be interpreted as an indication that *bicinctus* invaded New Zealand from Australia. The migration of several European birds now breeding in Greenland and Baffinland offers some support for this interpretation, but there is no basis for accepting it as a general hypothesis. One year at the beginning of the breeding season, a female *alexandrinus* was seen with a male *bicinctus* in New Zealand. It was assumed that it had flown to New Zealand with a returning flock of *bicinctus*. The female *alexandrinus* paired with the *bicinctus* male and nested. Both birds were seen incubating. After the first set of eggs was washed away by a flood, a second set of two eggs was laid which were later collected. One egg was infertile, the other contained a dead, partly developed embryo. Three years later another pair of female *alexandrinus* and male *bicinctus* was seen in the same area. It was implied that the female was the same one that had nested there three years before. Two chicks were raised, one of which was collected when it was a year old, and described. All facts indicate a close relationship between the two species which while they are able to interbreed, are distant enough so that the hybrids are not very viable.

It is possible that *C. alexandrinus ruficapillus* has given rise to *bicinctus* which in turn reached South America and gave rise to *falklandicus* and hence to *alticola*. On the other hand, *bicinctus* and *falklandicus* may have nothing to do with each other and the similarity between them may be due to convergence. This is entirely possible, but as they are the only species of sand plovers with two heavy breast bands, and unless a similar selection force is shown to exist to explain this convergence, it is far more likely that the two species are related. Considering all of the facts, I would prefer to read the series as *alexandrinus ruficapillus* — *bicinctus* — *falklandicus* — *alticola*, and regard the resemblance between *alticola* and *collaris* as the result of parallelism.

Peters combined the formerly accepted species *alexandrinus*, *ruficapillus*, *marginatus* and *nivosus* into a single species, an arrangement that has been generally accepted. However, there has been some doubt as to whether or not the ranges of *alexandrinus* and *marginatus* overlap. Mackworth-Praed and Grant (1952, pp. 340-342) claim that the two forms are distinct species on the grounds that their ranges overlap in the region of British Somaliland. Meinertzhagen (1954, pp. 478-479) and Chapin (1939, p. 67) agree with Peters and state that there is no overlap between *alexandrinus* and *marginatus* in either East or West Africa. Further study of the distribution of these forms is needed before we can be sure of their status, but for the present the best evidence is that there is no overlap in range and therefore Peters' classification will be followed.

Group C. The mountain or plains plovers, composed of *mongolus, leschenaultii, asiaticus, modestus* and *montanus,* have probably evolved from an *alexandrinus*-like ancestor. The rufous crown and head markings of *mongolus* are similar to those seen in some of the Far Eastern races of *alexandrinus.* The rufous breast of *mongolus* is foreshadowed in *peronii. Charadrius leschenaultii* is almost identical to *mongolus* and would be regarded as conspecific with that form if they were not sympatric. However, as their ranges are almost allopatric (Dementiev and Gladkov, 1951, pp. 81, 85), they are placed in the same superspecies to express their close relationship. Closely allied to this superspecies is *asiaticus* which differs from *mongolus* in its sharp white superciliary line, the black border to the posterior edge of the reddish breast and the faintness of the black line between the bill and the eye, all of which are modifications of the *mongolus* pattern. I have followed Hartert (1912-1921) and Dementiev and Gladkov (1951, p. 88) in placing *asiaticus* and *veredus* in the same species. They are extremely similar to one another in size and plumage color and as their ranges do not overlap at all, there is no basis for maintaining them as distinct species. The South American *modestus* resembles *asiaticus* except that its throat is grey, not white, and the markings on the head and breast are sharper. I have placed it in the same superspecies as *asiaticus*, in spite of the great gap between the ranges of these species, to show their relationship. The mountain plover, *montanus*, although it is a plain colored bird, shows its affinities to *asiaticus* by its white superciliary line, white forehead, and faint black line between its bill and eye. The anterior part of the crown is black as in many of its congeners.

The plains plovers are the largest and chunkiest species of *Charadrius* as well as being the species in which the head and breast pattern is developed the least. In these respects they are similar to *Pluvialis* and may be the species "connecting" the two genera.

Group D. The Australian *melanops* appears to be an aberrant offshoot of the ringed plover group for it has a black pectoral band and head markings similar to those of *hiaticula*. Its mottled back and wings are unusual for this genus and set it apart from the other species.

Group E. Charadrius cinctus seems to be another aberrant derivation of the ringed plovers. It has a broad black breast band that extends down the flanks to end in a series of red markings on the thighs. The solid brown of the head is continuous with the brown of the back which is very unlike the *hiaticula* pattern of a white collar separating the brown color of the head from that of the back.

Groups F and G. The two black-headed species, *rubricollis* and *novaeseelandiae*, are similar in some respects, but probably are not very closely allied. The head and foreneck of *rubricollis* are black and contrast with the white hindneck. A black band on the upper back delimits the posterior border of the hindneck. There is no breast band. Instead, a short ventral bar is present on each side of the breast. The black on the head and back is lost in the winter plumage which makes the bird look very much like a nondescript ringed plover. The forehead, sides of the face and foreneck of *novaeseelandiae* are black and separated from the brown crown by a narrow white line. There is no breast band; however, there is a thin black band about the upper back. The bill is slender and is the chief feature separating *novaeseelandiae* from the other species of *Charadrius*. Yet the difference between the bill of *novaeseelandiae* and *hiaticula* is largely bridged by some species as *melanops*, *tricollaris* and *thoracicus*.

Anarhynchus Quoy and Gaimard (frontalis) 1830

Included species: frontalis.

Diagnosis: The outstanding feature of this monotypic genus is its unusual bill which bends sharply to the right at its midpoint. The angle of the bend is about 20 degrees and is already present in the chick. The dorsal surface is grey; underparts are white with a black breast band of even width throughout. For a time it was believed that the band was wider on the left side; however, this is not so. The tail is grey, sometimes with lighter edges. The flight feathers are dark grey with a faint wing bar;

the rest of the wing is lighter grey similar to the back. In the fall molt the black breast band and head marks are lost. The immature bird is similar to the adult winter plumage. The wrybill breeds inland in the shingly (rocky) river beds; the nest is placed among the rocks (Oliver, 1955, p. 269). During the rest of the year it is found on mud and sand flats along the coast. Habits and behavior are in all respects like those of *Charadrius* (Stead, 1932).

Range. Resident in New Zealand; breeds on South Island and winters along the coast of North Island.

Remarks: In spite of its remarkable bill, *Anarhynchus* is a poorly marked genus. In fact, save for structure of the bill which is unique among birds, there would be no basis for separating *Anarhynchus* from *Charadrius.* Because of the importance of the bill in the differentiation of *Anarhynchus*, an inquiry into the feeding habits of the wrybill and the functional significance of the bend in the bill would be most desirable.

The habits of the wrybill have been discussed in a number of papers (Potts, 1871, pp. 93-97; Hutton and Drummond, 1923, pp. 216-218; Smith, 1926, p. 41; Stead, 1932; Oliver, 1937; and summarized in Oliver, 1955, p. 269). The habitat and distribution of the wrybill which are vital to the problem of the function of its bill are described in the above papers, especially by Stead, and also by Sibson (1943), and Urquhart and Sibson (1952). Yet the feeding habits have never been adequately described. According to Potts (p. 96) the bend in the bill would aid the bird in capturing insects that are found abundantly under the water-worn rocks of the river beds of its breeding grounds. Stead's conclusions (pp. 91-92) are somewhat colored by his beliefs, so that, although his evidence supports Pott's earlier statement, he does not believe that the wrybill gains any advantage from its deflected bill. Smith (p. 41) says: "in North Island, where the bird migrates in the winter he had observed it sweeping the wet sands with a remarkable scythe-like action of its bill for some minute food supply." Despite the fact that the wrybill is a common and easily observed bird, this constitutes our entire knowledge of its feeding habits. A complete description of its feeding habits on both the breeding and wintering grounds is sorely needed. The use of motion pictures and a statistical approach to the problem would be desirable.

Even though the evidence is poor, there is enough to indicate that *Anarhynchus* utilizes the bend in the bill in two ways. When it is on its rocky breeding grounds, the bend is advantageous in obtaining insects found under the rocks. On the mud flats of its wintering grounds, it may make use of the crook in the sweeping motions described by Smith. Until we have careful observations, these suggestion are the best that can be offered. However, it is certain that the bill is used in some special way(s); there had to be some selection force(s) responsible for the evolution of this peculiar bill.

The second aspect concerns the anatomical features of the skull and how they became modified with the change in the shape of the bill and feeding habits. It would be most interesting to see if the asymmetry of the anterior part of the bill is reflected in the hind part of the skull. A thorough study of the functional anatomy and evolution of the deflection in the bill of *Anarhynchus* should provide a most fascinating study of adaptation in the bill of birds.

Related to the structure of the bill is the problem of whether this species should be given generic rank. Aside from its bill, the wrybill agrees with *Charadrius* in all respects. It has with little doubt evolved from some member of *Charadrius*, and except for the shape of its bill, would be placed in that genus without hesitation. The handling of cases in which a species differs from its nearest relatives in a single character, no matter how remarkable, was discussed in connection with *Cochlearius* in my revision of the herons (Bock, 1956, pp. 31-35). *Anarhynchus* has not yet given rise to any new radiation of forms and may well represent an evolutionary dead-end. I do not consider *frontalis* markedly different from *Charadrius* and it is with much hesitation and reluctance that it is kept in a separate genus, but done only to point out the truly unique structure of its bill. However if the generic limits in the plovers are further broadened, this genus will almost automatically have to be merged with *Charadrius*.

EUDROMIAS C. L. Brehm (MORINELLUS) 1830

Synonymy: Oreopholus Jardine and Selby, 1835 (*ruficollis*); *Morinellus*

Bonaparte, 1856 (*morinellus*).

Included species: morinellus and *ruficollis.*

Diagnosis: Medium sized plovers with medium to long bills. The back is mottled, but unlike that of *Pluvialis.* The crown of the adult is solid brownish and bordered by a white superciliary line. The breast is uniformally colored, reddish or tan. The wing is similar to the back in color and pattern and without a wing stripe. Winter plumage (*morinellus* only ?) lacks the color of the underparts of the breeding plumage. The immature is similar to the winter plumage of the adult.

Range: E. morinellus breeds in the tundra and mountains of northern Eurasia and winters in the Mediterranean region and southern Asia. *E. ruficollis* is a permanent resident in the mountains and plains of southern South America.

Remarks: The grouping of these species into one genus may well be artificial. However the two species agree in many points of color pattern that are not seen in any other plover. The large gap between the ranges of the two species is a problem, but not an insurmountable one when compared to the many disjunct ranges in other genera. The number of similarities that exist in these two species makes it reasonable to regard them as congeneric unless additional evidence should prove otherwise.

PLUVIANELLUS G. R. Gray (SOCIALIS) 1846

Included species: socialis.

Diagnosis: This medium-sized plover has a solid grey back and white underparts with a broad grey breast band in the female while the breast of the male is mottled grey. The wings are dark grey with a broad white wing stripe much like the wing stripe of *Vanellus.* The central tail feathers are dark grey; the lateral ones are dirty white. The bill is rather flattened laterally for a plover and is sharply pointed. In some ways the bill resembles that of the turnstones. The habits of this species are given in Goodall *et al.* (1951, pp. 216-217) and seem to be like those of the rest of the charadriine plovers.

Range: Found only in Tierra del Fuego.

Remarks: Pluvianellus is a nondescript and rather strange plover. Nothing that can be seen in a museum skin gives any clue to its relationships. I have not seen any anatomical material of this species, nor has its anatomy ever been described. Most of its features, except for the broad wing stripe, are more charadriine-like than vanelline-like, but are still not very convincing. I have considered it as allied to the *Charadrius* group on the basis of past usage rather than on any strong evidence, and should like to emphasize that much more must be known about the anatomy and behavior of this plover before we can be reasonably sure of its position.

Genera Incertae Sedis

PHEGORNIS G. R. Gray (MITCHELLII) 1846

Included species: mitchellii.

Diagnosis: A small bird, about the size of *C. hiaticula.* The head is dark brown with a narrow white band across the forehead, continuing around the sides as a superciliary line and completing the circuit about the rear of the head. The back of the neck is reddish-brown while the back is dark brown. Chin and throat are black, the rest of the underparts are barred with black and white transverse strips. The tail is dark brown except for the lateral feathers which are white with dark bars as seen in the tail of many sandpipers (*e.g. Tringa solitaria*). Wings are dark brown with the secondaries tipped with white. The bill is quite long and thin compared to that of the plovers.

Range: High Andes from Peru south to central or southern Chile.

Remarks: The relationships of this genus are still obscure and there are good reasons to doubt that it is even a plover. Seebohm placed it with the sandpipers (Scolopacinae) and included *cancellatus* (=*Aechmorhynchus cancellatus* and *A. parvirostris* of Peters) and *leucopterus* (=*Prosobonia leucoptera* of Peters) in the same genus. Sharpe kept the three species in the Scolopacidae *sensu stricto*, but separated them into three genera. In his first paper on plovers, Lowe (1922, p. 491) stated that he did not have anatomical material of *mitchellii* and hence did not commit himself as to its systematic position.. However in his major work (1931b, p. 743) he placed *Phegornis* in the Charadriidae *sensu stricto* on the basis of its color pattern (no elaboration given) and the nature of its maxillo-palatine strut which is illustrated on page 769 (see Figure 6). The difference between the plovers and the sandpipers in this structure, according to Lowe, is that in the plovers the maxillo-palatine strut meets the jugal bar at right angles, while in the sandpipers the strut runs forward from the maxillo-palatines to meet the jugal bar at a rather sharp angle. In addition to the differences given by Lowe, the maxillo-palatine strut of the plovers fuses to the jugal bar

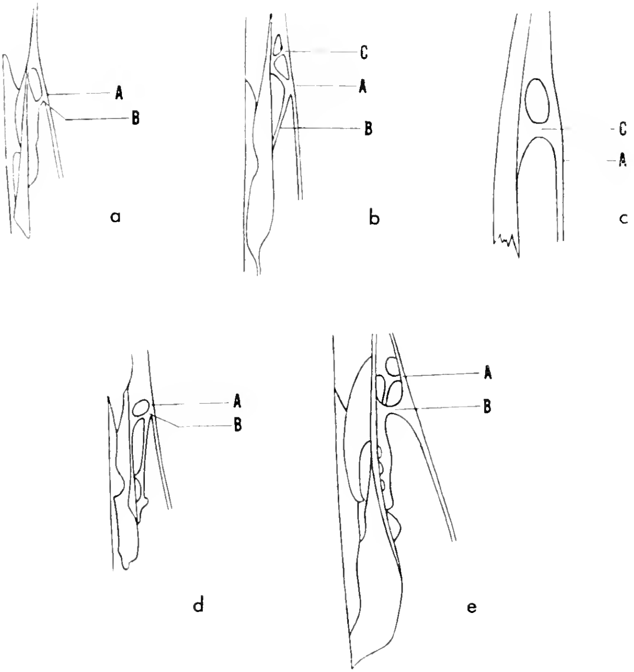

Figure 6. Ventral view of the left side of the palate of a) *Erolia*, b) *Tringa*, c) *Phegornis* (after Lowe, 1931b, p. 769), d) *Arenaria*, and e) *Pluvialis* to show the nature of the maxillo-palatine strut. The anterior end of the palate is at the top, midline is to the left. The labeled structures are: A) the point of junction between the jugal bar and the lateral ramus of the nasal bone (not shown in the drawing), B) the maxillo-palatine strut, and C) an unnamed strut anterior to the maxillo-palatine strut. Figures are twice life size.

at a point posterior to the junction of the jugal bar and the lateral ramus of the nasal. In the sandpipers, on the other hand, the junction of the strut is at a point where the lateral ramus of the nasal fuses to the jugal bar. This is quite evident in Lowe's drawings but is not mentioned by him in the text. In the plovers, the maxillo-palatine strut is always as described by Lowe. The sandpipers, however, exhibit a considerable amount of variation which was appreciated and described by Lowe. Usually the strut is as described above or a minor variation of it. But in some genera, notably *Tringa* and its allies, the strut meets the jugal bar almost at a right angle at a point slightly posterior to the junction of the lateral process of the nasal bone and the jugal bar. In spite of its variation in the sandpipers, the nature of the maxillo-palatine strut seems to be a good means of separating the plovers from the sandpipers. In Lowe's drawing of *Phegornis* on page 769, the process labeled as the maxillo-palatine strut, while it does meet the jugal bar at right angles, is anterior to the junction of the jugal bar and the lateral ramus of the nasal, not posterior as in all other plovers. Also the more dorsal parts of the palate included in the drawings on pages 735 and 736 illustrating the strut in other plovers and sandpipers seem to be omitted in this plate. If the drawing of *Phegornis* is compared to the one showing the palate of *Tringa* (Figure 6. and see also Lowe, 1931b, p. 375, fig. b), the bone marked as the maxillo-palatine strut in *Phegornis* seems to correspond to an unnamed process in *Tringa* which is anterior to the maxillo-palatine strut and which meets the jugal bar at right angles, but which is just anterior to the junction of the jugal bar and the lateral bar of the nasal bone. Because of these differences, I would hesitate to definitely label the strut shown by Lowe in his drawing of *Phegornis* as the maxillo-palatine strut seen in other species of plovers and sandpipers, but instead suggest that it corresponds to the above mentioned, but unnamed strut in *Tringa*. I have not seen any anatomical material of this species and until I do, I cannot make a more definite statement about the condition of the maxillo-palatine strut in *Phegornis*.

Lowe (1927; 1931 a, b) studied the anatomy of *Aechmorhynchus cancellatus*, one of the species considered closest to *Phegornis* by Seebohm. He concluded that *Aechmorhynchus* was a sandpiper and most closely related to the group that he called the Limosinae (*Bartramia*, *Numenius*, *Limosa*, etc.). In regard to the maxillo-palatine strut in this species, Lowe said only that: "the maxillo-palatine region seems to conform to the arrangement seen in the curlews" (1927, p. 129), but further on he says that this region was badly decalcified, thus making the determination of the morphological features very difficult.

According to Lowe, the color of *Phegornis* agrees with that of the plovers, but did not cite any definite points of resemblances. The barred underparts and tail (underside and edges) of *Phegornis* match the plumage of some sandpipers and are quite unlike any plover. The pattern of the head is, however, similar to that found in many charadriine plovers. It should be stressed that as a general rule, it is unsafe to determine the family status of a bird on the basis of its color pattern. In *Phegornis* the taxonomic implications of the plumage color and pattern are certainly unclear.

Phegornis is found along mountain streams in pairs or singly where it walks on the rocks looking for aquatic animals under the algae that cover the rocks. It is protectively colored, silent and tame so that it is difficult to see until it flushes at the last possible moment and flies off with strong wing beats. The nest is a depression in the grass, not far from water. This account taken from Goodall *et al.* (1951, p. 218) is the extent of our knowledge of this species and is of no help in discovering its true position.

Peters and other recent workers follow Lowe and assign *Phegornis* to the Charadriinae *sensu stricto*. No one has studied the anatomy of this species since Lowe and indeed we are still completely ignorant of its morphology. While I believe that future work will prove that *Phegornis* belongs to the Scolopacinae, perhaps allied to *Aechmorhynchus* and *Prosobonia*, there is no evidence at present to support this belief. I must also emphasize that there is at present no reason other than past usage to retain *Phegornis* in the plovers. However, the most practical solution is to keep *Phegornis* in the Charadriinae until evidence proves otherwise, but to remember that its true affinities are still unknown.

PELTOHYAS Sharpe (AUSTRALIS) 1896

Included species: australis.

Diagnosis: The upper parts of this medium-sized bird are mottled brown, much like those of *Eudromias.* The throat, breast and belly are tannish, the lower breast is reddish brown, and the under tail coverts whitish. The white forehead is bordered behind by a black bar extending between the eyes and continued below the eye as a short vertical bar. There is a black breast band that is continuous about the back. The breast band extends down the mid-ventral line as a narrow streak as far as the lower breast. The wings are similar to the pattern of the back with no wing bar. The tail is brownish with lighter outer tail feathers. The immature is like the adult, but lacks the black markings on the head and breast. The hind toe is lacking. The bill has an expanded distal portion, and while it is slightly pointed, it is no more so than the bill of *Pluvianellus.*

Range: Australia.

Remarks: This puzzling genus was originally described as a species of *Eudromias* by Gould and placed in that genus or *Charadrius* until Sharpe placed it in a separate genus and subfamily of the Charadriidae *sensu stricto.* Seebohm included *australis* in *Charadrius* near *C.* (=*Eudromias*) *morinellus,* but was not sure of its proper position as indicated by his remark (1888, p. 110): "It is difficult to say which it most resembles, *Charadrius hiaticula, Charadrius morinellus* or *Cursorius bicinctus,* but its resemblance to the latter is probably an example of analogy rather than affinity."

Mathews (1913-1914, pp. 335-336) placed *Peltohyas* in the Glareolidae on the basis of the shape of the bill, the scutellation of the tarsus, and the flattened nature of the claws. Lowe (1931b, p. 771) listed several anatomical characters such as the thigh muscle formula, the patagial wing muscles, the feather tracts of the neck, and some aspects of the skull and vertebral morphology in which *Peltohyas* agrees with the glareolids and not with the charadriids. A number of these characters are those given by Gadow (1893, pp. 195-203) and Beddard (1898, pp. 336-350) to separate the two groups and thus may be of considerable taxonomic importance.

Externally, *Peltohyas* in all respects resembles the plovers. In plumage it is closest to *Charadrius* which it resembles in the head markings, breast band and tail pattern, and does not match in any way the plumage of any species of the Glareolidae. The bill is that of a plover and is completely unlike the arched, pointed bill of the glareolids. While the scutes of both the anterior and posterior surfaces of the tarsus are rectangular, they are not like those of the glareolids, especially the scutes of the plantar surface, but rather more like those of some species of *Vanellus* or *Eudromias ruficollis*. A number of species of plovers have rectangular scutes on the front surface of the tarsus, but at best the scutes of the plantar surface are hexagonal. The middle claw of most genera of the Glareolidae is pectinate (lacking in *Stiltia* and rudimentary in *Rhinoptilus*), but while the claws of *Peltohyas* are flattened, the middle claw is not pectinate.

In view of the strongly conflicting evidence — the external features being charadriine-like while some of the features of the internal anatomy (as reported by Lowe) agree very closely with the Glareolidae — *Peltohyas* must be placed with the other genera of uncertain position. A careful comparative anatomical study of *Peltohyas* and the Charadriinae and the Glareolidae is needed before it can be assigned to the proper family.

The Turnstones ("Arenariini")

The genera *Arenaria* and *Aphriza* may be thought of as a tribe of shorebirds of uncertain affinities, "Arenariini." They have been placed either in the Charadriinae *sensu lato* or in the Scolopacinae *sensu lato*, but a convincing argument for either proposal has never been given. Most authors include the turnstones in the plovers, basing their action on such external features as the shape of the bill and the plumage pattern. At present, this is the most widespread opinion. Lowe, on the other hand, cites several features of the skull in which the turnstones agree with the Scolopacinae *sensu lato* and not with the Charadriinae (see Lowe, 1931b, p. 747). These characters are: the type of maxillo-palatine strut (see Figure 6, and for a discussion of this structure, see above, p. 81), the nature of the articulation of the quadrate with the skull, and lastly the shape of the mandibular articular surfaces of the quadrate. I have compared skulls of

Arenaria and *Aphriza* with skulls of a number of genera of plovers and sandpipers and thus far have confirmed Lowe's earlier findings and conclusions. The condition of the supraorbital rims in *Arenaria* is illustrated in Figure 1e. The rims do not resemble those of any of the plovers and are similar to those of sandpipers in the narrow shelves of bone. Within the sandpipers, Lowe places the turnstones closest to the eroliine group and proposes the following "evolutionary sequence": *Erolia* (perhaps more definitely *E. maritima* or *E. ptilocnemis*) — *Aphriza* — *Arenaria,* a reasonable hypothesis that deserves serious attention. However, Lowe's works need to be checked before they can be accepted and until the anatomy of the turnstones is further studied and compared with that of the plovers and the sandpipers, they must be regarded as a group of doubtful affinities. Yet for the present there is better evidence for placing the turnstones in the Scolopacinae *sensu lato* and they will be considered as members of this group for the purposes of this paper. If future work shows that the turnstones are in reality related to the plovers rather than to the sandpipers, the present evidence indicates that they probably would have to be considered as a group distinct from the species studied in this paper; perhaps the two groups would be best regarded as separate tribes.

Zoogeographic Considerations

A careful examination of the ranges of closely related species of plovers reveals a number of interesting zoogeographic problems. For example, some members of the same species or superspecies are separated by ocean gaps of 1000 to 5000 miles. Equally interesting are the species that are confined to a small area somewhere in the southern tips of the southern land masses. There are enough problems of general zoogeographic interest to warrant a full discussion of some aspects of the distribution and dispersal of the plovers. In a recent paper, Larson (1957) discusses the past and present distribution of the North Temperate and Arctic shorebirds, including the plovers, to which the interested reader is referred.

The present day center of distribution for the lapwings is Africa and for the charadriine plovers, the Holarctic region. All Arctic species migrate south in the winter often as far as the southern tips of South America, Africa and Australia. Many of these species make extremely long flights (1000 miles or more) over the ocean; an excellent example is the flight of the golden plover (*Pluvialis dominica*) from Nova Scotia to South America or from Alaska to Hawaii. They may rest on long flights by settling on driftwood (Nicholson, 1928, pp. 126-127), or by swimming if they are forced to (Cottam, 1928, and numerous other reports). Except for *Phegornis*, which may not even be a plover, most species are highly gregarious or at least occur in small flocks. Lastly, there are a few records of northern species breeding in their winter range: *P. dominica* in New Zealand (Robson, 1884), which apparently bred in its winter plumage, nest found on January 9, 1883, eggs hatched two days later; and the chick of *C. leschenaultii* has been found in the region of the Red Sea (Archer and Godman, 1937, pp. 384-385, and Meinertzhagen, 1954, pp. 482-483). It should be pointed out that some species of plovers are wintering in the temperate areas of the Southern Hemisphere at a time when the day length is increasing and reaching a maximum in these regions. Nothing is known of the annual cycle of these species and its correlation to day length, and especially the possible effects of wintering in the south temperate zone.

Apparently for plovers, ocean gaps are not important barriers to successful colonization of new areas. Two examples of recent invasions may be cited. In 1927, during the winter, large flocks of the European lapwing, *V. vanellus*, flew from England to Newfoundland and Labrador when they missed their course in a storm (Spencer, 1953, p. 88). *Vanellus miles novaehollandiae* has recently successfully invaded New Zealand from Australia (Oliver, 1955, p. 270).

Thus the three species of lapwings found in South America had with little doubt come from the west coast of Africa. The two species *chilensis* and *resplendens* represent one invasion, and the third species, *cayanus*, represents a separate invasion. *Charadrius alexandrinus* has probably also travelled over this route.

The close relationship between *Pluvialis obscura* of New Zealand and the Arctic *apricaria-dominica* and *squatarola* can best be explained by regarding *obscura* as descended from a group of individuals of some species of *Pluvialis* that remained in New Zealand to breed. The old nesting record of *dominica* in New Zealand offers some support for this hypothesis.

Charadrius bicinctus (New Zealand) and *falklandicus* (South America) belong to the same superspecies, but their ranges are separated by many thousands of miles of open ocean. It is possible that the invasion was direct from New Zealand to South America. There is, however, another possibility that may be more likely. It is well known that at times in the past, Antarctica was not always covered with ice (Axelrod, 1952 a, b). If the ice at the edges of the Antarctic Continent melted and a tundra-like vegetation developed, there is no reason why plovers should not have bred there and migrated north in the fall. If this is true, then *bicinctus* could have reached South America by way of Antarctica. More likely *falklandicus* and *bicinctus* differentiated from each other in Antarctica, one migrating north to South America and the other to New Zealand and Australia. This may well be the explanation of the relict nature of the species (ten in number) of Southern Hemisphere plovers that are found today breeding in a small area in the very southernmost tips of the southern land masses. It is of interest that the relict plovers are all related to the present-day Arctic species and that there are no plovers confined to the Cape of Good Hope region of Africa.

The gaps between the ranges of *Charadrius asiaticus* and *modestus* or between *Eudromias morinellus* and *ruficollis* are the largest of any that exist in the plovers. In both cases it is a gap between northern Asia and the southern Andes. But even here, it could be explained by invasion and perhaps a partly relict nature of the southern species.

It is hoped that these considerations of the migration and dispersal habits of the plovers have shown that there is nothing in the proposed classification of the Charadriinae that is in conflict with currently accepted principles of zoogeography.

History and Future Studies

The shorebirds, including the plovers, being conspicuous birds became well known early in the history of ornithology. A brief survey of the dates of the original descriptions shows that less than half a dozen species were discovered in the past century and all were known before the turn of the century. It is quite safe to say that no species of plovers remains to be discovered, but much must still be done before we understand the geographic variation and status of many species (*e.g. Charadrius hiaticula*).

Much has been published on the generic and suprageneric relationships of the Charadriinae; however, few of the conclusions have stood the test of time. The same is true of the past anatomical work. While it is hoped that the delimitation of genera proposed in the present study is reasonable, little can be said of their relationships and evolution. We cannot even set limits to the Charadriinae or determine whether several genera such as *Phegornis, Peltohyas, Aphriza* and *Arenaria* belong to this subfamily or to some other group. Our knowledge of the anatomy of these groups is almost nonexistant so that a good comparative study of the anatomy of the entire shorebird group is sorely needed. Perhaps after this is done, we may gain some understanding of the evolution of the Charadriinae and their position in the Charadriidae.

Behavior was briefly mentioned several times in the discussions, but never gone into fully. Despite the fine work that has been done on the behavior of several species (Rinkel, 1940; Laven, 1940; Laven, 1941; Deane, 1944; Williamson, 1948; Simmons, 1952, 1953, 1955; and Smith and Hosking, 1955), the comparative ethology of the plovers is still in its beginnings and of no help to our understanding of the specific relationships of the plovers at this time. Yet all indications point to the fact that the relationships within the large genera, *Charadrius* and *Vanellus*, and perhaps even between the genera will be understood only after their behavior is well known, so that the need and desirability of behavioral studies comparable to those done on the ducks, gulls and terns cannot be urged too strongly.

A knowledge of the ecology, even a rough indication of their habitat, is necessary for a proper understanding of several features of the anatomy and plumage and here again careful studies are not available and are much needed.

It can be seen that while much work has already been done, our knowledge of the biology of the plovers must be greatly increased if we hope to understand the relationships and evolution of this group. This review must then be thought of, not as a definitive study, but rather as a preliminary work with the hope of clearing the path for future studies.

Summary

The structure and variation of the skull of the plovers were studied. It was shown that the degree of ossification of the supraorbital rims is strongly correlated with the size of the nasal glands and hence with the salinity of the water, and is of no taxonomic value. Some other features of the skull were also studied.

The important earlier works on the classification and anatomy of the Charadriinae were discussed, especially those of Lowe upon which much of the current accepted classification is based. It is shown that Lowe's interpretations of the morphology of the skull, color and color pattern are at variance with many of the observed facts and with many of the ideas and principles of evolution and classification. Any classification of the plovers resulting from these interpretations would, therefore, be highly artificial.

In addition to the skull, the major characters studied were the hind toe, the wattles, the wing spur, the color and color pattern of the plumage, and the osteology. Each character is described and its variation and possible evolution within the subfamily, and its value in the proposed classification is discussed. The importance of the habitat is mentioned.

A new classification of the plovers, based on a comparative study of the above mentioned characters, is presented. The plovers, following Mayr and Amadon, are considered as a subfamily Charadriinae of the Charadriidae. The subfamilies Charadriinae and Vanellinae of Peters are dropped and the 56 recognized species are placed in 6 genera as compared to the 61 species and 32 genera of Peters. No new species or genera are proposed. A diagnostic description is given for each group within the Charadriinae, but not for the subfamily as a whole. The status of several genera remains uncertain. *Phegornis* is retained in the plovers only on the basis of past usage, but it is believed that more study will prove it to be a member of the Scolopacinae. *Peltohyas* may belong either to the Charadriinae or to the Glareolidae; at present its status is very uncertain. The turnstones and surf-birds, *Arenaria* and *Aphriza*, are for the purposes of this

paper considered as sandpipers, but their position is still doubtful. A discussion of subspecies lies outside the scope of this review.

A brief mention of the zoogeographic implications of the proposed classification is given. Lastly, a brief summary of past investigations of the group including an outline of the largest gaps in our knowledge of the biology of the plovers is presented.

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STUDIES ON THE ANT FAUNA OF MELANESIA. I. THE TRIBE LEPTOGENYINI. II. THE TRIBES AMBLYOPONINI AND PLATYTHYREINI

By E. O. Wilson

CAMBRIDGE, MASS., U. S. A.
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BULLETIN (octavo) 1863 — The current volume is Vol. 118.

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JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 35 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 21 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

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No. 3.—*Studies on the Ant Fauna of Melanesia*

I. The Tribe Leptogenyini

II. The Tribes Amblyoponini and Platythyreini

By E. O. Wilson
Biological Laboratories, Harvard University

I. THE TRIBE LEPTOGENYINI

The tribe Leptogenyini, principally composed of the large genus *Leptogenys,* is exceptionally well developed in the Melanesian region and in terms of individual species and colonies must be counted among the dominant ant groups there. During the present revisionary study three zoogeographic divisions have been recognized as feasible at the species or species-group level within Melanesia:

(1) The *Leptogenys* of western and central Melanesia, from New Guinea to the New Hebrides, containing at least six distinct species groups, most of which are precinctive or of recent Indomalayan origin.

(2) The *Leptogenys* of the Fiji Islands, composed of a homogeneous group of six species, apparently all derived from the Papuan-based *L. bituberculata* stem.

(3) The *Leptogenys* and *Prionogenys* of New Caledonia, with four species representing at least three phyletic groups, two of which are apparently of Australian origin and the third with uncertain relationships.

These three faunal divisions have been accorded separate systematic treatment in the present paper. The fauna of the Moluccas has also been reviewed and an account of it included with the first section (western and central Melanesia). There are two reasons for this procedure. First, the Moluccan fauna is closely allied to that of New Guinea, so close in fact as to represent little more than a depauperate extension of it. Second, by taking all of the Moluccan species into account, there is a better chance of obtaining a complete coverage of the New Guinea fauna, since the Moluccas have been more intensively collected, and there are undoubtedly many species and even genera of ants known at present only from the Moluccas that will eventually be found on New Guinea also.[1]

DESCRIPTION OF COLLECTING STATIONS

Most of the material on which this revision is based was collected by the author during field work in Melanesia in 1954-55. In order to document more fully the distributions presented in this and future parts of a proposed review of the Melanesian ant fauna, a gazetteer of collecting stations is given below, including a brief ecological characterization of each locality. The classification of New Guinea forest types follows that of Lane-Poole (in P. W. Richards, *The Tropical Rain Forest,* Cambridge University Press, 1953).

NEW GUINEA

Bandong, upper Bunbok Valley, Northeast New Guinea (1100 meters). May 26, 1955. Disturbed foothills rain forest near the village, which is located approximately 12 kilometers north of Boana.

Bisianumu, near Sogeri, Papua (500 meters). March 15-20, 1954. Field work at Bisianumu was conducted almost entirely in the second-growth foothills rain forest partly surrounding the Government experimental rubber plantation. A few accessions were made in similar forest several kilometers farther inland along the Kokoda Trail.

Boana, Bunbok Valley, Northeast New Guinea (1100 meters). May 25, 1955. Partly disturbed foothills rain forest on the steep western slope of a hill rising just east of the Boana airstrip.

Brown River Road, 1.5 km. south of Karema, Papua. March 8-11, 1955. Most of the collecting at this locality was conducted in undisturbed lowland rain forest. Several accessions were made in an enclave of eucalyptus savanna several kilometers to the south.

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[1] To cite an example, the aberrant formicine genus *Mesoxena* was previously known only from a single specimen of *M. mistura* Fr. Smith from Batjan, collected by Wallace more than a century ago. A second species was recently discovered by the present author at Bisianumu, Papua.

Bubia, 12.5 km. northwest of Lae, Northeast New Guinea. March 26-27, May 18-19, 1955. Lowland rain forest, moderately disturbed.

Upper Bunbok Valley, southern slope of Saruwaged Range. May 27-June 1, 1955. The southern slope of the central portion of the Saruwaged Range was climbed to a point on the crest at approximately 4000 meters. Insect collections were made all along the altitudinal transect, and in all of the major vegetational belts, including mid-mountain forest, mossy forest, high mountain forest ("tree-line" zone), and alpine savanna. Ants diminished rapidly in the mid-mountain forest belt, above 1500 meters, and appeared to be altogether absent above the lowermost levels of the mossy forest, the last colonies being encountered in a clearing at approximately 2500 meters. In this connection it is interesting to note that Dr. J. J. H. Szent-Ivany and a party of native assistants were unable to turn up a single ant during several hours search in mossy forest at 2600 meters on the Asoro-Chimbu Divide, in the Central Highlands (Szent-Ivany, pers. commun.). All present evidence points to the complete absence of a high-alpine ant fauna in New Guinea.

Lower Busu River, near Lae (100-150 meters). March 27, April 28-May 17, 1955. Collecting was conducted principally between the Busu and Bupu Rivers in the area indicated in Figure 1. At the time of my visit this area was covered for the most part by primary lowland rain forest, which was in the process of being high-graded by the South Pacific Lumber Company. Through the courtesy of officials of the Company, I was able to reside for a period of three weeks in a camp on the forest border, and was thus presented with a superb opportunity to collect in the tops of the large trees as they were felled, in forest clearings at various stages of overgrowth, and in and around logs at all stages of decomposition. The ant fauna of the area proved exceptionally rich, and in one section of less than two square kilometers an estimated minimum of 170 species was collected. Several short excursions were also made into the extensive grassland fringing the western banks of the Busu River.

Didiman Creek, Lae, Northeast New Guinea. March 27, 29, May 8, June 3, 1955. Moderately disturbed lowland rain forest adjacent to the Government Botanical Gardens at the head of Didiman Creek. (See Figure 1.)

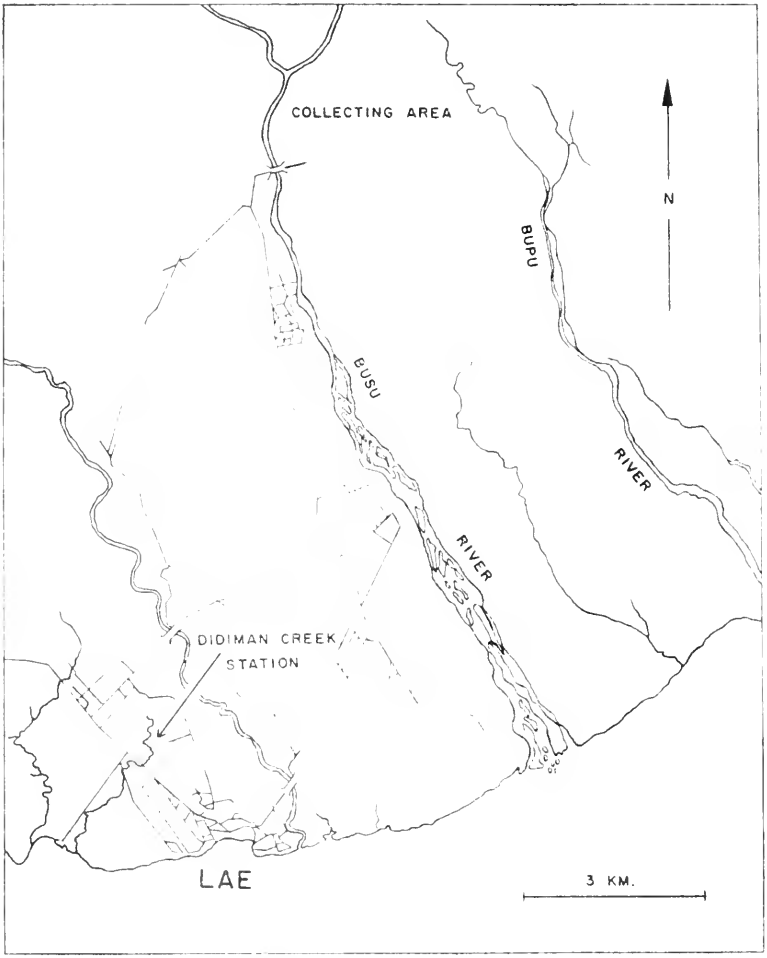

Fig. 1. The Lae area in 1955, showing the Didiman Creek and lower Busu River collecting stations.

Karema. See *Brown River Road.*

Laloki River, 16 km. northeast of Port Moresby, near Little Mt. Lawes, Papua. March 8, 1955. Collecting was limited to the terraced, forested floodplain of the Laloki.

Mongi-Mape Watersheds, eastern Huon Peninsula, Northeast New Guinea. April 2-23, 1955. In the company of Mr. Robert Curtis, of the Territorial Department of Agriculture, Stock, and Fisheries, the author made a three-week collecting trip through the mountainous country of the Dedua and Hube districts, embracing the headwaters of the Mongi and Mape (Go rivers. The route of this trip is shown in Figure 2; the localities indicated are villages, the elevations of which range from sea level to 1800 meters. Collecting was conducted in the forests and clearings along native foot trails.

Nadzab, Markham Valley, Northeast New Guinea. May 20-22, 1955. The collecting station was a plantation managed by Mr. Keith Smith, located at the southwestern corner of the old wartime Nadzab airstrip, 1.5 km. east of the junction of the Markham and Erap rivers. Most accessions were made in dry broadleaf evergreen forest, marked by dense undergrowth, open canopy, and prevalence of palms in all stories. At the time of the author's visit, the area was suffering from a record drought, not having received rain in over two months. On the forest floor leaf litter and mold were thin and dry, while the interiors of the larger rotting logs were generally moist.

Port Moresby, Papua. March 5-7, 1955. Collecting was conducted in open *Eucalyptus* woodland in and around Port Moresby, and in *Eucalyptus* woodland and dense second-growth monsoon forest on the summit of Kini-Kini, a 250-meter-high hill on the southeastern outskirts of the town

Saruwaged Range. See *Bunbok Valley.*

NEW HEBRIDES

Eight kilometers north of Luganville, Espiritu Santo (100-150 meters). January 10, 1955. Second-growth rain forest.

Aubert Ratard Plantation, 8 km. southwest of Luganville. January 7-13, 1955. Collecting was limited to the border and interior of primary lowland rain forest in the western section of the Ratard Plantation.

FIJI ISLANDS

Eight miles west of Korovau, on King's Road, Viti Levu. December 3, 1954. Second-growth rain forest.

Nadala, near Nadarivatu, Viti Levu. December 1-2, 1954. Partly disturbed rain forest on the slope of a steep hill just north of Nadala. The soil was clayey, with numerous fragments of volcanic rock at the surface, and covered by fairly thick leaf litter. The canopy was open, due to native lumbering operations, and the undergrowth was moderately to very dense. Despite the obviously disturbed condition of the forest, the

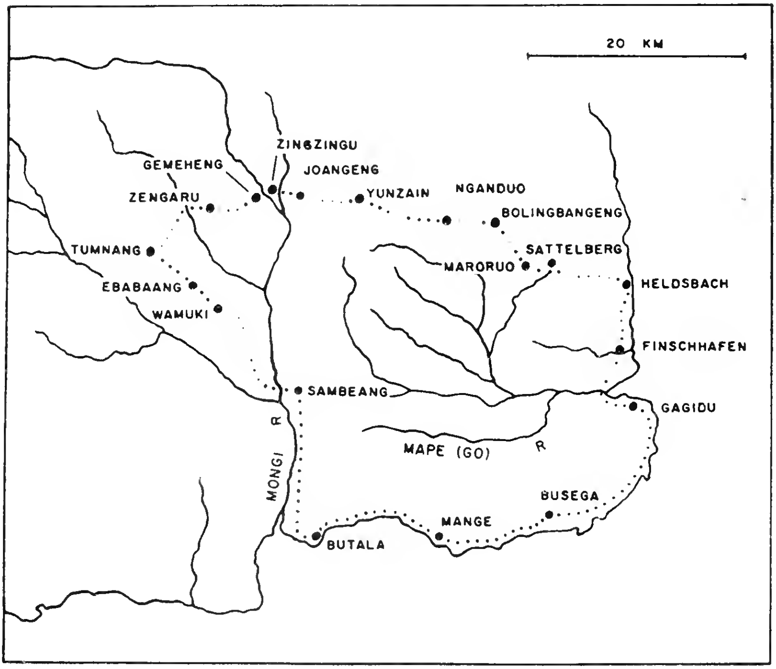

Fig. 2. Southeastern part of the Huon Peninsula, showing the itinerary of a collecting trip in the region of the Mongi-Mape watersheds in April, 1955.

local ant fauna was almost entirely endemic in composition, and a large percentage of the known Viti Levu species was encountered during the course of only two days' work.

NEW CALEDONIA

Anse Vata, Nouméa. December 4, 15, 1954. Most collecting was conducted in open *Melaleuca* and *Santalum* woods within several hundred meters distance of the Anse Vata beach. A few accessions were made in *Ficus* groves on the beach itself.

Le Chapeau Gendarme, near Yahoué. December 5-7, 1954. Most of the hills in the area immediately to the north of Nouméa are covered by open *Melaleuca* woodland, occupied chiefly by introduced ant species, but along the stream running down the southern slope of Chapeau Gendarme there was during the time of the author's visit a section of rich, semi-deciduous angiosperm forest that yielded many of the New Caledonian endemic ants. The forest contained two strata — an upper, discontinuous stratum exceeding twelve meters in height, and a lower, denser stratum of small trees and shrubs ranging mostly three to seven meters in height. Much of the forest floor was covered by bracken, and the leaf litter was generally thin, patchy, and dry. (See Figure 3.)

Ciu, near Mt. Canala. December 21, 1954; December 31, 1954-January 3, 1955. Field work was conducted at three stations in the vicinity of Ciu. (1) On the property of Mr. D. Fèré, on the west bank of the Canala River at 300 meters elevation, collections were made in an isolated section of broadleaf evergreen forest completely surrounded by pastures. The floor of this woodlot had been badly disturbed by cattle, but many of the endemic New Caledonian ant species were found nesting under deep-set rocks and in the occasional stable accumulations of leaf litter. (2) On the east bank of the Canala River, only several hundred meters from the Fèré woodlot, was the start of an extensive stretch of relatively undisturbed broadleaf evergreen forest that was made the second site of intensive collecting. The more remote sections of the forest probably approached a mature (primary?) condition and resembled the Chapeau Gendarme forest in being two-storied. Epiphytes and lianas were uncommon. The floor was well insolated and covered in most parts by moist leaf litter up to a meter in depth. Rocks and rotting logs were everywhere common on the ground. (3) The third collecting station was two kilometers southwest of the Ciu Falls, on the trail to Koindé, at an elevation of 500 meters. The forest here was limited to deep stream valleys and was similar in form and composition to that at the second station, apparently differing only in being somewhat denser and moister.

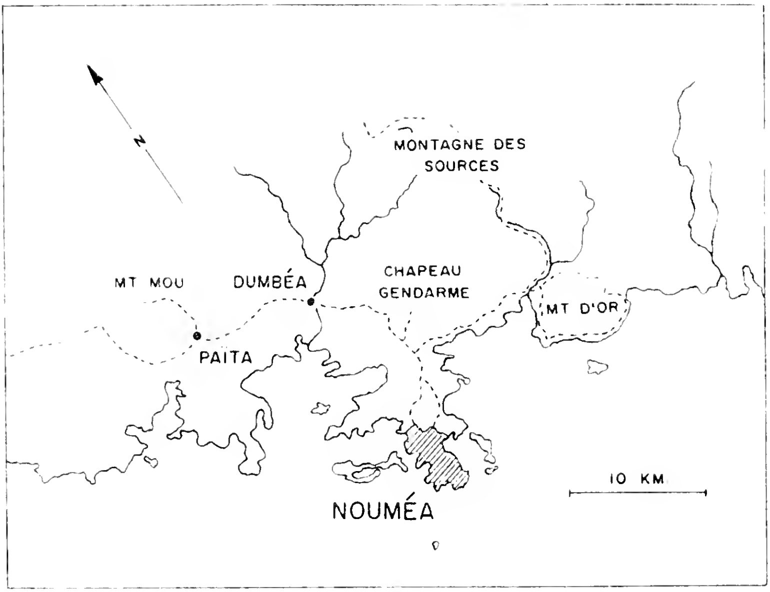

Fig. 3. The Nouméa area, southwestern New Caledonia, showing the route followed during collecting in December, 1954, and January, 1955.

Koh (*ca. 500 meters*). December 20, 1954. This locality is on the eastern slope of the central New Caledonian massif. Collections were made in moist broadleaf evergreen forest along a steep stream course crossing the main La Foa-Canala road.

Montagne des Sources. December 17, 1954. Collections were made at two stations in this montane area: at 800 meters, mixed *Araucaria-Agathis*-angiosperm forest on the steep valley walls at the head of the Dumbéa River; at 1000 meters, a pure stand of second-growth *Araucaria* forest.

Mt. Mou (180-1200 meters). December 10-12, 1955. At lower elevations collecting was conducted near the Bourdinat residence in valley-pocket forest very similar to that on Chapeau Gendarme. On December 12 an ascent was made of Mt. Mou to a point on the summit ridge at about 1200 meters. Between approximately 300 and 700 meters the trail led through dense bracken scrub, toward the latter elevation passing into a belt of scattered, low, shrubby trees. Beyond this marginal zone

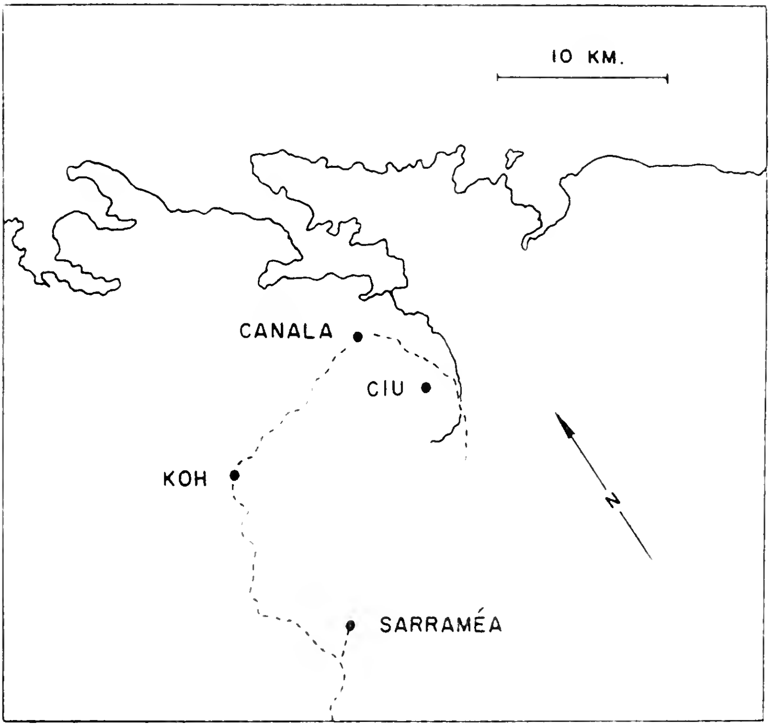

Fig. 4. The Canala area, north-central New Caledonia, showing the route followed during collecting in 1954-55.

the summit cloud forest was encountered, dominated by large *Araucaria* and *Podocarpus*, and with abundant ground moss and epiphytes. Somewhat higher the cloud forest gave way to true mossy forest, consisting of gnarled, twisted trees averaging only eight to ten meters in height and bearing thick layers of mosses and other epiphytes. Ants were present but relatively scarce in both the cloud and mossy forest zones.

Nouméa. See *Anse Vata.*

Sarraméa (160 meters). December 22, 1954. Most of the accessions came from under rocks in moist, well shaded pastureland in the rich farming country around Sarraméa. Several stands of second-growth broadleaf evergreen forest were also visited and proved to contain most of the same ant species as the surrounding cultivated land.

Yahoué. See *Chapeau Gendarme.*

REFERENCE COLLECTIONS

Most of the available study material of Melanesian ants, both in original and duplicated series, is currently housed in the Museum of Comparative Zoology, Harvard University (MCZ). Below are listed other principal collections from which material has been drawn for the present study; these are preceded in each case by the abbreviation by which they are cited in the formal synonymies of the systematic section to follow.

(Bishop Museum)	B. P. Bishop Museum, Honolulu
(BMNH)	British Museum (Natural History), London
(CAS)	California Academy of Sciences, San Francisco
(Emery Coll.)	Emery Collection, Museo Civico di Storia Naturale, Genoa
(Forel Coll.)	Forel Collection, Museum d'Histoire Naturelle, Geneva
(OUM)	Hope Department of Entomology, Oxford University Museum, Oxford, England
(Paris Museum)	Museum National d'Histoire Naturelle. Paris

(USNM)	United States National Museum, Washington, D. C.
(Yasumatsu Coll.)	Collection of Dr. Keizô Yasumatsu, University of Kyushu, Japan

ACKNOWLEDGEMENTS

The author is indebted to Dr. W. L. Brown and Mrs. Eleanor Lowenthal for preparing a large part of his Melanesian collections and shipping them to him for advance study in Europe on his return from the Pacific in 1955. Dr. Brown also supplied a set of preliminary taxonomic notes and inquiries that proved most helpful during examination of type material in the major European collections. As a result of this cooperation, the author was able to firmly identify many of the little known and critical Melanesian forms, as well as settle a number of pressing nomenclatural problems pertaining to other parts of the world fauna.

Appreciation is also expressed to the following individuals for their help in assembling the study collection and granting access to type material: Mr. J. Auber (Paris Museum), Dr. Ch. Ferrière (Forel Coll.), Dr. H. Gisin (Forel Coll.), Dr. J. L. Gressitt (Bishop Mus.), Dott. Delfa Guiglia (Emery Coll.), Mr. G. E. J. Nixon (BMNH), Dr. E. S. Ross (CAS), Dr. M. R. Smith (USNM), Dr. K. Yasumatsu (Yasumatsu Coll.).

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MEASUREMENTS

Measurements in the present study follow the conventions already adopted by the author and W. L. Brown in previous taxonomic work.[1] The dimension *head length*, over which there

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[1] See W. L. Brown, 1953, Amer. Midl. Nat., **50**, p. 7; or E. O. Wilson, 1955, Bull. Mus. Comp. Zool., **113**, p 22.

has been some disagreement in the past, is taken as follows: maximum length of the head, measured from a transverse through the posteriormost point or points along the occipital border to a transverse through the anteriormost point or points on the anterior clypeal border (after Brown, 1953).

THE LEPTOGENYINI OF THE MOLUCCAS AND WESTERN MELANESIA

In the area extending from the Moluccas to the New Hebrides, six species groups of *Leptogenys* are currently recognizable. These are listed below, along with their constituent species and attendant new synonymy.

Group of *L. caeciliae* Viehmeyer

caeciliae Viehmeyer
optica Viehmeyer

Group of *L. chinensis* Mayr

bituberculata Emery
drepanon Wilson
hebrideana Wilson
indagatrix Wilson
papuana Emery
triloba Emery

Group of *L. diminuta* (Fr. Smith)

diminuta (Fr. Smith)
  = *Ponera simillima* Fr. Smith
  = *Ponera ferox* Fr. Smith
  = *Leptogenys diminuta* var. *bismarckensis* Forel
  = *Leptogenys diminuta* subsp. *santschii* Mann
  = *Leptogenys diminuta* var. *stitzi* Viehmeyer
  = *Leptogenys diminuta fruhstorferi* var. *amboinensis* Karawajew
  = *Leptogenys diminuta fruhstorferi* var. *buruensis* Karawajew
nitens Donisthorpe
oresbia Wilson
purpurea Emery
violacea Donisthorpe

Group of *L. emeryi* Forel

emeryi Forel
foreli Mann
= *walkeri* Donisthorpe
truncatus Mann

Group of *L. keysseri* Viehmeyer

keysseri Viehmeyer

Group of *L. processionalis* (Jerdon)

breviceps Viehmeyer
= *Pseudoponera lubbocki* Donisthorpe
= *Euponera niger* Donisthorpe

Key to the species, based on the worker caste

1. When the mandibles are in a closed position, there is a gap between the point where their inner borders overlap and the midpoint of the anterior clypeal border which is at least as wide as the width of the individual mandibles at their insertions; mandibles linear and with no more than a single tooth besides the apical. 2
When the mandibles are in a closed position, there is little or no gap between the point of overlap of their inner borders and the midpoint of the anterior clypeal border; mandibles varying in shape among species and frequently, but not always, bearing numerous teeth in addition to the apical 9

2. Alitrunk completely lacking standing hairs; entire body surface opaquely sculptured and covered with pruinose pubescence (Polynesia; possibly occurring also in Melanesia as a tramp species) ... *insularis* Fr. Smith
Alitrunk with abundant standing hairs; body surface smooth and shining at least in part, and lacking pruinose pubescence 3

3. Smaller species, the pronotal width 1.14 mm or less; almost all of the head and alitrunk densely foveate-punctate and subopaque to opaque 4
Larger species, the pronotal width 1.30 mm or more; almost all of the head and a large part of the alitrunk smooth and shining 6

4. Dorsal face of propodeum only slightly longer than the posterior face (New Britain) ... *emeryi* Forel
Dorsal face of propodeum about twice as long as the posterior face 5

5. Median anterior clypeal projection nearly twice as broad as long (Santa Cruz Islands) .... *truncata* Mann
Median anterior clypeal projection as long as broad or longer (widely distributed, New Guinea to New Hebrides) .... *foreli* Mann

6. When the mandibles are in a closed position, the gap between the point of intersection of their inner borders and the midpoint of the anterior clypeal border is approximately three times the maximum mandible width .... *triloba* Emery
When the mandibles are in a closed position, the gap described above is about equal to the maximum mandible width or a little less 7

7. The petiolar node about 1.1 × longer than broad, its dorsal surface distinctly tuberculate .... *indagatrix* Wilson
The petiolar node at least 1.3 × longer than broad, its dorsal surface smooth or at most bearing shallow foveae 8

8. Petiolar node about 1.3 × longer than broad; its width measured just behind the anterior margin 0.7-0.8 × the maximum width, which is located just in front of the posterior border; body surface showing bluish reflections .... *papuana* Emery
Petiolar node about 1.5 × longer than broad; its width measured just behind the anterior border only about 0.5 × the maximum width; body lacking bluish reflections .... *drepanon* Wilson

9. Petiolar node compressed antero-posteriorly, forming a narrow, transverse dorsal crest; head nearly as broad as long; dark brown, robust, small-eyed species .... *breviceps* Viehmeyer
Petiolar node not compressed antero-posteriorly, its crest longitudinally oriented; head much longer than broad; mostly, but not all, jet-black, slender species with moderately large eyes 10

10. Very small, slender species, the pronotal width not exceeding 0.79 mm; the petiolar node strongly compressed laterally and seen from above strongly tapered in an anterior direction 11
Larger species, the pronotal width 0.82 mm or greater, and if approaching the smaller size class (pronotal width 0.82-1.17 mm) then the petiolar node is neither markedly compressed laterally nor strongly tapered in an anterior direction 12

11. Head almost entirely smooth and shining (New Guinea) .... *bituberculata* Emery
Entire head foveate-punctate and opaque (New Hebrides) .... *hebrideana* Wilson

12. Showing the following combination of characters: medium-sized (pronotal width 1.06-1.23 mm), most of the body surface showing strong

steel-blue or violaceous reflections, the entire head surface finely and densely striate . . 13

Not showing all of the above characters 14

13. Entire alitrunk covered with long erect hairs; bluish-violaceous reflections absent or very weakly developed on the gaster and appendages (New Guinea mainland) . . . . *purpurea* Emery

Alitruncal pilosity limited to a few short hairs on the declivitous faces of the propodeum; bluish-violaceous reflections well developed on the first several gastric tergites and on the appendages (Waigeo) . . *violacea* Donisthorpe

14. Smaller species, the pronotal width not exceeding 1.02 mm. Showing in addition the following combination of characters: petiolar node seen from above shaped like a half-ellipse; sculpturing of the head limited almost entirely to longitudinal striation; the lower halves of the sides of the propodeum longitudinally striate, the upper halves mostly or entirely smooth 15

Larger species, the pronotal width at least 1.17 mm. Not showing all of the additional characters given above . . 17

15. The area between the posterior margin of the eye and the occipital corner at least partly striate and feebly shining to subopaque . . . . *diminuta* (Fr. Smith)

Cephalic area described above lacking striae, completely smooth and shining 16

16. Longitudinal striae just mesad of the eye extending for a short distance posterior to the level of the posterior margin of the eye; head proportionately longer, cephalic index 71; scapes proportionately longer, scape index 138-145 (Netherlands New Guinea and Waigeo) . . . . . . *nitens* Donisthorpe

Longitudinal striae just mesad of the eye not surpassing the level of the posterior margin of the eye; cephalic index 76; scape index 121-125 (Solomons) . . . . . . *oresbia* Wilson

17. Distance from the posterior margin of the eye to the posterior margin of the head only slightly greater than the maximum eye length; circumocular sulcus lacking; entire body smooth and shining . . . . *keysseri* Viehmeyer

Distance from the posterior margin of the eye to the posterior margin of the head more than twice the maximum eye length; the eye mostly or entirely surrounded by a shallow but distinct sulcus; body in large part sculptured and opaque 18

18. In full face view, the eyes do not quite reach the lateral margins of the head; the eyes are completely surrounded by the circumocular sulcus . . *caeciliae* Viehmeyer

In full face view, the eyes slightly surpass the lateral margins of the head; the circumocular sulcus does not extend around the anterior margin of the eye *optica* Viehmeyer

LEPTOGENYS BITUBERCULATA Emery

(Figure 5)

Leptogenys bituberculata Emery, 1902, Természetr. Füz., 25: 160, worker. Original localities: Tamara I., Oudemaine I., and Sattelberg, N.-E. New Guinea. (Syntype examined — Emery Coll.)

Material examined. PAPUA: Dobodura (P. J. Darlington); Bisianumu, 500 m. (Wilson, nos. 637, 640, 663).

Taxonomic notes. The Dobodura specimens were compared with a syntype in the Emery Collection and found to be nearly identical. The series from Bisianumu, however, differ in their slightly larger size and more rounded propodeum, and may prove to belong to a distinct species. For descriptive data on *bituberculata*, see under the comparative descriptions of *L. hebrideana* Wilson and *L. sagaris* Wilson.

Ecological note. At Bisianumu, a colony containing about 300 workers and a quantity of brood was found nesting in and under loose leaf litter on the floor of second-growth foothills rain forest.

LEPTOGENYS BREVICEPS Viehmeyer

(Figure 5)

Leptogenys (Lobopelta) breviceps Viehmeyer, 1914, Arch. Naturgesch., 79A(12): 30, fig. 4, worker. Type locality: Wareo, N.-E. New Guinea.

Pseudoponera lubbocki Donisthorpe, 1938, Ann. Mag. Nat. Hist., (11)1: 593, 596, fig., worker. Type locality: Mt. Lina, Cyclops Mts., Neth. New Guinea. (Syntype examined — MCZ). NEW SYNONYMY.

Euponera (Brachyponera) niger Donisthorpe, 1949, Ann. Mag. Nat. Hist., (12)2: 405, male. Type locality: Maffin Bay, Neth. New Guinea. (Holotype examined — CAS). NEW SYNONYMY.

Material examined. N.-E. NEW GUINEA: lower Busu River (Wilson, no. 873); Boana, upper Bunbok Valley, 1100 m. (Wilson, no. 1116). NETH. NEW GUINEA: Mt. Lina, Cyclops Mts., 160 m. (*Pseudoponera lubbocki* Donisthorpe syntype); Maffin Bay (*Euponera niger* Donisthorpe holotype).

Taxonomic notes. This is the only known Papuan member of the *L. processionalis* group, the species of which are predominantly Indomalayan in distribution. The series collected by myself and a single syntype of *Pseudoponera lubbocki* Donisthorpe agree well with Viehmeyer's description of *breviceps*, except in slight color characters. Viehmeyer states that *breviceps* is colored similarly to *L. processionalis*, whereas the series examined by me are slightly darker than *processionalis*, as I conceive that species, and show metallescent reflections not exhibited by *processionalis*. There is a good possibility that this difficulty may be resolved by the fact that Viehmeyer was using as his standard some species of the taxonomically difficult *processionalis* group other than *processionalis*, e.g. *L. iridescens* (Fr. Smith). The holotype of *Euponera niger* Donisthorpe, on loan from the California Academy of Sciences, has been compared with a male of *breviceps* from the Busu River and found to be nearly identical.

Ecological notes. At Boana a large colony was found nesting in open soil in a partial clearing in second-growth rain forest. The nest was marked externally by a low, irregular pile of excavated earth about a meter in diameter and bearing multiple entrance holes. At the Busu River a group of workers were found foraging in leaf litter during the day. The workers are unusually aggressive when disturbed and capable of delivering a powerful, shocking sting. No observations were made to determine whether *breviceps* conducts raids on termite nests as do other members of the *processionalis* group. A male determined as *breviceps* was taken at light at the Busu River on May 13, 1955.

LEPTOGENYS CAECILIAE Viehmeyer

Leptogenys (*Lobopelta*) *caeciliae* Viehmeyer, 1912, Abh. Zool.-anthrop.-ethn. Mus. Dresden, 14: 6, figs. 5, 5a, worker. Type locality: Torricelli Mts., N.-E. New Guinea.

This large and striking species is known only from the single type worker. As indicated in the key, it is closely allied to *L. optica* Viehmeyer.

LEPTOGENYS DIMINUTA (Fr. Smith)

Ponera diminuta Fr. Smith, 1857, J. Linn. Soc. Zool., 2: 69, worker.* Type locality: Sarawak.

Leptogenys diminuta, Mayr, 1867, Tijdschr. Ent., 10: 57, worker, distribution.

Ponera simillima Fr. Smith, 1860, J. Linn. Soc. Zool., 5 (suppl.): 104, worker. Type locality: Batjan. NEW SYNONYMY (provisional). *Nec Ponera simillima* Fr. Smith, *op. cit.*, p. 105 (= *Prionopelta majuscula* Emery).

Leptogenys (Lobopelta) simillima, Donisthorpe, 1932, Ann. Mag. Nat. Hist., (10)10: 462.

Ponera ferox Fr. Smith, 1865, J. Linn. Soc. Zool., 8: 70, worker. Type locality: Salawati. NEW SYNONYMY (provisional).

Leptogenys (Lobopelta) ferox, Donisthorpe, 1932, Ann. Mag. Nat. Hist., (10)10: 472.

Leptogenys (Lobopelta) diminuta var. *bismarckensis* Forel, 1901, Mitt. Zool. Mus. Berlin, 2(1,b): 7, worker. Type locality: Muarlin, New Britain. (Syntype examined — Emery Coll.). NEW SYNONYMY.

Leptogenys (Lobopelta) diminuta var. *papuana* Stitz, 1912, Sitzber. Ges. Naturf. Freunde Berlin, no. 9: 498, fig. 1, worker. *Nec Leptogenys papuana* Emery 1897; see *L. diminuta* var. *stitzi* Viehmeyer 1924.

Leptogenys (Lobopelta) diminuta subsp. *santschi* [!] Mann, 1919, Bull. Mus. Comp. Zool., 63: 299, worker, ergatogyne, male. Type locality: Malapaina I., Three Sisters Group, Solomons. (Syntypes examined — MCZ). NEW SYNONYMY.

Leptogenys (Lobopelta) diminuta var. *stitzi* Viehmeyer, 1924, Ent. Mitt., 13: 310, nom. pro *L. diminuta* var. *papuana* Stitz. NEW SYNONYMY (provisional).

Leptogenys (Lobopelta) diminuta subsp. *fruhstorferi*, Karawajew, 1925, Konowia, 4: 276.

Leptogenys (Lobopelta) diminuta fruhstorferi var. *amboinensis* Karawajew, 1925, *ibid.*, p. 277, worker. Type locality: Amboina. NEW SYNONYMY.

Leptogenys (Lobopelta) diminuta fruhstorferi var. *huruensis* [!] Karawajew, 1925, *ibid.*, p. 278, worker. Type locality: Tifu, Buru. NEW SYNONYMY.

Material examined. This abundant ponerine species ranges from Ceylon and India east to Botel Tobago and south through Indonesia to New Guinea, the Solomons, and Queensland. Below are listed the records from Melanesia that have been verified during the present study.

WAIGEO: Camp Nok, 800 m. (L. E. Cheesman). N.-E. NEW GUINEA: Nadzab, Markham Valley (Wilson, nos. 1087, 1106, 1107); Bubia (Wilson, no. 1059); lower Busu River (Wilson, nos. 934, 940); Mongi River at Sambeang (Wilson). PAPUA: Karema, Brown River (Wilson, no. 539); Bisianumu, 500 m. (Wilson, nos. 608, 644, 659). SOLOMONS: Wai-ai, San Cristoval (W. M. Mann).

Significant literature records include Amboina and Buru (Karawajew, 1925); Muarlin, New Britain (Forel, 1901); and Malapaina and Ugi, Solomons (Mann, 1919).

Taxonomic notes. The status of *diminuta* is complicated by the existence of at least four closely related species that occupy restricted distributions within its range. On Negros Oriental and Luzon, Philippines, there is a species, apparently undescribed, which is distinguished from *diminuta* by its denser, heavier body sculpturing. A second species occurs in northern Borneo and Sarawak and is distinguished from sympatric samples of *diminuta* by much feebler body sculpturing and smaller size; this species may well be Frederick Smith's *Ponera laeviceps*. A third species, *L. nitens* Donisthorpe, is widespread in Netherlands New Guinea, while a fourth, *L. oresbia* Wilson, occurs in the Solomons. The possibility exists that sibling species additional to *L. nitens* occur with *diminuta* on New Guinea. A single stray worker (or ergatogyne?) from Bisianumu, Papua (acc. no. 644) appears identical with other workers from the same locality except for a much thinner petiolar node; it has been treated tentatively as a pathological specimen of *diminuta* but may represent a distinct species.

The single definitely associated ergatogyne collected in New Guinea (Nadzab; acc. no. 1106) is distinguished from connidal workers by its slightly larger size, proportionately thinner petiolar node, and proportionately much larger gaster. The alitrunk is worker-like. Lateral ocelli are developed but the median ocellus is represented only by an empty pit.

Geographic variation in the worker caste of *L. diminuta* is most conspicuous in body sculpturing. In this character at least three separate surface areas show independent variation. In the accompanying table I have indicated the records of the species that I have personally verified or that are adequately described in the literature, and I have attempted to indicate by means of a crude classification of sculpturing form and relative sculpturing density the geographic variation in the three body areas. Most

GEOGRAPHIC VARIATION IN LEPTOGENYS DIMINUTA

Locality	Postocular Cephalic Surface	Lateral Pronotal Surface	Mesopleural Surface
Lengoo, Kwantung Prov., China	heavily striate	feebly punctate-striate	heavily striate
Botel Tobago	heavily striate	completely smooth	heavily striate
Misamari, Assam	feebly striate	smooth to feebly striate	feebly shagreened
Rangoon, Burma	heavily striate	feebly punctate-striate	feebly punctate-striate
Walajanagar, E. Madras Prov., India	feebly striate	completely smooth	feebly shagreened
Kandy, Ceylon	feebly striate	completely smooth	feebly shagreened
Batu Caves, Kuala Lumpur, Malaya	heavily striate	feebly striate	feebly striate
Pang Mop, Sumatra	heavily striate	feebly striate	feebly striate
North Borneo and Sarawak	heavily striate	feebly striate with smooth patches	moderately striate
Pemalang, Java	heavily striate	feebly striate with smooth patches	feebly striate
Bali	heavily striate	moderately striate	heavily striate

Locality	Postocular Cephalic Surface	Lateral Pronotal Surface	Mesopleural Surface
Binaluan, n. Palawan	heavily striate	feebly punctate-striate	feebly striate
Zamboanga, Mindinao, P. I.	heavily striate	feebly punctate-striate	moderately striate
Cebu and Limay, Luzon	heavily striate	feebly punctate-striate	heavily striate
Buru (after Karawajew, 1925)	heavily striate	smooth to feebly striate	?
Waigeo	heavily striate	completely smooth	heavily striate
New Guinea	heavily striate	smooth to feebly striate	moderately to heavily striate
Wai-ai, Solomons	feebly striate	completely smooth	heavily striate
Kuranda, Queensland	heavily striate	moderately punctate-striate	moderately striate

of the records involve single nest series. This is only a preliminary sketch and will serve merely to indicate the extensive nature of the variation and the marked discordance between the independent areas.

L. diminuta should prove in the future one of the most satisfactory of all ant species for the detailed study of geographic variation. However, the unfortunate circumstance prevails that even the most elementary analysis will be hampered by the large number of infraspecific names that have been attached to this species during its long taxonomic history. In the present treatment I have accounted for only those names applied to material originating from Melanesia and the Moluccas. Some of the names placed in synonymy, such as Karawajew's Moluccan varieties and subsp. *santschii* Mann from the Solomons, are clearly geographic variants or less and do not need further comment. Several other names, however, present more complex problems and, in the absence of type material, have been placed in provisional synonymy. Their cases are treated individually below.

Ponera simillima Fr. Smith. In the original description this species was compared with *Ponera laeviceps* Fr. Smith, in such a way as to suggest its probable identity with *L. diminuta.* There is no clue in the descriptions of either *laeviceps* or *simillima* as to any character by which the latter can be separated from *diminuta.*

Ponera ferox Fr. Smith. In the original description this species was stated to differ from *diminuta* by its larger size and weaker sculpturing. The present author made a special attempt to locate the type of *ferox* during a recent visit to the British Museum (Natural History) and Hope Department of Entomology, but was not successful.

Leptogenys diminuta var. *stitzi* Viehmeyer. This form was described as differing from "typical" *diminuta* by (1) larger size, (2) somewhat more elongate alitrunk, and (3) less flattened petiolar node. In my opinion the *stitzi* types probably fall within the extreme range of the New Guinea *diminuta* population in the first two characters. I have seen no specimens with the precise petiolar node form shown by Stitz in his figure, but an exceptionally large worker from Sambeang approaches it, and if the node of this specimen is turned slightly so as to be seen from a posterior-oblique view, the outline actually corresponds well to that in Stitz's figure. Until a species is defined which corresponds with Stitz's characterization, it will probably be best to leave this form in provisional synonymy.

Ecological notes. Leptogenys diminuta has been found in a variety of habitats in New Guinea, from dry evergreen forest at Nadzab to primary lowland rain forest at the Busu River and foothills rain forest at Bisianumu. It sems to favor forest borders and partial forest clearings. Nest sites are variable, from logs of various degrees of decomposition to cavities in open leaf litter.

The following estimates of colony size and composition were made:

1. *Acc. no. 1087.* May 20-22, 1955. 70 to 80 workers, 10 males, and an undetermined amount of brood, consisting of larvae, one-quarter to full grown, and cocoons, the latter predominating.
2. *Acc. no. 1106.* May 20-22, 1955. One ergatogyne, about 150 workers, 10 males, and an undetermined amount of brood, consisting of larvae, one-half to full grown, and cocoons, the latter predominating.
3. *Acc. no. 539.* March 9, 1955. Somewhat in excess of 300 workers; brood not examined.
4. *Acc. no. 608.* March 15-20, 1955. About 200 workers and several males; brood not examined.

The ethology of *L. diminuta* has already been described in some detail in another paper.[1] The species shows what I have considered to be true legionary behavior, involving both frequent colony movement between temporary nests and the tendency of the workers to forage in groups. The following prey were recorded in New Guinea: a large adult millipede (Karema), 2 small pentatomid bugs (Nadzab), and a large passalid larva (Nadzab).

LEPTOGENYS DREPANON Wilson, n. sp.

(Figure 5)

Diagnosis (*worker*). A large member of the *chinensis* group, with almost completely smooth and shining body surface and elongate, non-tuberculate petiolar node.

Holotype worker. HW 1.49 mm, HL 2.15 mm, SL 2.68 mm, ML 0.50 mm, CI 69, SI 179, EL 0.38 mm, PW 1.30 mm, petiolar node length 1.03 mm, petiolar node height 0.94 mm, dorsal petiole width 0.69 mm. Mandibles linear, their maximum width (at the level of the junction of the apical and basal segments of the masticatory border) 0.29 mm. Apical tooth narrow but blunt; apical segment of masticatory border 0.40 mm in length, concave, meeting the basal segment in an obtuse, rounded angle. When the mandibles are in a closed position the distance between the point of overlap of the masticatory borders of the two mandibles

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[1] Wilson, E. O., 1958. The beginnings of nomadic and group-predatory behavior in the ponerine ants. *Evolution,* in press.

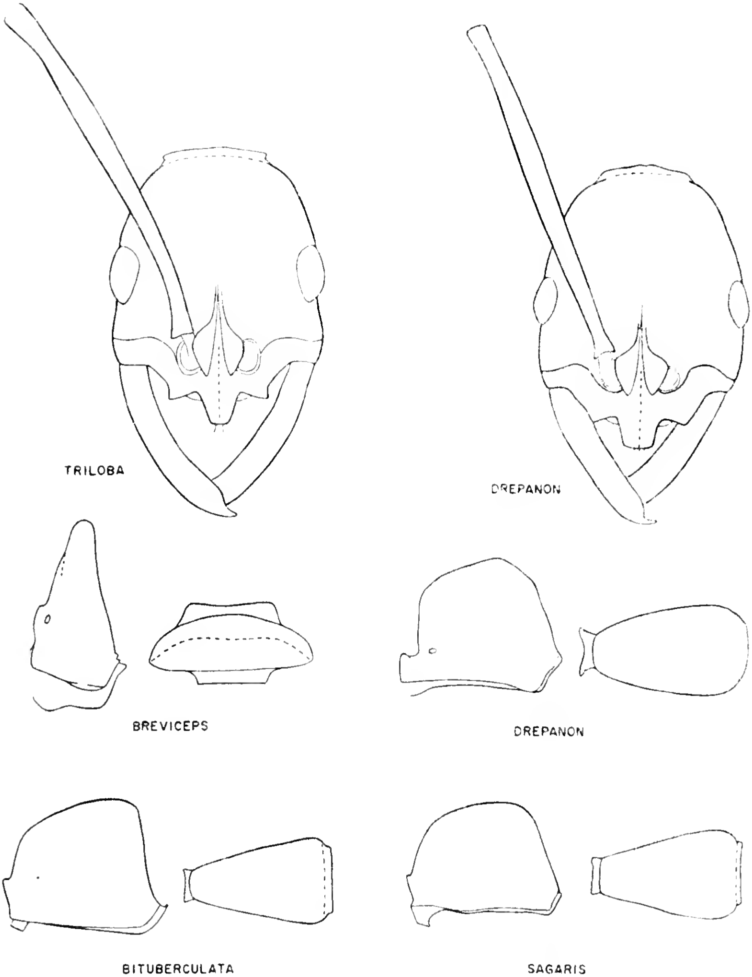

Fig. 5. Heads and petiolar nodes of the workers of selected species of *Leptogenys*. *L. triloba* Emery, worker from Bandong, N.-E. New Guinea; *L. drepanon* Wilson, worker holotype; *L. breviceps* Viehmeyer, drawn from syntype worker of the synonymous *Pseudoponera lubbocki* Donisthorpe; *L. bituberculata* Emery, worker from Dobodura, Papua; *L. sagaris* Wilson, holotype worker.

and the anterior clypeal projection is 0.32 mm. Eyes well developed, completely surrounded by a narrow sulcus, their outer margins extending well beyond the lateral margins of the head when the latter is viewed in full face. Median anterior clypeal projection 0.19 mm in length, trapezoidal, tapering slightly anteriorly, bearing three stout bristles 0.04 to 0.05 mm in length on its anterior border. Anterior clypeal border bearing on each side of the median projection a smaller, triangular projection the apex of which forms an angle of slightly more than 90°. Between the median and lateral projections the clypeal border is strongly convex. Posterior margin of head evenly rounded, grading into the lateral margins through a continuous curve. Head broadening anteriorly, so that its maximum width is just posterior to the mandibular insertions. Petiolar node as shown in Figure 5.

Entire body, including gula and appendages, covered by abundant, long, coarse, predominantly erect hairs. Scapes covered by predominantly oblique hairs, the longest of which are 0.14 mm in length, or more than 0.7 X the maximum scape width, which is 0.19 mm. The longest hairs of the posterior lateral margins of the head are 0.23 mm; those on the gula are 0.40 mm; those on the pronotum are 0.44 mm; and those on the petiolar node are 0.22 mm in length. As in *L. triloba* Emery, the body surface is almost entirely free of underlying pubescence; the scapes are also bare, but the funiculi and remainder of the appendages bear variably abundant appressed pubescence.

Mandibles feebly and irregularly striate; occiput bearing scattered small, low tubercles; remainder of the head almost entirely smooth and moderately to strongly shining. Entire pronotum, mesonotum, and propodeum (except the posterior propodeal face) smooth and shining. Upper one-fifth of episternum covered by rugae oriented transversely to the long axis of the body; lower four-fifths of episternum and entire metapleuron covered by obliquely oriented, anteriorly descending rugae. Basal two-thirds of posterior propodeal face covered by transverse costulae. Petiolar node nearly smooth and moderately shining, bearing broad, extremely shallow, indistinct, contiguous depressions which give it a very feebly wavy outline when viewed from the side. Gastric tergites completely smooth and shining.

Entire body, except mandibles and apical gastric segments, jet-black. Coxae also jet-black. Antennae, apical gastric segments, and leg segments distal to the coxae medium to dark brown.

Material examined. N.-E. NEW GUINEA: Bialowat, Morobe District (H. Stevens); a single worker.

Taxonomic notes. L. drepanon is closely related to *L. indagatrix* Wilson and can be distinguished by the characters given in the comparative description of that species. It is also close to *L. papuana* Emery, from which it can be distinguished by its more slender, tapering petiolar node, and lack of bluish surface reflections. From the more distantly related *L. triloba* Emery it differs by its smaller size, shorter mandibles, different clypeal outline, and longer and denser pilosity.

LEPTOGENYS EMERYI Forel

Leptogenys (Leptogenys) Emeryi Forel, 1901, Mitt. Zool. Mus. Berlin, 2(1,b): 7, worker. Type locality: Lowon Valley, near Ralum, New Britain.

Known from the holotype worker only. This species is closely related to *L. foreli* Mann, a species widely distributed in western and central Melanesia, but should be easily distinguished by the distinctive propodeal proportions as given by Forel in his original description.

LEPTOGENYS FORELI Mann

Leptogenys (Leptogenys) foreli Mann, 1919, Bull. Mus. Comp. Zool., 63: 297, fig. 9 (*nec* fig. 10, which is labelled as this species but is actually *L. truncata*), worker, male. Type locality: Malapaina I., Solomons. (Syntypes examined — USNM).

Leptogenys (Leptogenys) walkeri Donisthorpe, 1942, Ann. Mag. Nat. Hist., (11)9: 704, worker. Type locality: Vila, Efate, New Hebrides. (Holo type examined — BMNH). NEW SYNONYMY.

Material examined. NETH. NEW GUINEA: Maffin Bay (E. S. Ross). SOLOMONS: Malapaina (type locality). NEW HEBRIDES: Vila, Efate (*walkeri* holotype); Aubert Ratard Plantation, Espiritu Santo (Wilson, no. 237). Mann (1919) also records *foreli* from Auki and Simoli, in the Solomons.

Taxonomic notes. The Maffin Bay series differs from the *foreli* types and New Hebrides series in having slightly longer anterior genal teeth and sparser appendage pilosity.

Ecological notes. Ross (unpublished notes) found the Maffin Bay colony nesting in a sago palm trunk. The colony that I found on Espiritu Santo was nesting in a large rotting log, partly elevated off the ground, in primary lowland rain forest. It contained approximately 25 workers, which were extremely timid and agile.

LEPTOGENYS HEBRIDEANA Wilson, n. sp.

Diagnosis (worker). Closely resembling *L. bituberculata* Emery of New Guinea, showing the following principal differences:

(1) The entire surface of the head is coarsely sculptured and opaque (as opposed to completely smooth and shining in *bituberculata*), with the sculpturing showing the distinctive pattern described herewith: All of the clypeus but the central raised portion is longitudinally costulate. Posteriorly the costulae extend onto the frons, where they turn into rugae, which in turn form into a rugoreticulum in the area between the eye and antennal insertion. At about the level of the posterior margin of the eye, the rugoreticulum gives way to flat, shallow foveae, 0.02 to 0.05 mm in diameter and separated from one another by distances of about the same magnitude as the diameters. The bottoms of the foveae are densely punctate, whereas the interfoveal spaces are sparsely punctate to smooth. The entire gular area is covered by similar foveae. At the dorsal occipital zone the foveae are crowded together and the interfoveal spaces form a rugoreticulum.

(2) In *hebrideana* the anterior half of the pronotum and entire dorsal surfaces of the mesonotum and propodeum are irregularly pitted and furrowed, while in *bituberculata* the same area is completely smooth and shining. In *hebrideana* the entire lateral surface of the alitrunk is coarsely sculptured, with oblique rugae predominating, whereas in *biturberculata* sculpturing is limited to the immediate vicinities of the metapleural-propodeal suture and metapleural gland.

(3) Both appendage and body pilosity are much denser in *hebrideana.*

(4) The petiolar node is proportionately shorter in *hebrideana.*

Holotype worker. HW 0.86 mm, HL 1.40 mm, SL 1.58 mm, CI 61, SI 184, EL 0.34 mm, PW 0.75 mm, petiole node length 0.74 mm, petiole node height 0.45 mm, dorsal petiole width 0.41 mm.

Paratype worker. HW 0.90 mm, HL 1.43 mm, SL 1.61 mm, CI 63, SI 179, PW 0.76 mm.

Material examined. NEW HEBRIDES: A. Ratard Plantation, near Luganville, Espiritu Santo (Wilson, no. 348; 2 workers).

Taxonomic notes. L. hebrideana also bears a close resemblance to *L. foveopunctata* Mann, *L. humiliata* Mann, and *L. navua* Mann, all of the Fiji Islands. The Fijian species have foveate head surfaces as in *hebrideana*, but *humiliata* and *navua* are considerably smaller in size and have nearly smooth alitruncal dorsa, while *foveopunctata* is larger than *hebrideana* and is further distinguished from all other members of the *bituberculata* complex by its coarsely sculptured petiolar node. There are other characters but the above should suffice for diagnostic purposes.

Ecological note. The two type workers of *hebrideana* were taken as strays foraging on the floor of undisturbed lowland rain forest.

LEPTOGENYS INDAGATRIX Wilson, n. sp.

Diagnosis (*worker*). Closely related to *L. papuana* Emery and *L. drepanon* Wilson, but easily distinguished from these two species by the following characters:

(1) Smaller size (see measurements of holotype worker).

(2) The petiolar node is proportionately shorter.

(3) The surface of the petiole is covered by relatively small, non-contiguous, rounded tubercles; the intermediate areas are feebly and irregularly shagreened and their surfaces only feebly shining.

(4) The head surface, but no other part of the body, bears very faint bluish reflections. *L. drepanon* completely lacks surface reflections, while they are prominently developed on the body (and head also?) of *papuana*.

The following additional difference between *indagatrix* and *drepanon* is noteworthy: in *indagatrix* the pilosity of the dorsal propodeal and petiolar node surfaces is predominantly oblique, the individual hairs set at an angle at about 45° from the cuticular surface, whereas in *drepanon* the pilosity is predominantly erect, the individual hairs set at an angle of about 70°; the comparison cannot be extended to *papuana* in the absence of material belonging to that species.

Holotype worker. HW 1.44 mm, HL 2.02 mm, SL 2.48 mm, CI 71, SI 172, EL 0.41 mm, PW 1.26 mm, petiolar node length 1.06 mm, petiolar node height 1.00 mm, dorsal petiole width 0.86 mm.

Worker paratype variation. HW 1.38-1.43 mm, HL 1.94-2.00 mm, SL 2.40-2.46 mm, CI 71-72, SI 171-175.

Material examined. PAPUA: Bisianumu, 500 m. (Wilson. no. 661); holotype and six paratype workers.

Ecological note. The types were collected together from the floor of somewhat disturbed foothills rain forest.

LEPTOGENYS INSULARIS Fr. Smith

Leptogenys insularis Fr. Smith, 1879, J. Linn. Soc. Zool., 14: 675, worker. Type locality: Oahu, Hawaii.

Although this distinctive tropicopolitan tramp species has not yet been recorded from Melanesia, it has been included in the key and mention made of it here on the basis of the high order of probability that it does occur somewhere in the area.

LEPTOGENYS KEYSSERI Viehmeyer

Leptogenys (Lobopelta) keysseri Viehmeyer, 1913, Arch. Naturgesch., 79A(12): 29, fig. 3, worker. Type locality: Sattelberg, N.-E. New Guinea.

Known from type material only

LEPTOGENYS NITENS Donisthorpe

Leptogenys (*Lobopelta*) *nitens* Donisthorpe, 1943, Ann. Mag. Nat. Hist., (11)9: 169, worker. Type locality: Camp Nok, Waigeo, Neth. New Guinea. (Syntypes examined — MCZ). *Ibid.*, pp. 444-445, male, doubtfully associated.

Material examined. WAIGEO: Camp Nok (lectotype). NETH. NEW GUINEA: Maffin Bay (E. S. Ross).

Taxonomic notes. One of two syntype workers deposited in the Museum of Comparative Zoology belongs to the typical Papuan form of *L. diminuta.* The other belongs to a distinct, related species to which the name *L. nitens* is correctly applied. In order to stabilize the nomenclature, the latter specimen is hereby designated the lectotype of *nitens.* This species resembles *L. oresbia* Wilson of the Solomons in its reduced cephalic sculpturing but is easily distinguished by the fact that the longitudinal striae mesad of the eye extend well beyond the level of the posterior margin of the eye, whereas in *oresbia* they just attain the level of the posterior margin. *Nitens* further differs from *oresbia,* and resembles *diminuta,* in its smaller size, distinctly lower cephalic index, and proportionately longer scapes. The lectotype has the following cephalic proportions: HW 1.23 mm, HL 1.72 mm, SL 1.70 mm, CI 71, SI 138. The largest of four workers examined from the Maffin Bay series has the following cephalic proportions: HW 1.26 mm, HL 1.78 mm, SL 1.83 mm, CI 71, SI 145.

LEPTOGENYS OPTICA Viehmeyer, new status

Leptogenys (*Lobopelta*) *caeciliae* var. *optica* Viehmeyer, 1914, Zool. Jahr. Syst., 37: 609, worker. Type locality: Wareo, N.-E. New Guinea. (Syntype examined — Forel Coll.).

Material examined. N.-E. NEW GUINEA: Wareo (syntype); lower Busu River (Wilson, no. 927); Zingzingu, Mongi Watershed, 1200 m. (Wilson, no. 761).

Taxonomic notes. Workers from the Busu River differ from the syntype in the Forel Collection in the following manner: in the type, the sculpturing of the occipital region consists of transverse rugae, whereas in the Busu specimens it consists of an irregular rugoreticulum with no tendency toward a transverse orientation.

In addition to the characters given in couplet 18 of the key, *L. optica* can be distinguished from the closely related *L. caecilia*
by the following characters: eyes larger and more convex, petiolar node lower, first gastric tergite more densely punctate.

Ecological notes. At the Busu River a small colony of this remarkable ant was found nesting in and under a large, partly buried "Zoraptera-stage" log on the floor of primary lowland rain forest. Workers and brood occupied several large galleries in the lower part of the log itself, as well as several smaller galleries that passed laterally from the bottom of the log into the soil. At Zingzingu a single worker was found in late afternoon crossing a foot trail that led through a clearing in second-growth midmountain forest. The workers are unusually sluggish and timid for *Leptogenys.*

LEPTOGENYS ORESBIA Wilson, n. sp.

Leptogenys (*Lobopelta*) *diminuta* var. *laeviceps,* Mann, 1919, Bull. Mus. Comp. Zool., 63: 300. *Nec Ponera laeviceps* Fr. Smith.

Diagnosis (*worker*). Closely related to *L. diminuta* (Fr. Smith), *L. nitens* Donisthorpe, and the writer's present conception of *L. laeviceps* (Fr. Smith),[1] but differing in the following characters:

(1) Larger size. The HW of a series of *diminuta* from Wai-ai, San Cristoval, ranges 1.10-1.18 mm; the maximum HW of a large number of individuals of *diminuta* measured from all over its range is 1.26 mm. The HW of the two available series of *nitens* varies 1.23-1.26 mm, while the HW of the putative Bornean *laeviceps* varies 1.02-1.08 mm.

(2) The body sculpturing is finer and less extensive. Dorsal cephalic sculpturing consists almost entirely of longitudinal striae, and these are limited to the lateral portions of the clypeus, to the area bordered by the eyes, antennal insertion, and mandibular bases, to a restricted area just ventral to the eye, and to the gula. In the gular area the striae are relatively feebly developed and wavy. All of the remainder of the head is completely smooth and shining. Sculpturing is distributed on the

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[1] Two series from northern Borneo and Sarawak in the Museum of Comparative Zoology have been tentatively determined as *laeviceps.* As noted under the discussion of *diminuta,* these specimens evidently represent a distinct sibling species that occurs sympatrically with *diminuta* on Borneo.

alitrunk as follows: a thin area at the base of the pronotal "neck" is covered by transverse striae; the episternum is covered by arcuate striae running parallel to the long axis of the sclerite; the metapleuron and lateral face of the propodeum below the level of the propodeal spiracle are covered by moderately wavy, longitudinally oriented striae; and the posterior face of the propodeum below the level of the dorsal margin of the metapleural gland bulla is covered by transverse striae. All the rest of the dorsal and lateral surfaces of the alitrunk, as well as the entire surfaces of the petiolar node and gastric tergites, are completely smooth and shining.

Holotype worker. HW 1.29 mm, HL 1.69 mm, SL 1.56 mm, CI 76, SI 121, PW 0.95 mm.

Paratype worker. HW 1.29 mm, HL 1.67 mm, SL 1.59 mm, CI 77, SI 123, PW 0.95 mm.

Paratype ergatogyne. HW 1.18 mm, HL 1.56 mm, SL 1.48 mm, CI 76, SI 125, PW 0.83 mm. This specimen is distinguished externally from the two associated workers by its smaller head and alitrunk, thinner petiolar node, and much larger gaster. The alitrunk is worker-like in form.

Material examined. SOLOMONS: near Fourafi, in the mountainous interior of Malaita (W. M. Mann); 2 workers, 1 ergatogyne. Nidotypes are on deposit in the United States National Museum.

Ecological note. According to Mann (1919), the types were taken running in file across a foot trail in montane forest. The presence of an ergatogyne in this series suggests that the colony may have been in the process of migration.

LEPTOGENYS PAPUANA Emery

Leptogenys papuana Emery, 1897, Ann. Mus. Civ. Stor. Nat. Genova, 38: 556, pl. 1, figs. 5, 6, worker. Type locality: "N. Guinea Mer."

Known from the holotype only.

LEPTOGENYS PURPUREA Emery, new status

(Figure 6)

Leptogenys Kitteli var. *purpurea* Emery, 1887, Ann. Mus. Civ. Stor. Nat. Genova, (2)5: 433, worker. Type locality: Andai, Neth. New Guinea. (Holotype examined — Emery Coll.).

Material examined. NETH. NEW GUINEA: Andai, near Manokwari (holotype); Maffin Bay (E. S. Ross). N.-E. NEW GUINEA: Gemcheng, Mongi Watershed, 1300 m. (Wilson, no. 781); Tumnang, Mongi Watershed, 1500 m. (Wilson, no. 803); Ebabaang, Mongi Watershed, 1300-1400 m. (Wilson, no. 828); Wamuki, Mongi Watershed, 800 m. (Wilson, no. 849); Finsch Harbor (N. G. L. Wagner). In eastern New Guinea, at least, this species is most abundant at intermediate elevations in the mountains. It was never encountered by the author during intensive collecting in the lowlands around Lae and Gagidu.

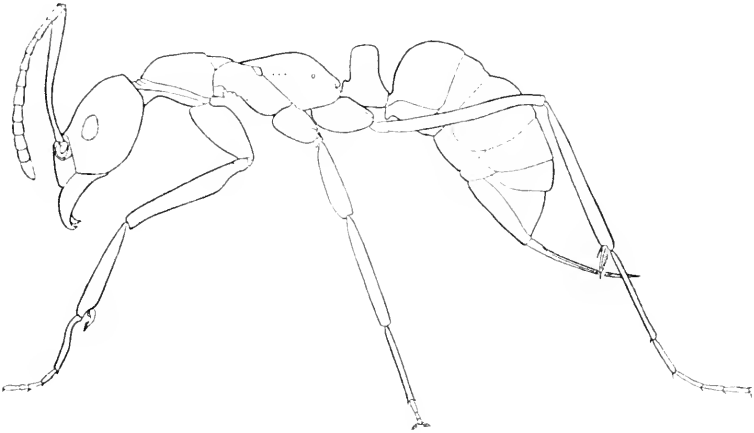

Fig. 6. Worker of *Leptogenys purpurea* Emery from Gemeheng, N.-E. New Guinea.

Taxonomic notes. Three species, *L. kitteli* Forel of the Asian mainland and Indonesia, *L. violacea* Donisthorpe of Waigeo, and *L. purpurea* Emery, together form what may be provisionally termed the *kitteli* superspecies. They are obviously closely interrelated, replace one another geographically, and yet seem too well marked to be considered as mere geographic variants of the same species.

L. purpurea can be distinguished from *L. kitteli* on the basis of the following set of worker characters: (1) purpurescent reflections common over most of the body surface of *purpurea*, as opposed to none in *kitteli;* (2) cephalic striae finer and denser in *purpurea* than in *kitteli;* (3) most of the lateral surfaces of the pronotum of *purpurea* smooth and shining, as opposed to this surface striate and subopaque in *kitteli;* (4) petiolar node somewhat thicker in side view in *purpurea*. *L. purpurea* can be separated from *L. violacea* by means of the characters given in couplet 13 of the key.

Ecological notes. In the mountains of the Huon Peninsula, *L. purpurea* inhabits both clearings and the interior of undisturbed forests. Its behavior has already been described in some detail in another paper (cited on p. 123). Like the related species *L. diminuta*, it has marked legionary habits, employing group-foraging to prey on large arthropods not ordinarily vulnerable to ants that forage solitarily.

LEPTOGENYS TRILOBA Emery

(Figure 5)

Leptogenys triloba Emery, 1902, Természetr. Füz., 25: 159, worker. Type locality: Sattelberg, N.-E. New Guinea.

Material examined. N.-E. NEW GUINEA: Tumnang, Mongi Watershed, 1500-1600 m. (Wilson, no. 811); 1.5 km. north of Bandong, upper Bunbok Valley, 1300 m. (Wilson, no. 1131).

Taxonomic notes. The Bandong worker agrees with Emery's description in having the gaster reddish and contrasting with the remainder of the body, which is jet black. The Tumnang worker differs, in that its gaster is as darkly colored as the remainder of the body. Both specimens agree well with the remainder of Emery's description. I have tentatively determined as this species a single male collected at light during the April, 1955, trip in the mountainous portion of the Huon Peninsula.

Ecological notes. Near Tumnang, in undisturbed midmountain forest, a worker was found at about 9 a.m. running along the top of a large rotting log, with a dead oniscoid isopod in its mandibles. Near Bandong another lone worker was found during the morning foraging on a native foot trail in midmountain forest.

LEPTOGENYS TRUNCATA Mann

Leptogenys (*Leptogenys*) *truncatus* Mann, 1919, Bull. Mus. Comp. Zool., 63: 296, fig. 10 (*nec* fig. 9, which is labelled as this species but is actually *L. foreli*), worker. Type locality: Graciosa Bay, Santa Cruz I.

Known from the holotype worker only.

LEPTOGENYS VIOLACEA Donisthorpe

Leptogenys (*Lobopelta*) *violacea* Donisthorpe, 1942, Ann. Mag. Nat. Hist., (11)9: 705, worker. Type locality: Camp Nok, Waigeo, 800 m. (Syntype examined — MCZ).

Known from type material only.

THE LEPTOGENYINI OF THE FIJI ISLANDS

Nothing has been published on the Fijian *Leptogenys* since Mann's pioneering monograph on the Fijian ant fauna (W. M. Mann, 1921, Bull. Mus. Comp. Zool., 64: 401-499). In this publication all six of the currently known species were described for the first time: *foveopunctata, fugax, humiliata, letilae, navua,* and *vitiensis.* A recent re-examination of the types of all of these species, with the exception of *L. foveopunctata,* has led me to the tentative conclusion that all are closely interrelated and even possibly derived from the same parental species. They are members of the *L. chinensis* Mayr group, which is represented by a large number of species in the Indo-Australian region, and their closest Melanesian relatives within the *chinensis* group are *bituberculata* Emery of New Guinea, *hebrideana* Wilson of the New Hebrides, and *sagaris* Wilson of New Caledonia. On the basis of morphological evidence it appears likely that *bituberculata, hebrideana,* and most or all of the Fijian species were derived from a single ancestral stock, while *sagaris* has been derived independently from near the related, possibly cognate Australian species *anitae* Forel. *Bituberculata, hebrideana, sagaris, navua,* and *humiliata* have undergone little change, while *foveopunctata, fugax, letilae,* and *vitiensis* have diverged along several independent morphoclines. The reason why this species complex has radiated so extensively on the proportionately tiny land mass of the Fiji Islands, while remaining restricted and conservative elsewhere, is perhaps that in the Fijis it faced relatively little competition from the depauperate endemic ponerine-myrmicine fauna and hence had more evolutionary "opportunity" than elsewhere.

THE LEPTOGENYINI OF NEW CALEDONIA

The four known New Caledonian species represent at least three, and possibly four, distinct species groups. Three of the species have obvious affinities with the fauna of tropical Queensland, while the fourth (*Leptogenys punctata*) is of uncertain position.

Key to the species, based on the worker caste

1. Large species, head width exceeding 1.5 mm; mandibles exceptionally long, their length measured from insertion to tip exceeding the head width. . . . . *Prionogenys rouxi* Emery
   Smaller species, head width never exceeding 1.2 mm; mandibles shorter, their length much less than the head width 2

2. Head entirely covered by coarse punctures, subopaque to opaque *Leptogenys punctata* Emery
   Head entirely smooth and shining 3

3. Larger species, head width not less than 0.90 mm; posterior corners of petiolar node seen from directly above forming distinct angles of 45-50° . . . . *Leptogenys acutangula* Emery
   Smaller species, head width not exceeding 0.75 mm; posterior corners of petiolar node seen from directly above thick and broadly rounded *Leptogenys sagaris* Wilson

LEPTOGENYS ACUTANGULA Emery

Leptogenys (*Lobopelta*) *acutangula* Emery, 1914, Nova Caledonia, 1: 398-399, pl. 13, fig. 2a, worker. Original localities: Vallée de la Ngoï, 200 m.; Yaté. (Syntype examined — Emery Coll.)

Leptogenys (*Lobopelta*) *acutangula* var. *brevinoda* Emery, *ibid.*, p. 399, pl. 13, fig. 2b, ergatogyne. Type locality: Vallée de la Ngoï. NEW SYNONYMY.

Material examined. NEW CALEDONIA: Ciu, 300 m. (Wilson, acc. nos. 196, 197, 198, 199, 227, 230, 237, 282).

Taxonomic notes. As Emery suggested in his original description of var. *brevinoda*, this form is nothing more than the ergatogyne of *acutangula*. Individuals were taken by the present author on three occasions in association with typical *acutangula* workers (acc. nos. 198, 199, 282).

L. acutangula is clearly a member of the Australian *conigera* group. Of all the Indo-Australian species examined during the present study, it is most closely approached by an undescribed species of the *conigera* group represented by a single series in the Museum of Comparative Zoology from Mt. Carbine, Queensland (P. J. Darlington). The two species share, among other characters, the angulate posterior petiolar corners in the worker caste.

Ecological notes. This species was one of the most abundant ants encountered in the isolated woodlot on the Fèré property at Ciu. Colonies were found occupying well formed chambers and galleries in the soil beneath rocks. Three colonies removed entire and examined consisted in each case of a single ergatogyne and approximately fifty workers. Callow males were found in one nest, on December 21, 1954. In the less disturbed forest near the Ciu Falls only a single colony was encountered; this was nesting in a small rotting log buried in thick leaf litter.

LEPTOGENYS PUNCTATA Emery

Leptogenys (Lobopelta) punctata Emery, 1914, Nova Caledonia, 1: 398, worker. Type locality: Coné, New Caledonia. (Syntype examined—Emery Coll.)

Material examined. NEW CALEDONIA: Coné (syntype); Ciu, 300 m. (Wilson, acc. nos. 228, 262).

Taxonomic notes. The Ciu specimens have distinctly lighter body sculpturing than the syntype but are otherwise nearly identical to this specimen. *L. punctata* is not closely related to any other Australian or Melanesian species known to me. Its worker caste is very similar to that of *L. punctiventris* Mayr, a widespread Indomalayan species, but the males of the two species are quite different, particularly in genitalic structure.

Ecological notes. One colony was collected in the Féré woodlot and one in the forest east of the Canala River. Each was nesting in the soil beneath a rock and contained probably less than a hundred workers. Males were found in the Canala River nest, on December 31, 1954.

LEPTOGENYS SAGARIS Wilson, n. sp.

(Figure 5)

Diagnosis (worker). Closely resembling *L. anitae* Forel of Queensland, differing principally in the following characters:

(1) Distinctly smaller in size. Head width of *sagaris* types 0.64-0.69 mm; head width in two nest series of *anitae* examined not less than 0.82 mm.

(2) Eyes proportionately smaller in size. In *sagaris* there are only five to six ommatidia along the maximum length of the eye, while in *anitae* there are approximately twelve to sixteen ommatidia along the same line of measurement.

(3) Petiolar node proportionately shorter in *sagaris.*

The above diagnosis will also serve to distinguish *L. sagaris* from its nearest Melanesian relative, *L. bituberculata* Emery. The latter species is further distinguished from both *sagaris* and *anitae* by the following characters: body pilosity proportionately longer; head tapering more posteriorly when viewed in full face; dorsal border of petiolar node viewed from the side descending more abruptly in an anterior direction.

Holotype worker. HW 0.67 mm, HL 0.97 mm, SL 0.83 mm, CI 69, SI 124, EL 0.12 mm, PW 0.53 mm, petiolar node height 0.69 mm, petiolar node length 0.56 mm, dorsal petiole width 0.35 mm.

Paratype worker variation. HW 0.64-0.69 mm (encompassed by a single nest series, acc. no. 240). The paratype series shows very little variation in external morphology.

Ergatogyne. HW 0.64 mm, HL 0.89 mm, SL 0.73 mm, CI 72, SI 114, EL 0.12 mm, PW 0.48 mm, petiolar node height 0.41 mm, petiolar node length 0.38 mm, dorsal petiole width 0.40 mm. The single individual examined (acc. no. 272) is very worker-like. The head is very similar to that of a small worker, lacking ocelli and showing no enlargement of the compound eyes. The alitrunk is smaller proportionate to the head than in the worker. A distinct metanotal groove is present which is lacking in the worker. The petiolar node is much shorter and broader than in the worker; seen from the side it approximates an isosceles triangle in outline, with a broadly rounded dorsal border. The gaster is large, its volume exceeding by 1.5 X that of a large worker.

Material examined. NEW CALEDONIA: Ciu, 300 m.; holotype nest series, Wilson acc. no. 272, one ergatogyne and 9 workers; acc. no. 230, one worker; acc. no. 240, 9 workers. Chapeau Gendarme, one worker.

Ecological notes. My accession no. 240 consisted of a colony found nesting under a rock on the floor of the Fèré woodlot. It contained an estimated 50-75 adult workers. The holotype nest series (no. 272) was taken from a colony nesting in a small rotting log buried in leaf litter in the Canala River forest. It contained an ergatogyne and an undetermined number of workers. As in the related species *L. bituberculata* and *L. hebrideana*, the workers of *sagaris* are relatively timid and fast, and scatter quickly when the nest is opened.

PRIONOGENYS ROUXI Emery

Prionogenys rouxi Emery, 1914, Nova Caledonia, 1: 399-400, pl. 13, fig. 3, worker. Type locality: Mt. Canala, 700 m., New Caledonia.

Material examined. NEW CALEDONIA: Fèré woodlot, Ciu. 300 m. (Wilson, acc. nos. 189, 303, 304).

Taxonomic notes. This species appears to be distinguished from the species of *Leptogenys* solely by its aberrant head form. In particular, the mandibles are extremely elongate, their length measured from insertion to tip nearly as great as the head length (standard measure); the masticatory borders are lined with distinctive stiff sensory hairs that project out at 60° and criss-cross when the mandibles are closed; and the eyes are placed far forward on the head, their anterior margins being less than maximum-eye-length distance from the mandibular insertions.

As far as I have been able to ascertain, *P. rouxi* is not marked by any other characters, in external morphology, that might be construed to be of generic magnitude. In fact, it bears a particular resemblance in body structure to *Leptogenys acutangula* and other members of the *L. conigera* group. The ergatogyne, collected for the first time during the present study, differs from the worker caste in the same manner already indicated by Emery for *L. acutangula*, i.e., ocelli lacking, head size about that of a small worker, alitrunk proportionately smaller relative to head size than in the worker, gaster approaching twice the volume of that of connidal workers, metanotal groove better developed, the petiolar node much shorter and broader.

The male of *P. rouxi*, also collected for the first time in 1954-55, shows no truly remarkable characteristics. Compared with *Leptogenys acutangula*, only two differences seem noteworthy: in

P. rouxi, the notaulices are better developed, and the subgenital plate is much shorter and lacks the paired posterior marginal hooks that are present in *L. acutangula*. Both of these structures, however, are extremely variable within *Leptogenys* and do not at the present time seem to offer much opportunity for generic divisions.

The precise relationships of *P. rouxi* are in need of further study. As noted already, the species bears a distinct resemblance to *L. acutangula*, appearing closer to this species than to any other known Melanesian species, and indeed may have been derived phylogenetically from *acutangula*, a common ancestral species, or a related Australian member of the *conigera* group.

Account must also be taken of the relationship of *P. rouxi* to the generitype *P. podenzanai* Emery of Queensland. The two species resemble each other, at least superficially, in several important features, including the peculiarly elongate mandibles. forward position of the eyes, and *conigera*-type structure of the petiolar node. But *podenzanai* differs strikingly from *rouxi* in the possession of well developed mandibular teeth, which are completely lacking in *rouxi*. There is an excellent possibility that further study will show that the *Prionogenys* diagnostic characters were evolved independently in the two species, in which case *Prionogenys* will have to be placed in the synonymy of *Leptogenys*, or else a separate monotypic genus erected to receive *rouxi*.

Ecological notes. All three of the colonies of *P. rouxi* found at Cin were in the Fèré woodlot. Each was nesting under a flat rock embedded in the soil. The nest of colony no. 189, discovered on December 21, 1954, consisted principally of a flat, irregular chamber about 10 centimeters in maximum diameter; a lateral gallery led for a short distance to the base of a small stump adjacent to the covering rock, and then descended vertically to a depth of approximately 12 centimeters. The colony contained an estimated 55 workers, 25 worker cocoons, 20 larvae at various stages of development, and an undetermined number of eggs. The ergatogyne, if present, was not recovered.

Colony no. 303, collected on January 3, 1955, was lodged in a single gallery, approximately 2.5 cm. in diameter and 10 cm. in length, that led from beneath a rock into the soil at one side.

It contained a single ergatogyne and an estimated 30 workers, 6 callow males, 20 cocoons of undetermined caste, and an undetermined number of larvae at various stages of development.

Colony no. 304, also collected on January 3, occupied a nest very similar to that of no. 303. It contained an ergatogyne and an estimated 40 workers, 6 callow males, and an undetermined quantity of brood.

Prionogenys rouxi is a very shy, timid species, and the colonies scatter swiftly when their nest is exposed. When captured and handled, the workers open their mandibles to a 90° angle in a threatening posture and are capable of inflicting a painful sting. The central nest chamber of colony no. 189 was partially filled with the chitinous remains of isopods and earwigs. Both types of arthropods are a prominent part of the cryptofauna at Ciu and are assumed to serve as the chief, if not exclusive, prey of the *Prionogenys*. It is probable that the workers are primarily nocturnal in habit, since they were never found foraging above ground in the vicinity of the nests during the day.

II. THE TRIBES AMBLYOPONINI AND PLATYTHYREINI

This section deals with five genera, *Amblyopone*, *Myopopone*, *Prionopelta*, *Mystrium*, and *Platythyrea*, represented by a small number of species mostly limited within Melanesia to New Guinea, the Bismarck Archipelago, and Solomon Islands. No member of these genera has yet been recorded from the Fiji Islands, while New Caledonia is known to harbor only two endemic species: *Amblyopone australis* Erichson, which is widespread in other parts of Melanesia as well as in Australia and Tasmania, and *Prionopelta brocha* n. sp., a remarkable relict form with primitive features reminiscent of *Amblyopone*. Western Melanesia contains a zoogeographic mixture, including old endemics (*Amblyopone celata*, *Prionopelta majuscula*), probable Indo-Malayan immigrants (*Myopopone castanea*, *Platythyrea* spp.), and a single probable Australian immigrant (*Amblyopone australis*). Certain species, e.g. *Myopopone castanea* and *Platythyrea parallela*, are widely distributed over the islands and are among the dominant ants in the lowland rain forests there.

AMBLYOPONE Erichson

Key to the species, based on the worker caste

Fontal carinae separated by a wide space; larger species, head width never less than 1.32 mm (widespread in Melanesia) *australis* Erichson

Frontal carinae contiguous; smaller species, head width not exceeding 0.64 mm (Solomons) *celata* Mann

AMBLYOPONE AUSTRALIS Erichson

Amblyopone australis Erichson, 1841, Arch. Naturgesch., 8: 261, pl. 5, fig. 7, worker. Type locality: Woolnorth, Tasmania.

Amblyopone laevidens Emery, 1887, Ann. Mus. Civ. Stor. Nat. Genova, 25: 447 worker. Type locality: Hatam, Arfak Mts., Neth. New Guinea. NEW SYNONYMY.

Amblyopone levidens, Mann, 1919, Bull. Mus. Comp. Zool. 63: 281.

Amblyopone australis subsp. *levidens*, Wheeler, 1927, Proc. Amer. Acad. Arts Sci., 62: 12.

Amblyopone nana Emery, 1914, Nova Caledonia, 1: 394-395, worker, queen. Original localities: Mt. Panié, 500 m., and Mt. Canala, 700 m., New Caledonia. NEW SYNONYMY.

Amblyopone australis subsp. *nana*, Wheeler, 1927, *op. cit.*, 16.

Material examined. N.-E. NEW GUINEA: Joangeng, 1500 m. (E. O. Wilson, no. 752); Ebabaang, 1400 m. (Wilson, no. 819). NEW HEBRIDES: Tanna (L. E. Cheesman). Mann (1919) records this species from near Fourafi, in the mountainous interior of Malaita, Solomon Islands. Outside western and central Melanesia, *A. australis* is widespread in Australia and occurs on Tasmania, New Caledonia, Norfolk I., Lord Howe I., and New Zealand. According to W. L. Brown (pers. commun.), the New Zealand population was probably introduced by man from Australia and is currently limited to the vicinity of cities and towns on North Island.

Taxonomic notes. In the present review I have followed Wheeler (1927) in considering *laevidens* and *nana* as no more than geographic forms of the widespread and highly variable *australis.* The New Guinea workers examined (*laevidens*) are relatively large, darkly colored, and with smooth dorsal mandibular surfaces. In these characters they most closely resemble material from Queensland and New Zealand. In contrast, the Tanna, New Hebrides, workers (*nana*) are small, light colored, and with heavily striate dorsal mandibular surfaces. They most closely resemble specimens from New Caledonia (*fide* Emery's description of the *nana* types) and southeastern Australia.

Ecological notes. At Ebabaang workers were found scattered under the bark of a large "Zoraptera-stage" rotting log in second-growth midmountain rain forest. At Joangeng a lone dealate queen was found under the bark of a log in a forest clearing. It is noteworthy that the western Melanesian collections, including that of the *laevidens* type and Mann's Solomons collection, were all made at higher elevations in cool forest zones. If this is indicative of its true distribution, *A. australis* makes only limited contact with its closest ecological equivalent in this area, *Myopopone castanea*, a predominantly lowland species.

AMBLYOPONE CELATA (Mann)

Stigmatomma (*Fulakora*) *celata* Mann, 1919, Bull. Mus. Comp. Zool., 63: 279-281, fig. 2, worker. Type locality: Fulakora, Santa Isabel, Solomons. (Syntypes examined — MCZ.)

Known from type material only. In his original description Mann records this species from additional Solomons localities: Auki, Malaita; Tulagi, Florida; Wai-ai, San Cristoval. He found it nesting in small colonies under rocks on the floor of lowland rain forests.

MYOPOPONE Roger

Key to the species, based on the worker caste

Dorsal surface of petiole bearing only scattered piligerous foveae, the extensive interspaces completely smooth and shining (Moluccas to Solomons) . *castanea* (Fr. Smith)

Dorsal surface of petiole longitudinally rugulose and subopaque (Moluccas only) *beccarii* Emery

MYOPOPONE BECCARII Emery

Myopopone Beccarii Emery, 1887, Ann. Mus. Civ. Stor. Nat. Genova, (2)5: 447-448, worker. Type locality: Ternate.

Known from type material only. According to Emery, this species differs from *M. castanea* principally in the following characters: mesonotum and petiole longitudinally rugulose, cephalic "striation" more extensive, and propodeal and dorsal petiolar foveae elongated into weak sulci.

MYOPOPONE CASTANEA (Fr. Smith)

Amblyopone castaneus Fr. Smith, 1860, J. Linn. Soc. Zool., 5 (suppl.): 105, pl. 1, fig. 6, worker. Type locality: Batjan. (Holotype examined — Oxford University Museum).

Myopopone rufula Roger, 1861, Berl. Ent. Z., 5: 52, worker. Type locality: Batjan.

Myopopone castanea, Forel, 1901, Mitt. Zool. Mus. Berl., 2: 5.

Myopopone castanea, Mann, 1919, Bull. Mus. Comp. Zool. 63: 281, distribution.

Myopopone moelleri, Santschi, 1932, Mém. Mus. Nat. Hist. Belg., 4: 11. *Nec M. moelleri* Bingham.

Myopopone picea Donisthorpe, 1938, Ann. Mag. Nat. Hist., (11)2: 493, worker. Type locality: Mt. Dulit, Sarawak. (Holotype examined — BMNH). NEW SYNONYMY.

Myopopone wollastoni Donisthorpe, 1942, Ent. Mon. Mag., 78: 29, queen. Type locality: Mimika River, Neth. New Guinea. (Holotype examined — BMNH). NEW SYNONYMY.

Myopopone smithi Donisthorpe, 1946, Ann. Mag. Nat. Hist., (11)13: 577, queen. Type locality: Nadzab, Markham Valley, N.-E. New Guinea. NEW SYNONYMY (provisional).

Myopopone rossi Donisthorpe, 1947, Ann. Mag. Nat. Hist., (11)14: 297-299, worker. Type locality: Finschhafen, N.-E. New Guinea. (Holotype examined — CAS). NEW SYNONYMY.

Myopopone similis Donisthorpe, 1949, Ann. Mag. Nat. Hist., (12)1: 488, queen. Type locality: Maffin Bay, Neth. New Guinea. (Holotype examined — CAS). NEW SYNONYMY.

Material examined. MOLUCCAS: Batjan (*castanea* holotype). NETH. NEW GUINEA: Maffin Bay (*similis* holotype). N.-E. NEW GUINEA: Finschhafen (*rossi* holotype); Tor River. PAPUA: Karema, Brown River (Wilson, no. 566); Bisianumu, 500 m. (Wilson, no. 652). SOLOMONS: Tenaru River, Guadalcanal (G. E. Bohart); Simba Mission, Bougainville (E. J. Ford, Jr.); Tulagi, Florida (W. M. Mann); Siota, Florida (Bohart); Fulakora, Santa Isabel (Mann); Lambeti, New Georgia (Mann); Star Harbor, Wai-ai, San Cristoval (Mann). In addition to the material listed above, I have seen series from Hainan, Sumatra, Borneo, Philippines, and North Queensland.

Taxonomic notes. This species shows considerable geographic variation in at least four independent characters, as indicated in the accompanying table. It is the author's present view that

GEOGRAPHIC VARIATION IN MYOPOPONE CASTANEA

Locality	Subpetiolar Process (Side View)	Cephalic Sculpturing	Sculpturing of Dorsal Surface of Petiolar Node	Sculpturing of First Two Gastric Tergites
Hainan	about as long as broad; apex posteriorly acute	feebly rugose	sparsely punctate; post.-central area non-striolate	finely punctate
Labuan I., N. Borneo	twice as long as broad; apex rounded	shallowly furrowed and punctate	sparsely punctate; post.-central area non-striolate	smooth and shining
Sindanglaja, Java	?	moderately rugose	moderately punctate; post.-central area non-striolate	densely punctate
Engano I., near Sumatra	about as long as broad; apex rounded	moderately rugose	moderately punctate; post.-central area non-striolate	densely punctate
N. Palawan (var. *proxima* Stitz syntype)	about 1.5 × longer than broad; apex rounded	shallowly furrowed and punctate	moderately punctate; post.-central area non-striolate	feebly shagreened
Philippine Islands — various localities	about 1.5 × longer than broad; apex rounded	shallowly furrowed and punctate	moderately punctate; post.-central area non-striolate	first tergite feebly shagreened, second smooth
Bisianumu, Papua	distinctly shorter than broad; apex rounded	moderately rugose	sparsely foveate; post.-central area non-striolate	smooth and shining
Finschhafen, N.-E. New Guinea	distinctly shorter than broad; apex rounded	moderately rugose	sparsely foveate; post.-central area striolate	feebly shagreened
Tor R., Neth. New Guinea	distinctly shorter than broad; apex rounded	moderately rugose	sparsely foveate; post.-central area striolate	feebly shagreened
Various Solomons localities	distinctly shorter than broad; apex rounded	moderately rugose	sparsely foveate; post.-central area striolate	feebly shagreened
McIlwraith Range, N. Queensland	distinctly shorter than broad; apex rounded	moderately rugose	sparsely foveate; post.-central area striolate	feebly shagreened

all of the Melanesian material examined, including the types of the several included Donisthorpe species, belongs to the single species *M. castanea*. The Philippine series,[1] on the other hand, appear sufficiently divergent to rank as a separate species and may be considered so by future revisers of *Myopopone*. The queen of *castanea* differs strikingly from the worker in its much larger size, darker color, and more extensive and deeper cephalic sculpturing. This circumstance has led to taxonomic confusion in the past and was undoubtedly the principal source of inspiration for the numerous new names proposed by Donisthorpe.

Ecological notes. Both the Karema and Bisianumu collections consisted of workers found under the thick bark of large rotting logs on the floor of rain forests. At Bisianumu workers were clustered with larvae around two large, freshly killed cerambycid larvae on the same log. Since the beetle larvae were well separated from one another, and appeared to be too large for the ants to transport through the preformed galleries under the bark, it is inferred that the ants had transferred their own larvae to feed on the prey after the latter had been attacked and killed. The *Myopopone* are singularly clumsy and shy ants, and immediately commence searching for cover when exposed to light, abandoning their brood in the process. When handled, however, they are capable of inflicting a painful sting.

PRIONOPELTA Mayr

Key to the species, based on the worker caste

1. Larger species, head width of single known specimen 0.64 mm; genal teeth strongly developed, at least 0.03 mm in length (New Caledonia) . . . . *brocha* Wilson
   Smaller species, head width not exceeding 0.54 mm; genal teeth feebly developed, not exceeding 0.01 mm in length (New Guinea) . 2

2. Cephalic and thoracic dorsa finely punctate and feebly shining; larger species, head width at least 0.48 mm . . . . *majuscula* Emery
   Cephalic and thoracic dorsa densely and coarsely punctate and opaque; smaller species, head width not exceeding 0.42 mm . . . . *opaca* Emery

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[1] Including a syntype worker of *M. castanea* var. *proxima* Stitz (MCZ).

Prionopelta brocha Wilson, n. sp.

Figure 7

Diagnosis. Distinguished in the worker caste from all other known members of the genus by several apparently primitive characters, including exceptionally large size, strongly developed genal teeth, and *Amblyopone*-like head shape. Two features of head shape are considered to be more typical of *Amblyopone* than of *Prionopelta* — the head is broadest near its anterior end, and the lateral borders are relatively straight. *Brocha* is thus seen to be a species intermediate in position between the remainder of *Prionopelta* and the presumably more primitive *Amblyopone*. It has been placed in *Prionopelta* primarily because of its mandible form, which is typical for that genus.

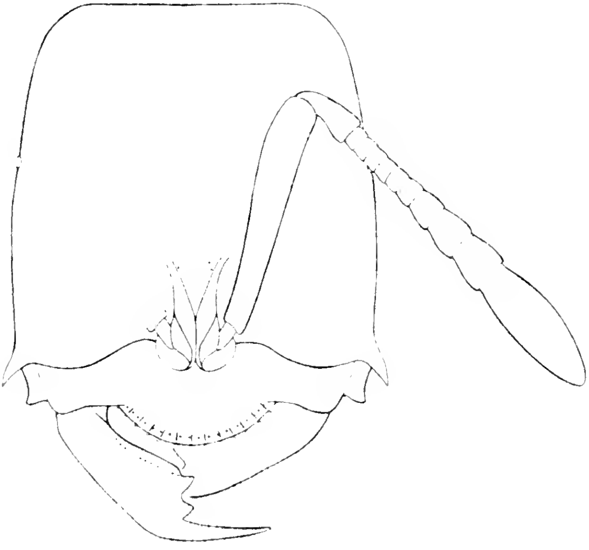

Fig. 7. ***Prionopelta brocha*** **n. sp., head of holotype worker.** Drawing by Mrs. **Nancy Buffler.**

Holotype worker. HW (exclusive of genal teeth) 0.64 mm, HL 0.79 mm, ML 0.16 mm, SL 0.45 mm, CI 81, SI 70, PW 0.43

mm, alitrunk length (maximum) 1.05 mm, dorsal petiole width 0.38 mm, petiolar node length (exclusive of ventral lobe) 0.42 mm, width of first gastric tergite 0.52 mm. Head as shown in Figure 7. Remainder of body similar to that of other *Prionopelta*, including the relatively large *majuscula* Emery.

Dorsal surfaces of mandibles finely and longitudinally striolate, and shining. Central portion of clypeus smooth and shining. Remainder of head covered by coarse, contiguous punctures, its surface for the most part completely opaque. Body posterior to the head sparsely punctate, its surface almost entirely feebly shining.

Pilosity very similar to that of most other *Prionopelta*, including *majuscula*. Abundant standing hairs present on most body and appendage surfaces, nearly or completely absent from posterior propodeal face, anterior and ventral surfaces of petiolar node, and most of extensor surfaces of legs; everywhere grading into equally abundant, predominantly oblique underlying pubescence.

Body uniformly light ferruginous, appendages clear to very light reddish yellow.

Material examined. NEW CALEDONIA: Mt. Mou, 180 m., December 12, 1954, a single worker (E. O. Wilson). This specimen was collected by means of a Berlese funnel from leaf litter on the floor of dry, semi-deciduous native forest.

PRIONOPELTA MAJUSCULA Emery

Ponera simillima Fr. Smith, 1860, J. Linn. Soc. Zool., 5 (suppl.): 105, worker. *Nec Ponera simillima* Fr. Smith, *ibid.*, p. 104 (= *Ponera diminuta* Fr. Smith).

Prionopelta majuscula Emery, 1897, Természetr. Füz., 20: 595, worker, queen. Type locality: Beliao I., near Friedrich-Wilhelmshafen (= Madang), N.-E. New Guinea.

?*Rhopalopone simillima*, Emery, 1911, Gen. Ins., 118: 35. (Generic re-allocation for *Ponera simillima* Fr. Smith, 1860, p. 105).

Prionopelta poultoni Donisthorpe, 1932, Ann. Mag. Nat. Hist., (10)10: 462, nom. pro *Ponera simillima* Fr. Smith, 1860, p. 105. Synonymy by Brown, 1953, Breviora, no. 11: 12.

Renea testacea Donisthorpe, 1947, Ann. Mag. Nat. Hist., (11)14: 183-186, fig., worker, queen. Type locality: Maffin Bay, Neth. New Guinea. Synonymy by Brown, *loc. cit.* (Syntypes examined — CAS).

Examblyopone churchilli Donisthorpe, 1949, Ann. Mag. Nat. Hist., (12)2: 401-402, queen. Type localtiy: Maffin Bay, Neth. New Guinea. Synonymy by Brown, *loc cit.* (Holotype examined — CAS).

Taxonomic note. Through the courtesy of Dr. E. S. Ross, I have been able to re-examine the type series of *Renea testacea* Donisthorpe and *Examblyopone churchilli* Donisthorpe and to confirm the earlier opinion of Brown that these two forms are unqualified synonyms of *P. majuscula.*

PRIONOPELTA OPACA Emery

Prionopelta opaca Emery, 1897, Természetr. Füz., 20: 596, pl. 15, figs. 44 45, worker, queen, male. Type locality: N.-E. New Guinea.

Prionopelta Mocsáryi Forel, 1907, Ann. Mus. Nat. Hungar., 5: 1, worker. Type locality: Asunción, Paraguay (Anisits leg.). NEW SYNONYMY (provisional; see below).

Material examined. N.-E. NEW GUINEA: Nadzab (Wilson, no. 1089); Bubia (Wilson, no. 687); lower Busu River (Wilson. nos 899, 963, 978); Wamuki, 800 m. (Wilson, no. 846). PAPUA: Karema (Wilson, nos. 563, 573, 575); Bisianumu, 500 m. (Wilson, no. 636). This species also occurs in Micronesia.

Taxonomic notes. A single worker collected in the mountains near Wamuki is slightly larger than all of the other specimens examined, including those from nearby localities in the lowlands (head width 0.39 mm as opposed to maximum head width in other material measured of 0.38 mm).

Dr. W. L. Brown has transmitted the following unpublished note concerning the status of *Prionopelta mocsaryi*: "A worker type of *P. mocsaryi* received from the Hungarian National Museum can not be distinguished from *P. opaca* samples from New Guinea (Wilson, Biró leg.) in any character, after long and careful examination and comparison. Since the original Biró New Guinea collections were housed in the Hungarian National Museum, and since some of this New Guinea material is known to have been included in the series sent Forel for his 1907 study, it seems likely that the label 'Paraguay/Anisits' is misplaced. No specimen of *Prionopelta* anything like this one has been reported a second time from the Americas, although other species of the genus have all been collected repeatedly in tropical America. My conclusion is that *P. mocsaryi* should be added to the synonymy of *P. opaca*."

Ecological notes. This species was found in a wide range of major habitats in New Guinea: dry, open tropical evergreen forest at Nadzab, foothills rain forest at Bisianumu and Wamuki, and primary lowland rain forest at the Busu River. Stray workers were very common on the forest floor, and could easily be secured by tapping loose material from the bottoms of small pieces of rotting wood buried in leaf litter. They also turned up frequently in leaf-litter berlesates. A single colony found at Karema was nesting in a rotting section of tree branch on the forest floor. It contained between 15 and 20 workers and a small quantity of brood.

MYSTRIUM Roger

MYSTRIUM CAMILLAE Emery

Mystrium Camillae Emery, 1889, Ann. Mus. Civ. Stor. Nat. Genova, 27: 491, pl. 10, figs. 1-3, worker, queen. Type locality: Bhamo, Burma. Wheeler and Chapman, 1925, Philippine J. Sci., 28: 55, dist. Karawajew, 1925, Konowia, 4: 73, dist. Brown, 1952, Psyche, 59: 25, dist.

A single male, collected by E. S. Ross at Maffin Bay, Neth. New Guinea, in July, 1944, has been tentatively determined as this species. Although this is the first time *Mystrium* has been recorded from Melanesia, its occurrence there is not surprising, since *M. camillae* was already known from the Philippines (Wheeler and Chapman, 1925), Java (Karawajew, 1925), and Northern Territory, Australia (Brown, 1952).

PLATYTHYREA Roger

Seen from above, the posterior border of the petiolar node is deeply concave, and its posterior corners are drawn out into long, flattened, blunt processes . . . *quadridenta* Donisthorpe

Seen from above, the posterior border of the petiolar node is sinuate, while its posterior corners are not drawn out into processes *parallela* (Fr. Smith)

PLATYTHREA PARALLELA (Fr. Smith)

Ponera parallela Fr. Smith, 1859, J. Linn. Soc. Zool., 3: 143, worker. Type locality: Aru. Donisthorpe, 1932, Ann. Mag. Nat. Hist., (10)10: 454, worker. *Ibid.*, 1943, (11)10: 434-435, male, doubtfully associated. (Holotype examined — Oxford University Museum).

Pachycondyla melancholica Fr. Smith, 1865, J. Linn. Soc. Zool., 8: 71, worker. Type locality: Morotai. NEW SYNONYMY (provisional).

Platythyrea pusilla Emery, 1893, Rev. Suisse Zool., 1: 188-189, worker. Type locality: Amboina. (Holotype examined — Emery Coll.). NEW SYNONYMY.

Platythyrea coxalis Emery, 1893, *ibid.*, p. 189, nota, worker. Type locality: Perak, Malaya. (Holotype examined — Emery Coll.). NEW SYNONYMY.

Platythyrea melancholica var. *aruana* Karawajew, 1925, Konowia, 4: 75, worker. Type locality: Wammar I., Aru Archipelago. NEW SYNONYMY (provisional).

Material examined. MOLUCCAS: Kalam I., Halmahera (C. S. Banks); Amboina (*pusilla* holotype). NETH. NEW GUINEA: Maffin Bay (E. S. Ross). N.-E. NEW GUINEA: Nadzab (Wilson, nos. 1086, 1090, 1097); Lae (N. L. H. Krauss); Bubia (Wilson, no. 683); Finschhafen (Ross). PAPUA: Bisianumu, 500 m. (Wilson, nos. 617, 644, 655, 659, 660). ARU: (holotype).

Taxonomic notes. This species shows non-geographic variation in several characters, notably total size, proportions of the petiolar node, form and placement of the petiolar teeth, sculpturing, and color, which is of similar magnitude to the differences separating many related species in other ponerine groups. Nevertheless, in an analysis of the sizable collections of material in the Museum of Comparative Zoology and Museo Civico di Storia Naturale, Genoa, I have been unable to detect any constant differences that might be construed as partitions along species lines. Variation in two of the characters, total size and relative thickness of the petiolar node, is indicated in the plot of petiolar length times width given in Figure 8. It can be seen that these data are distributed along a single regression zone. The other characters examined show a similar pattern of variation.

The form *melancholica* is placed in provisional synonymy here because of its inadequate definition in previous literature. The holotype is probably lost, since neither Donisthorpe (1932) nor the present author (in 1955) were able to find it among the extant Frederick Smith types. The chances are very remote that this specimen represented anything more than a variant of *P. parallela.*

Ecological notes. All of the author's collections consisted of stray workers found in leaf litter and rotting logs. At Nadzab a worker was found carrying a small moth larva in its mandibles.

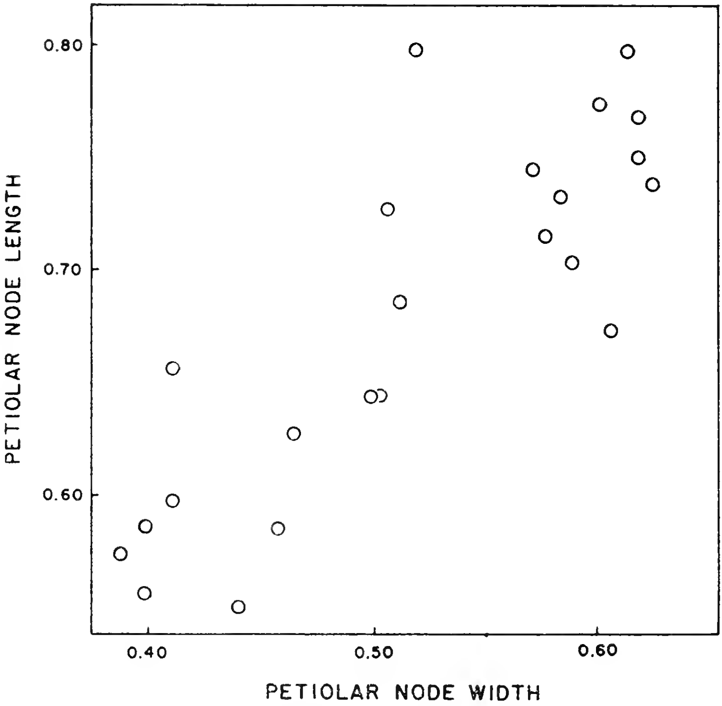

Fig. 8. Variation in petiolar node proportions in Indo-Papuan material of *Platythyrea parallela.* No more than two workers were measured from each nest series.

Platythyrea quadridenta Donisthorpe

Platythyrea quadridenta Donisthorpe, 1941, Ann. Mag. Nat. Hist., (11)7: 134, worker. Type locality: Wharton Range, Kokoda, Papua. (Syntype examined — BMNH).

Material examined. PAPUA: Wharton Range (syntype);

Karema, Brown River (Wilson, nos. 550, 570); Bisianumu, 500 m. (Wilson, no. 642).

Taxonomic note. *P. quadridenta* is closely related to the Indo-Malayan species *P. sagei* Forel, but can be easily separated by its smaller size, thicker petiolar node, and unique possession of abundant, short, erect hairs over most of the dorsal surface of the body.

Ecological note. At Karema a colony consisting of approximately 50 workers and an undetermined quantity of brood was found nesting under the bark of a large, "Zoraptera-stage" log on the forest floor.

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AT HARVARD COLLEGE

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THE FOSSIL CARNIVORE AMPHICYON INTERMEDIUS FROM THE THOMAS FARM MIOCENE. PART I: SKULL AND DENTITION

By Stanley J. Olsen
Florida Geological Survey

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM

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No. 4 — *The Fossil Carnivore* AMPHICYON INTERMEDIUS *from the Thomas Farm Miocene, Part I: Skull and Dentition*[1]

By STANLEY J. OLSEN

INTRODUCTION

The lower Miocene beds of the Thomas Farm quarry, located in north central Florida, have in recent years yielded numerous vertebrates that are complete enough to fill in many of the gaps in our knowledge of species originally described from fragmentary material. Among the rarer remains that fall in this category are those of the large carnivore *Amphicyon*, which was first recorded from the Gilchrist County deposit by Simpson (1932), who briefly described some specifically undetermined fragments. White (1940) described *Amphicyon intermedius* on a left mandible with incomplete dentition, and later (1942) described a second species, *A. longiramus*, based on a right mandible with $P_2 - M_2$.

In the time that has elapsed since these species were described, much new evidence has come to light. The present restudy was undertaken to determine if the characters given as diagnostic would hold up when subjected to analysis with a larger sample of specimens for comparison. Variation in *Canis lupus* and *Ursus americanus*, which have to some degree a similar form and size in the skull and mandible, has also been taken into consideration.

All material used by White in his type descriptions has been examined, together with all specimens since found. Casts of the types of the majority of described North American species of *Amphicyon* have been available for comparison.

A discussion of the broader affinities of *Amphicyon* will be given in the paper describing the postcranial skeleton.

CANIDAE

AMPHICYONINAE

AMPHICYON Lartet

Amphicyon intermedius White

Figures 1 to 5

Amphicyon sp. Simpson, 1932, pp. 20, 21, fig. 5.
Amphicyon intermedius White, 1940, p. 32, pls. 3, 4.
Amphicyon longiramus White, 1942, pp. 6, 7, pl. 5.

Horizon and locality. Lower Miocene, Thomas Farm, Gilchrist County, Florida.

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[1] The postcranial skeleton will be treated in a subsequent contribution.

Material examined. M.C.Z. 3630, right mandible with $P_3 - M_1$, alveoli for M_{2-3}; 3631, left mandible with $P_3 - M_2$, alveoli for C, P_{1-2}, M_3 (type); 3632, left mandible with dm_4, and detached molars, alveoli for P_{1-3}, (original hypodigm); 3919, right mandible with $P_2 - M_2$, alveoli for $I_1 - P_1$, M_3 (type of *A. longiramus*); 4060, palate with left and right $P^4 - M^2$; 4424, partial braincase and sagittal crest; 5832, right $M_1 - M_2$; 5833, left M^1, M^2; 7140, restored skull; 7141, 16 miscellaneous teeth; 7142, left dm_4; 7143, left M^3. F.G.S. V-5257, right P_4; V-5258, trigonid of right M_2; V-5648, right M_1; V-5649, right M_2; V-5650, lower canine; V-5659, lower canine; V-5663, right M_2. U.F. 6501, nearly complete skull.

White distinguished this species as follows: ". . . intermediate in size between *A. frendens* Matthew and *A. superbus*[2] Peterson; diastema between P_2 and P_3 the longest yet recorded, . . . cusps of the molars resembling those of *A. sinapius* Matthew, but distinguished from that species by the smaller size and the greater length of the diastema between P_2 and P_3. It differs from *A. pontoni* Simpson in that M_2 is longer for its width, and that the basin between the hypocone and entocone[3] is shallower." *A. longiramus* was characterized by: "P_1 and M_3 single-rooted, M_3 with groove on outer side of root but not on the inner side, P_4 with heel and accessory cusp, two mental foramina . . . about one-fourth larger than the preceding, and differs from it also in the double-rooted P_2 and in the single-rooted M_3. In dental characters, in size, and in the relative proportions this form is difficult to distinguish from the jaws from the Snake Creek beds referred by Matthew to *A. sinapius* (Matthew, 1924) and perhaps does not merit specific designation."

Synonymy. Simpson (1932) referred a partial right M_2 (F.G.S. V-5258) and a right P_4 (F.G.S. V-5257) to *Amphicyon* sp. These specimens are morphologically indistinguishable from *A. intermedius* and must be referred to this species.

The stated differences between the two species of *Amphicyon* described by White are such that they can be attributed to individual variation and to age and do not appear to warrant taxonomic separation; examples of comparable dental variation are known in other carnivores.

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[2] This species was made the type of ***Daphoenodon*** (Peterson, 1909).

[3] Hypoconid and entoconid in this paper.

A wide range of variation in premolars, especially as regards numbers of roots, is of rather common occurrence in carnivores. Colbert for *Hemicyon teilhardi* (1939), Merriam for *Canis dirus* (1912), Scott (1890), and Matthew and Gidley (1904) for *Aelurodon haydeni*, Peterson (1910, pp. 213, 214) for *Daphoenodon superbus*, Hall (1928) and Simpson (1949) for *Ursus americanus*, Kurtén (1955) for *Ursus spelaeus* have all recorded variations of a similar nature to those used by White to establish *A. longiramus*, and have shown that they are individual in nature.

Furthermore, on comparing P_2 in the types of the two species, it is noticeable that P_2 in the type of *A. intermedius* is not fully single-rooted. The dividing wall in the alveolus is incipient but distinct. In an immature specimen (M.C.Z. 3632) referred by White to *A. intermedius*, the alveolus for P_2 is definitely for a double-rooted tooth. Measurements of the Thomas Farm rami show that, proportionately, the types of *A. intermedius* and *A. longiramus* are almost exactly comparable in dimensions to M.C.Z. 46547, the longest (and the oldest) and M.C.Z. 46553, the shortest (and the youngest) of a series of *Canis lupus* rami from Alaska[4]. The morphological differences, such as tooth cusp arrangement and pattern between *intermedius* and *longiramus*, are within the range of variation found in comparable groups of Recent carnivores.

I, therefore, believe that the species *longiramus* should be reduced to the synonymy of *A. intermedius*.

Amphicyon intermedius is now known also from the Garvin Gulley of Texas. The material will be described by Dr. J. A. Wilson.

It should be pointed out that caution must be exercised in comparing the type of *A. longiramus* (M.C.Z. 3919) with specimens of other members of this genus. It is an aberrant individual, at least in regard to the premolar region (Fig. 1A, and White, 1942, p. 5), having a fully formed P_4 that never erupted. I have figured this specimen (Fig. 1A), inasmuch as it is the only complete lower jaw of the Thomas Farm *Amphicyon* known to date. All measurements, with the exception of those anterior to P_2, are comparable to those of other specimens of the species.

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[4] Measurements taken by Dr. E. E. Williams and Prof. Bryan Patterson.

MORPHOLOGY

Skull and mandible (Figs. 1, 2 and 3). Although the skull of *Amphicyon intermedius* (Fig. 2) has been crushed and distorted to a certain extent, nevertheless the form is sufficiently well preserved that its characters may be readily seen and compared, without recourse to paper reconstructions or other means of interpretation usually resorted to in interpreting buckled or misshapen material.

The general form and proportions of the skull are more canid than ursid-like. One of the most prominent characters of the skull is the very high and strongly developed sagittal crest. This crest arises on the interparietal apex and terminates at a point which is midway along the median sagittal plane, and is much larger than the crest found in the Recent members of the Canidae and Ursidae or that which is present in the extinct genus *Hemicyon*, to which *Amphicyon* has been compared (Colbert, 1939; Frick, 1926). The base of this attachment for the powerful temporal muscle is formed by two compact layers of bone, separated by cancellous tissue, which tend to fuse into a denser structure at the sagittal suture. The structure of this crest was disclosed by a break. The smaller occipital crest runs laterally downward on either side to meet the heavy, expanded posterior roots of the zygomatic arches.

Since the described individual (U.F. 6501) is of advanced age, as evidenced by the worn condition of the dentition, it is difficult to determine the synostosed sutures or to distinguish them from the post-fossilization cracks, and thus nearly impossible to define the limits of the different bones of the skull roof and palate.

The braincase is quite small, in proportion to the rest of the skull, for a carnivore of this size. This observation is confirmed by another skull fragment (M.C.Z. 4424) which has a portion of the parietal and sagittal crest preserved in an undistorted condition.

The supraoccipital extends far back, to overhang the occipital condyles. The occiput is narrow and triangular as seen from the posterior view, having a central, vertical, occipital ridge much the same as *Hemicyon teilhardi* or the Recent members of *Canis*.

Although this ridge is also found in members of the Ursidae, the same region in these animals has less overhang and the occipital area tends to be more square in shape when viewed posteriorly.

Proportions of the frontals are much the same as those found in *Canis dirus* or *Canis lupus;* these bones have the "dished" appearance in the area of their union with the maxillaries and nasals — a condition not usually encountered in the bears.

The palate is long and narrow, expanding sharply posterior to P^4, much more so than in *Ursus* or *Hemicyon*, but to nearly the same degree when compared with that of *Canis*. The anterior palatine foramina have been destroyed but a remaining partial border of one of these openings locates them as being between the posterior margin of the canine alveolus and the anterior face of P^2. The posterior palatine foramina are present opposite M^2. The glenoid fossa of *A. intermedius* is shallower than that of *Canis*. There is a small postglenoid process, as in the bears and *Hemicyon*, rather than the definite recurved or hook-like process of the dog and wolf. The palatine-pterygoid area has been crushed and broken so that very little in the way of comparisons can be made with these elements.

Auditory region (Fig. 2C). The auditory region as a whole is of an ursid rather than of a canid type.

The bullae in *A. intermedius* are partially destroyed in the figured specimen, but this structure is known in *A. sinapius* (A.M.N.H. 18257), where it is flattened and flask-shaped and not highly inflated as in the bullae of the dog and wolf. As pointed out by Van der Klaauw, the name "bulla" is not very appropriate, in the literal sense, when applied to this region in the Ursidae (Van der Klaauw, 1931). This statement also holds true for the Amphicyoninae.

The external meatus, as in *Ursus americanus*, is quite long and exhibits the form of a gutter rather than that of a cylinder or closed tube as found in the Canidae. The superior roof of the meatus is formed by the squamosal (Segall, 1943).

The basioccipital in *A. intermedius* possesses wings or crests similar to those found on this element in the bears and *Daphoenus* but not in the dogs or wolves.

By far the largest single element of the auditory region is the paroccipital process which is composed of heavy, thickened bone having a deflected plane nearly parallel to that of the palate and forming the posterior border of the foramen lacerum posterius and the stylomastoid foramen.

In most cases, the courses of the various basicranial foramina cannot be followed to completion, due to the fragmentary nature of this area, and the fact that this entire region is supported by sand that has been artificially hardened in order to make the skull hold together, makes further preparation hazardous.

The condylar foramen is situated in much the same position as that found in *Ursus*. Immediately anterior to this opening is the foramen lacerum posterius which is the largest external opening in the auditory region. Located on the anterior and anteroexternal margins of this large opening are, respectively, the carotid canal (in part) and the stylomastoid foramen. This latter foramen forms a groove along the inner face of the mastoid process.

The eustachian opening and foramen lacerum medium are located at the junction of the postglenoid process with the squamosal, and are separated by a well defined wall into two surface openings instead of one as is present in *Ursus americanus*.

The foramen ovale and the foramen rotundum are located together, slightly anteromedial to the postglenoid process. Laterally and slightly anterior to these openings, there seems to be a part of a margin of what might be the alisphenoid canal but due to the damage in this particular area it is too doubtful to record as such with any degree of confidence.

The auditory region in *Amphicyon* and other primitive carnivores has been used as a clue to relationships for some time. However, this area does not give us a necromantic insight into the relationships of these animals. Hough, in speaking of the ties between primitive carnivores, has this to say: "The structure of the auditory region leaves no doubt of the affinity of *Daphoenodon* and *Amphicyon* or the relationship of these two genera to *Daphoenus*. . . . . It seems probable, therefore, that *Amphicyon* and *Daphoenodon* represent different branches of the same subfamily rather than having a directly ancestral relationship and that neither was in the direct line of the bears" (Hough, 1948a, pp. 598–600). Speaking of the same animals in a subsequent contribution (1948b, pp. 108, 109), Hough placed *Amphicyon* in the Ursidae and came to the following conclusions concerning this carnivore: "A dissection of the auditory region shows this region to be ursid. . . . There is no basis in the auditory region for the association of *Amphicyon* and *Daphoenus* . . . a close relationship with *Daphoenus* seems improbable."

Hough sums up the significance of the auditory region as a means of classification by pointing out that this area does preserve ancestral characters and that it would be a mistake to depend wholly upon it, or upon any one feature, in determining relationships.

The lower jaw is canid-like with the ascending ramus describing a gentle curve from $\overline{\mathrm{M}}_3$ to the apex of the coronoid process, as in the wolf and dog. In the bear and *Hemicyon* this same margin of the ascending ramus takes a vertical rise preceding the curve and ends in a decided, posteriorly deflected hook at the terminus of the coronoid process.

A single masseteric fossa occupies the greater portion of the ascending ramus in the Thomas Farm carnivore as compared to an additional premasseteric fossa in the mandible of *Hemicyon*.

The dental foramina in carnivores in general are subject to considerable variation both as to number and location and the use of these openings as specific keys is not practicable.

Dentition. The dental formula is $\mathrm{I}-\frac{3}{3}$, $\mathrm{C}-\frac{1}{1}$, $\mathrm{P}-\frac{4}{4}$, $\mathrm{M}-\frac{3}{3}$. The upper incisors are missing in the nearly complete skull but the alveolus for I^3 indicates that this was a heavier and larger tooth than the other two. The canines show the wear of an old adult, that of the right side being worn to a level of the gum line in life and the other to one-half of its original length. As noted by Matthew (1924, p. 105) for *Amphicyon*, it has a double cutting edge, and is similar in form to the corresponding lower tooth (Fig. 1C). Kurtén (1955) has found that the relative proportions of the canines in *Ursus spelaeus* show a stronger dimorphism than that found in the cheek teeth. Whether or not this will hold for *Amphicyon* is still to be determined. P^1 is missing on both sides but is a single-rooted tooth. P^2 is a simple, double-rooted structure with a slightly expanded heel, having no accessory cusp present in the known examples. P^3 has the same features as the preceding premolar with the exception of being larger and more expanded in the heel. P^4 is of a definite canid pattern. The protocone (=deuterocone) is at the antero-lingual end of the tooth instead of being more centrally located along the inner margin as it is in *Hemicyon* and the modern bears. M^1 is canid-like, being similar in proportion to the corresponding tooth in *Cynodesmus* and other primitive dogs, rather than having the more square outline found in *Hemicyon* and *Ursus americanus*. The metaconule found on M^1 and M^2 in *A. intermedius* is a variable character in other members of this genus.

M^2 is highly variable, both in size and form[5]. The examples found in the described skull differ but slightly from M^1 in general proportions, although the size and outline of this tooth do not adhere to a typical shape (Fig. 5). Both M^1 and M^2 are triple-rooted and exhibit considerable wear in the figured specimen (Figs. 2C, 4B). The heel in the upper molars of unworn specimens has fine crenulations along the cingulum, not unlike those found on the surface of these same teeth in the bears.

The alveoli for the third molars are perfectly preserved in the skull and furnish us with more accurate information concerning the location of these teeth than has been heretofore known. M^3 in *A. intermedius*, known only from a single specimen (M.C.Z. 7143), is a strongly developed single-rooted tooth, roughly oval in shape, having a single principal cusp, the paracone, and an internal cingulum of large proportions. The presence of M^3 has been the cause of much confusion in assigning specimens to the genus *Amphicyon*. In some cases it was the only reason given for the generic assignment. Although M^3 is typical of this genus, it is also present in several other canids, such as *Daphoenodon superbus* (originally described as *Amphicyon superbus*) and *Daphoenus*.

The proportions of the area occupied by the lower premolars in relation to the total jaw length are nearer to those of *Canis* than to those of *Ursus*. There is a wide variable diastema between each of the premolars, with no crowding evident in any of the known specimens. The canine as mentioned earlier is double-edged with

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[5] For similar variation in Recent Canidae see plates in Young and Jackson (1951), and Young and Goldman (1944).

fine serrations along these edges (Fig. 1C). The first premolar is single-rooted, and is absent in the known specimens of the jaw of this animal but its position is located by the alveolus. P_2 varies from a double-rooted tooth to one having a single root with an incipient division. The first three premolars have the same shape and cusp pattern as those found in the upper series and are progressively larger from P_1 to P_3. P_4 has a strong accessory cusp posterior to the principal cusp, and the cingulum is well defined. M_1, as in other members of this genus, has a high prominent protoconid with the metaconid posterior to it, with little or no separation between the two. The heel is large with the hypoconid and entoconid forming ridges on the labial and lingual edges. The talonid is expanded lingually being wider than the trigonid. The paraconid is a shearing cusp and is placed, in relation to the other cusps, as in *Canis*. The general structure of this lower carnassial is of a dog-like form. M_2 has three principal cusps; the metaconid and protoconid are equidistant from the anterior face of the tooth and of the same height. The hypoconid is prominent and is similar in form to that of M_1. The entoconid varies from being well defined to being subordinated in the cingulum. M_3 may be either single or double-rooted, judging from alveoli. Only one specimen of this tooth has been collected (M.C.Z. 7141); this is well preserved and single-rooted. As in the corresponding upper molar, it is roughly oval in shape with the principal cusp, the protoconid, situated on the anteroexternal margin. The heel has a cingulum which terminates in a small but distinct cusp just posterior to the protoconid.

The upper and lower dental series are not ursid-like and more nearly approach the canids in shape, form, and proportions.

Deciduous dentition (Fig. 3A, B). Very little is known of the immature dentition in *Amphicyon*. However, a note concerning the lower sectorial of *A. intermedius* is inserted here, if only as a warning to students of the possibility of confusing this deciduous tooth with an adult carnassial of one of the smaller carnivores found in the same quarry as *A. intermedius*.

Two specimens of dm_4 are known. One is associated with a nearly complete lower jaw (M.C.Z. 3632, Fig. 3A) and was referred to in White's description of *A. intermedius* (1940). The other is an isolated tooth (M.C.Z. 7142, Fig. 3B). The roots of both are spread in anteroposterior direction due to the pressure of the permanent tooth pushing up from below. This spreading of the roots in the milk molars, not present in the permanent dentition, is also obvious in many Recent carnivores. As may be seen from the figures, both teeth are well preserved and little worn.

During this study, I had occasion to refer to the type of *A. frendens* (A.M.N.H. 18913) which was described more than two decades ago (Matthew, 1924). Mrs. Rachel Nichols of the American Museum of Natural History brought to my attention the fact that this specimen has a supernumerary M_4 which has never erupted. This tooth was mentioned by Matthew but no detailed description was given. The tooth is circular and button-shaped with a principal, central cusp and two cuspules situated close together along the outer margin. The undersurface of the tooth is concave imparting a caplike structure to the whole. It is difficult to determine how the tooth was oriented in life, due to its circular structure and lack of identifying characters. It was situated well up in the ascending ramus, the walls of which are very thin around the crypt.

Comparison with other American species of *Amphicyon*

Amphicyon americanus Wortman, 1901. Type, Yale Peabody Museum 10061, upper Miocene, Nebraska.

This is a much smaller species than *A. intermedius*. The upper teeth, and the molars in particular, have quite different proportions from those of *A. intermedius*. The heel of M^1 is quite constricted with no noticeable metaconule. M^2 is very narrow compared to its length, with the metaconule absent. M^3 has the general form of *A. intermedius* but is, in the type at least, triple-rooted.

Amphicyon sinapius Matthew, 1902. A.M.N.H. 9358, upper Miocene, Colorado. Also A.M.N.H. 18258, 18257, 18259B; California Institute of Technology 207 (Stock, 1930), Miocene, Oregon; and California Institute of Technology 1621, 1622, 1616, 1619, 1620 (Bode, 1935), upper Miocene, California.

The type of this species, a right M_2, agrees fairly well with the Thomas Farm species, with the exception of being rather wider on the anterolabial surface. This is not a profound difference in such a variable tooth. The remaining teeth of the lower dentition (A.M.N.H. 18258) agree closely with those of *A. intermedius* (M.C.Z. 5832) except for the heavier heel and greater width of M_1 in the former. The paraconid of M_1 in *A. intermedius* tends to curve inward rather than maintain a straight line with the protoconid and hypoconid as it does in *A. sinapius.* The upper dentition in *A. sinapius* shows but little difference from that in *A. intermedius.*

Matthew found nothing to separate *A. amnicola* (Matthew and Cook, 1909; Cook, 1915) from *A. sinapius* and my comparisons of these species uphold Matthew's observations relating to this synonymy.

Amphicyon idoneus Matthew, 1924. Type, A.M.N.H. 18912, middle Miocene, Nebraska.

The skull and dentition (A.M.N.H. 20495) differ very little, if at all, from *A. sinapius;* Matthew noted that the only essential difference in this species from *A. sinapius* was its smaller size. If more material of this animal were available, I believe it would be found to be synonymous with *sinapius.*

Amphicyon frendens Matthew, 1924. Type, A.M.N.H. 18913, middle Miocene, Nebraska. California Institute of Technology 376, 377 (Gazin, 1932), Miocene, Oregon; California Institute of Technology 3192 (Wallace, 1946), Miocene, Oregon.

This species has a much shorter, heavier jaw proportionally than that of *A. intermedius* with nearly the same general form as *Osteoborus* and its relatives. P_2 has the same transverse crowding of the alveolus that is found in the borophagines, due to the short space occupied by these teeth. M_1 is a much heavier tooth with a higher hypoconid than that which is found in the other members of the genus *Amphicyon.* The upper dentition is also of a more robust nature than that possessed by *A. intermedius* but has the same cusp arrangement as those teeth in the Florida form.

Amphicyon pontoni Simpson, 1930. Type, Florida Geological Survey V-4112, lower Miocene of Florida.

The type, a left M_2 is morphologically indistinguishable from *A. intermedius*, but is much larger in size. There is a difference of 42 percent between it and the largest known M_2 of *A. intermedius.*

Amphicyon riggsi McGrew, 1939. Type, Chicago Natural History Museum P12029, upper Miocene, Montana.

A. riggsi has much shorter tooth rows than *A. intermedius*, with little or no diastema between the lower premolars. The heel of M_1 has a distinct swelling in the postero-external margin of the tooth that is peculiar to this species alone. Otherwise, this molar has the same general shape as in *A. sinapius.* The general form and shape of the upper dentition is the same as in other species of *Amphicyon,* with the exception of a concavity on the anterior base of the protocone of P^4 at its junction with the paracone.

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I wish to express my thanks to Professors A. S. Romer and Bryan Patterson for the full use of all of the *Amphicyon* material in the collections of the Museum of Comparative Zoology at Harvard University. Thanks are also due Dr. Herman Gunter, Director of the Florida Geological Survey, for permission to use the specimens which are a part of the collections in that institution, and to Dr. W. Auffenberg of the Biology Department of the University of Florida, for the loan of the fine skull of *A. intermedius,* which is a part of the collections of that university, and for permission to describe and figure the specimen.

The following people have aided me by furnishing casts of types or other related material in the collections under their care: Dr. G. G. Simpson and Mrs. R. H. Nichols of the American Museum of Natural History, Dr. H. J. Cook of Agate, Nebraska, Mr. W. D. Turnbull and Dr. E. C. Olson of the Chicago Natural History Museum and the University of Chicago, Dr. J. T. Gregory of Yale Peabody Museum and Dr. J. A. Wilson of the University of Texas.

The figures are the work of Mr. Andrew Janson, artist for the Florida Geological Survey.

TABLE OF MEASUREMENTS

All Measurements in Millimeters

REFERRED SPECIMENS AND SYNONYMS	Antero-Posterior Diameter M_1	Greatest Transverse Diameter M_1	Antero-Posterior Diameter M_2	Greatest Transverse Diameter M_2
A. intermedius F.G.S. V5648	33	17	....	....
A. intermedius M.C.Z. 5832	32.5	17.5	26	19
A. intermedius F.G.S. V5649	....	....	25.5	17
A. longiramus (Type) M.C.Z. 3919	32.5	17	23.5:	16.5
A. intermedius M.C.Z. 3632	....	....	23	15.5
A. intermedius F.G.S. V5663	....	....	21	15.5
A. intermedius (Type) M.C.Z. 3631	30	15.5	20.5	16
A. intermedius M.C.Z. 3630	29	14.5	....	....
	M^1	M^1	M^2	M^2
A. intermedius U.F. 6501	27.5	32.5	20.5	29.5
A. intermedius M.C.Z. 4060	26.5	30.5	21.5	29
A. intermedius M.C.Z. 5833	26	32	23	31.5
A. intermedius M.C.Z. 7140	24	29	19	26
A. intermedius M.C.Z. 7141 (in part)	....	....	19	26.5

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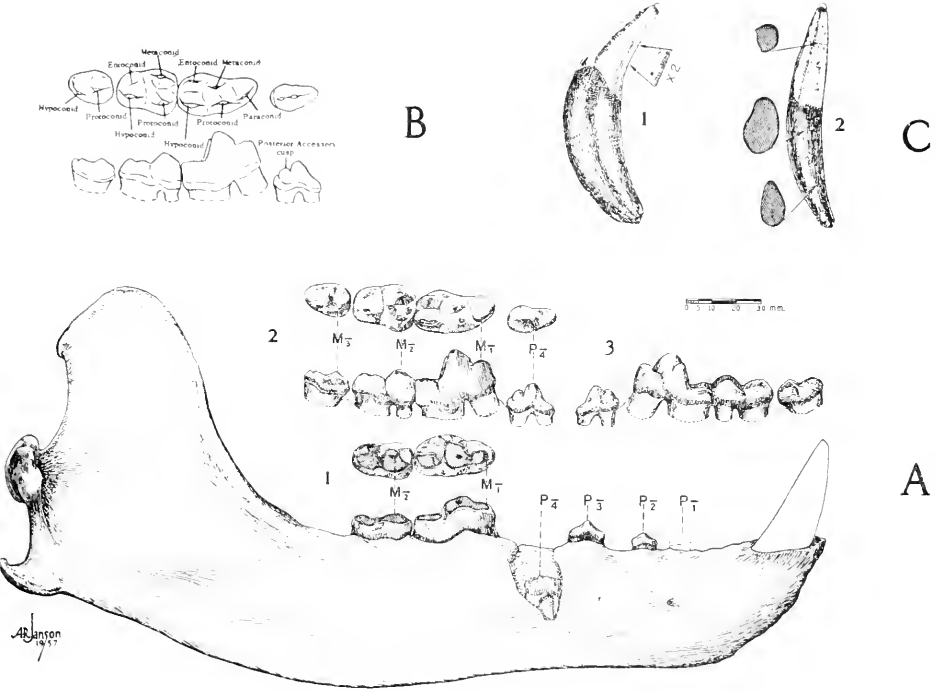

Figure 1

Lower jaw and dentition of *Amphicyon intermedius*

A — (1) Lower jaw and dentition, labial and occlusal views showing wear pattern of old adult, M.C.Z. 3919.

(2) Adult $P_4 - M_3$, labial and occlusal views showing no perceptible wear; P_4, F.G.S. V-5257; $M_1 - M_2$, M.C.Z. 5832; M_3, M.C.Z. 7141.

(3) Same as 2, lingual view.

B — Cusp nomenclature for lower dentition.

C — Left lower canine; (1) lingual view, with detail of serrations.

(2) Posterior view with sections.

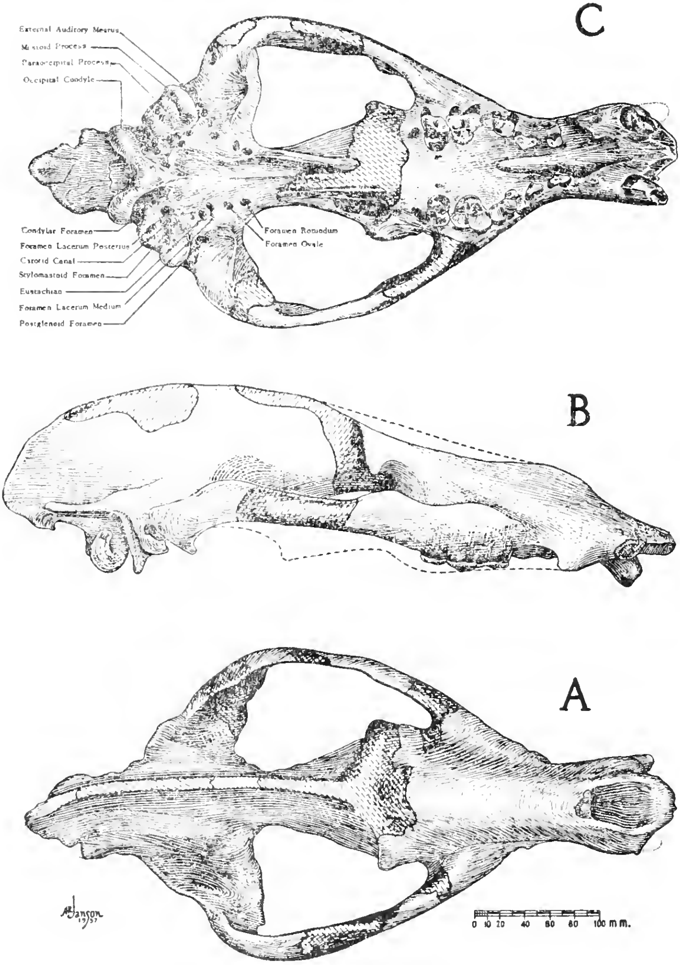

Figure 2

Skull of *Amphicyon intermedius*
U. F. 6501

A — Dorsal view.
B — Lateral view.
C — Palatal view with detail of auditory region — crushed and restored areas as indicated by dashed lines.

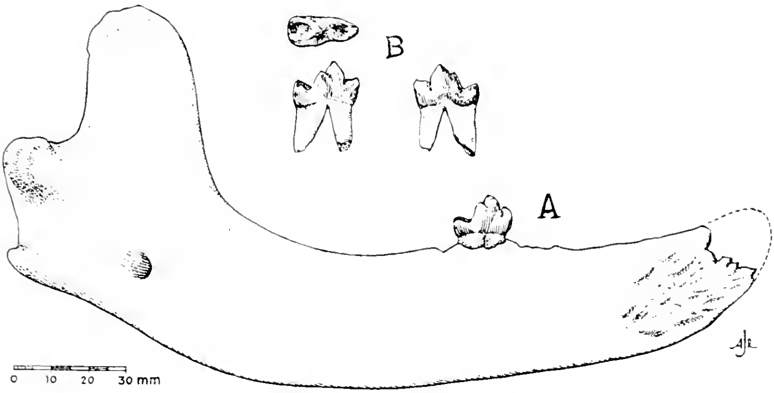

Figure 3

Immature jaw and deciduous carnassial
A — Immature jaw with dm_4 (replaced by P_4), M.C.Z. 3632.
B — Dm_4, M.C.Z. 7142.

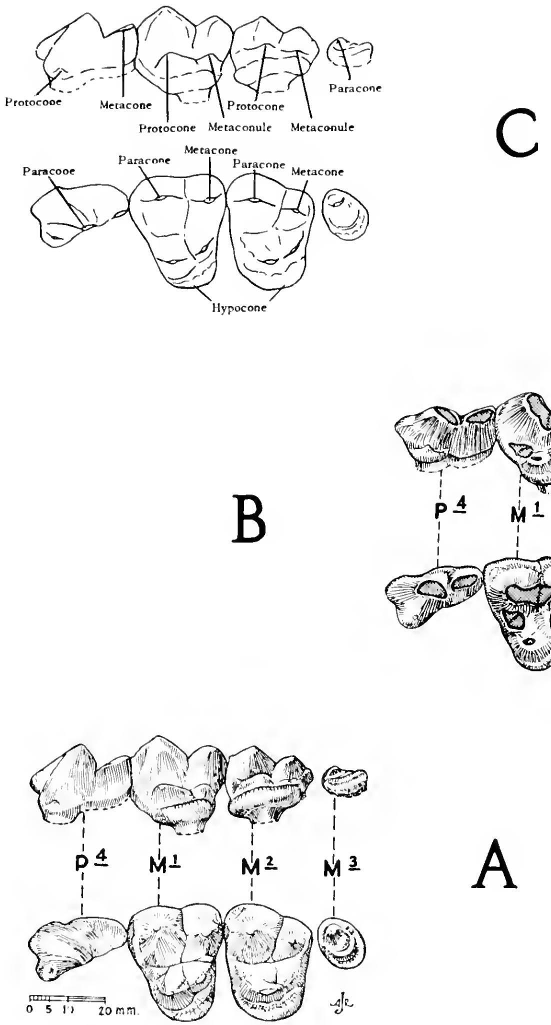

Figure 4

Upper dentition of *Amphicyon intermedius*

A — Occlusal and lingual views of adult showing no perceptible wear P^4 – M^3. P^4, M.C.Z. 4060; M^1, M^2, M.C.Z. 5833; M^3, M.C.Z. 7143.

B — Occlusal and lingual views of P^4 – M^2 of old adult showing pattern of wear. U. F. 6501.

C — Cusp nomenclature of upper dentition.

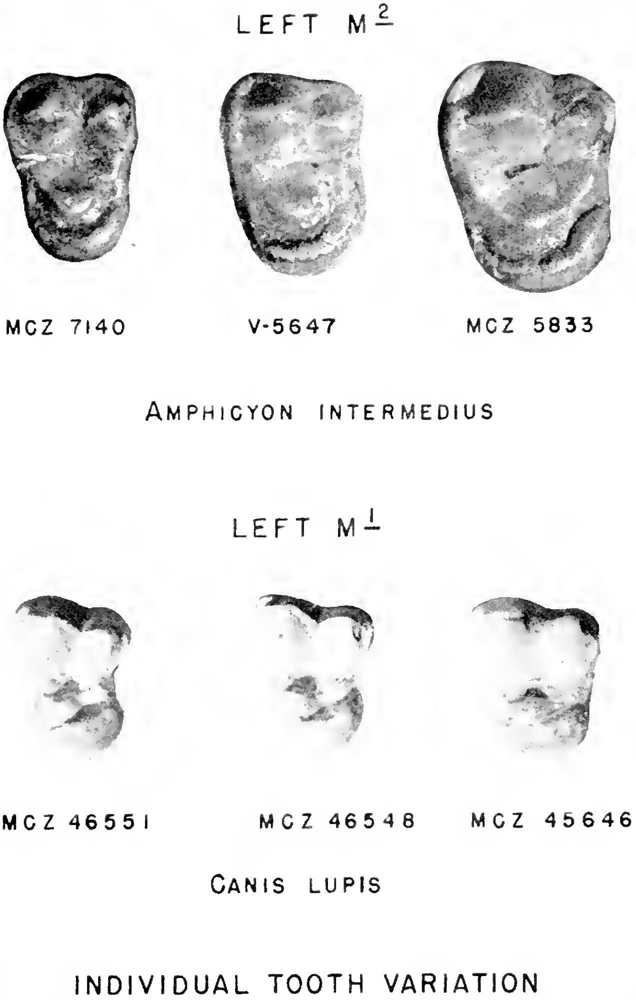
LEFT M^{2}
MCZ 7140
V-5647
MCZ 5833
AMPHICYON INTERMEDIUS
LEFT M^{1}
MCZ 46551
MCZ 46548
MCZ 45646
CANIS LUPIS
INDIVIDUAL TOOTH VARIATION

Figure 5

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 118, No. 5

CONTRIBUTIONS TOWARD A RECLASSIFICATION OF THE FORMICIDAE. II. TRIBE ECTATOMMINI (HYMENOPTERA)

By William L. Brown, Jr.

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
June, 1958

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The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5 and 7 are sold by the Museum, and future volumes will be published under Museum auspices.

Bulletin of the Museum of Comparative Zoology

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No. 5 — *Contributions toward a Reclassification of the Formicidae. II. Tribe Ectatommini (Hymenoptera)*

By William L. Brown, Jr.

CONTENTS

INTRODUCTION

This section deals with a large group of species in the subfamily Ponerinae, including most genera formerly placed in the old tribes Ectatommini, Paraponerini and Proceratiini. These genera are now grouped in a single, broadened tribe Ectatommini.

The previous "standard" classification of the subfamily Ponerinae, stabilized by Emery in his 1911 fascicle of the Genera

Insectorum, was altered but little when Wheeler made additions to it in his generic key of 1922. In 1911, Emery's system was a great advance over older arrangements in many respects, but the flood of description in more recent years has swamped it completely. Since basic classification has been neglected for so long a time, we are now faced with the necessity of constructing a completely new system. I have undertaken to make this replacement through the revision of tribes or similar-sized taxa, one at a time, and the publication of the results of tribal units. Thus, at least some of the results will be available for the necessary use and testing by other specialists long before a full subfamily revision could possibly be completed. It is hoped, however, that after the series of tribal sections is complete, there will be an opportunity to make final adjustments and to construct a grand key to the genera of the subfamily.

The Emery-Wheeler classification of the Ectatommini, Paraponerini and Proceratiini, with a summary of the changes here proposed

Emery recognized the Ectatommini, Paraponerini and Proceratiini as separate tribes within the Ponerinae, but the present evidence of their close relationship seems to make any such tribal division unnecessary and unrealistic. The Paraponerini include a single genus with one species, and the conclusion reached after a close consideration of the characters of all castes of *Paraponera clavata* is that tribal rank was granted in this case almost solely on the basis of the extraordinarily large size of the individuals of the species. Admittedly, *Paraponera* is unique in a couple of other respects as well, but its ectatommine relationships are so clear in its habitus in all adult castes, in its behavior, and in details of morphology such as the male genitalia (Weber, 1946) that it can no longer be considered as more than a slightly aberrant ectatommine.

The Proceratiini have even less claim to tribal separation from the Ectatommini, at least on adult characters. In fact, there is grave difficulty to be encountered in separating *Proceratium* of the Proceratiini from *Heteroponera* of the Ectatommini even at the generic level. The only doubts here rest on the unusual nature of the proceratiine larvae, but then these are known for only a few species in one genus, *Proceratium*, and for none of the *Heteroponera* species. The Ectatommini appear to make up one reasonably clearcut tribe with these inclusions.

Emery divided his tribe Ectatommini into two subtribes: Ectatommini, *sensu stricto* and Typhlomyrmicini. It has already been shown that two of the three genera of the Typhlomyrmicini (*Typhlomyrmex* Mayr and *Prionopelta* Mayr) are members of different ponerine tribes, and that they should be excluded from consideration under the Ectatommini (Brown, 1950, 1953a, 1953b). The third genus in this subtribe is *Rhopalopone* Emery, the species of which have been consistently characterized, and wrongly so, as lacking median teeth on the tarsal claws. In fact, such teeth are present in most, if not all species that have been placed in *Rhopalopone*, and a separation between these species and others now placed in *Gnamptogenys* is considered impossible. The synonymy of *Rhopalopone* with *Gnamptogenys* removes the last genus from subtribe Typhlomyrmicini, and thus removes all necessity for recognizing this subdivision any longer. I had considered retaining Paraponerini and Proceratiini as subtribes in the Ectatommini, *sensu lato*, but in the end this subdivision seemed misleading and an unnecessary complication to the system, and it was rejected.

Among the genera of the ectatommines, *Acanthoponera* is worthy of generic rank on present evidence. The erstwhile subgenus *Anacanthoponera* is a straight synonym of genus *Heteroponera* Mayr (Brown, 1952c), and *Paranomopone* is also considered to belong to *Heteroponera* in this revision. *Aulacopone* is retained as a genus, at least until more is known about it. *Rhytidoponera* is retained as a separate genus, also, and *Chalcoponera* is included as a synonym (Brown, 1953b). *Ectatomma* is considered to be a genus apart from *Gnamptogenys* and the remainder of its erstwhile subgenera. *Gnamptogenys* is preserved as a separate genus and, despite long and earnest attempts to find some basis for separation of two or more generic or subgeneric groups, I have been forced to place in its synonymy a number of generic and subgeneric names, including some much-used and familiar ones: *Holcoponera*, *Stictoponera*, *Emeryella*, *Parectatomma*, *Rhopalopone* and *Alfaria*, as well as some less well known names: *Wheeleripone, Spaniopone, Poneracantha, Barbourella, Opisthoscyphus, Tammoteca* and *Commateta.* Of the genera formerly included in the Proceratiini, *Probolomyrmex* Mayr and its probable synonym *Escherichia* Forel have been transferred to tribe Platythyreini (Brown, 1952a). *Proceratium* has been found to grade into *Sysphingta* (*Sysphincta* of authors), so synonymy is indicated here, with *Proceratium* the prior name. For similar reasons, *Discothyrea* becomes the senior synonym of *Prodiscothyrea* and *Pseudosysphincta.*

The Ectatommini come in this way to contain nine reasonably distinct genera: *Acanthoponera, Heteroponera, Rhytidoponera, Paraponera, Ectatomma, Aulacopone, Gnamptogenys, Proceratium* and *Discothyrea.*

Characters and Relationships among the Genera of Ectatommini

Taxonomy in the Ectatommini is chiefly dependent upon the characters of the adult worker, for this is the caste most commonly collected and described, and the one with the clearest differentiation of external morphological features. Queens follow workers in generic and specific characters for the most part, and many of them are present only as wingless ergatoids scarcely distinguishable from workers, or perhaps not distinct at all (*Rhytidoponera* spp.). The degree of caste divergence in the female sex is moderate, therefore, to nearly or quite non-existent.

The males show marked divergence from the females, but sexual dimorphism is not as strong as among some other formicid genera, even in the Ponerinae. The size is usually a little smaller than the corresponding female, and the sexual differences are otherwise much as seen in other ponerines. Males are rare in collections, and often are not in association with workers or females in the cabinet. Within the tribe, the males show greater conservatism in morphology than do the workers and queens, and, with few exceptions, the male characters are not known to furnish clear generic distinctions. The males of a species may often be distinguished by characters reflecting those shown more strongly by its workers and queens, so that males in association with workers are normally determined through the workers.

Perhaps a study of such characters as wing venation, genitalia, palpal segmentation, antennal form, and so on, will eventually furnish good male distinctions independent of those seen in the workers, but such a study must await much more complete collections. Some male characters will be mentioned below for the genera in which this caste is known.

The larvae of the ectatommines are also relatively incompletely known, and before the pioneering work of the Wheelers on the ponerine larvae (1952a: 117-139, pls. 2-5; 1952b, 657-661), there was virtually nothing in print of any value for morphological or systematic purposes. The larval findings agree in most respects at the generic level with the new classification adopted here. The Wheelers have been hampered in their work by a lack of material in some of the rare, but taxonomically critical genera. It is hoped that those specialists having access to the material needed to fill these gaps will see that larval specimens are forwarded to colleagues ready to study them.

At the present time, the relationships of the Ectatommini are not entirely clear, but it does seem likely that tribes Ponerini and Platythyreini are approximately cognate members of the Poneroid Complex (Brown, 1954a). There is evidence in the form of the male alitrunk, wings and genitalia, in the integumental consistency, proventricular structure, propodeal form and armament of all castes, and especially in the structure and proportions of the post-propodeal segments and their organs, that subfamily Myrmicinae arose from an ectatommine ancestor, and this supposition is strengthened by the characteristics of the fossil *Agroecomyrmex* Wheeler, which seems to provide a near-ideal intermediate form. These speculations on ectatommine connections seem reasonably safe to put forward at this time, but beyond this, nothing is gained by suggesting detailed relationships in the absence of the necessary comparative morphological data.

Within the tribe Ectatommini, the genus surviving with the greatest number of primitive characters appears to be *Acanthoponera*. This genus retains (in the female castes) the primitive palpal formula for ants: 6 maxillary, 4 labial segments. *Acanthoponera* also bears the strong extra tooth on each tarsal claw found in the most primitive ponerines and myrmeciines, and the alitrunk has a complete and possibly flexible articulation between pro- and mesonotum. It is interesting to note that this genus, like some other genera primitive within their respective tribes, is fitted with the large eyes and strong spinous armament marking an arboreal forager, and it is now known that *Acanthoponera* is in fact a nocturnal arboreal forager. All of the characters mentioned above, which happen to be generalized conditions for the ants as a family, oppose the tendency toward ankylosis of antennae, palps, and alitrunk. Other trends that cause the body to become more compact, such as reduction of spinous armament, and also the reduction of the eyes, accompany the ankylotic tendencies more or less consistently, apparently in correlation with a change from arboreal through ground-foraging to hypogaeic or otherwise cryptobiotic habits of the ants. This trend is clearly observable within the single myrmicine tribe Dacetini, as it is within the ectatommines. The frequent association of arboreal, tropical forms with characters generally considered to be the generalized ones for ants indicates a greater likelihood that the forested tropics were a more prolific evolutionary source in terms of major groupings than were the more arid regions usually cited as important to formicid major-group evolution (see also Bernard, 1948).

Acanthoponera is advanced in one respect, however; the known winged specimens of both sexes lack the anal lobe of the hind wing. All other ectatommines lack this lobe, too, except *Paraponera* and *Ectatomma*, each of which has well-developed lobes in all of the species so far seen. The loss of the anal lobe may mark a monophyletic lineage within the ectatommines, since there are additional grounds for linking most of the genera without it. *Heteroponera*, for instance, can be derived directly from *Acanthoponera*, and *Rhytidoponera* is very closely related to *Heteroponera*, especially through the species *H. relicta*. Judging from the original description and figures, *Aulacopone* also seems to be close to *Heteroponera*, but this needs to be confirmed by a new examination of the type or additional material that may have accumulated in collections. *Proceratium* and *Discothyrea* seem, on the basis of adult characters, to be closest to *Heteroponera*, and the amber species *Bradoponera meieri* (Mayr, 1868; Wheeler, 1914) looks like a reasonable intermediate step in this line. A comparative study of the larvae in this group is needed in order to decide how real the link between the "proceratiines" and *Heteroponera* may be.

The large and heterogeneous *Gnamptogenys* group is difficult to relate precisely to other genera, but it seems closer to the *Acanthoponera-Heteroponera* line than to *Ectatomma*, despite previous placements to the contrary. This leaves *Ectatomma* and *Paraponera* as offshoots from near the base of the ectatommine stock. The poorly-known Baltic Amber genus *Electroponera* Wheeler may represent an intermediate link between these genera and the main line of the tribe.

Two other fossil species, *Ectatomma europaeum* Mayr (1868) and *Archiponera wheeleri* Carpenter (1930; see also Wheeler, 1930) appear to belong either in or very close to *Gnamptogenys* in the present broad sense. *Gnamptogenys europaea* (Mayr) is the **new combination** for the Baltic Amber species, proposed tentatively on the basis of the original description of the winged female and Wheeler's (1914) characterization of the supposed male of this species. As Wheeler suggests, *Archiponera* may be near the *schmitti* group of *Gnamptogenys* (= *Emeryella*), although the state of preservation of the fossil, from the Oligocene Florissant Shales, leaves something to be desired. All of the fossils are interesting chiefly in that they show a widely diversified group of ectatommines to have existed at least as far back as the Oligocene, in northern areas from which the tribe is now absent completely or nearly so.

Geographical Distribution of the Genera

The pattern of ectatommine distribution is today essentially a peripheral one. The relatively large-bodied, epigaeically-foraging stocks are developed almost exclusively in the Neogaeic and Indo-Australian (especially Australian) Regions, where they are largely confined to tropical and warm temperate climates. From this, it will be clear that by "peripheral," I mean peripheral to the larger continental land masses of Eurasia, North America and Africa. However, since the presence of epigaeically-foraging stocks is clearly indicated in the fossil record of the Northern Hemisphere, we know that the distribution of ectatommines has not always been an essentially fringing one, and we suspect that the group may have had its principal source of evolutionary change in the central regions during earlier times. In the same central regions now, we find only a thin and discontinuous representation of specialized cryptobiotic types, like the species of *Proceratium* and *Discothyrea,* managing to survive by remaining ecologically unobtrusive.

Among the epigaeic genera, *Paraponera, Ectatomma,* and *Acanthoponera* are restricted to the New World in warm climates and are all clearly distinct from Old World members of the tribe. *Heteroponera,* a rather conservative stock, is distributed rather widely in both the Australian and Neogaeic Regions, but shows no obvious tendency to split into two groups following the geographical separation. *Rhytidoponera* is a very successful and luxuriantly radiating stock of the Australian Region; it halts at New Caledonia in the east, but ranges widely through Melanesia to the islands stretching from Timor to the southern Philippines on the west. *Rhytidoponera* looks as though it may have originated in the Australian region from some *Heteroponera*-like stock. *Aulacopone* has so far been reported only from the type locality in Russian Armenia; obviously, it has cryptobiotic tendencies.

Gnamptogenys is a large and wide-ranging genus, occurring both in the Indo-Australian Region (Ceylon and western China to Fiji, but not known from Australia, New Caledonia or New Zealand) and in the New World (Argentina to Texas, West Indies). This genus can be grouped into different lines, more or less equivalent to the genera and subgenera here synonymized, and reflecting in part the separation between New and Old World, as well as the water gap between archipelagic and continental faunas. However, these lines have not lost their associations through intergradient species, and these intergradient species, most of which exist in the New World, show that the lines still belong to the same genus at the present time level. It thus appears that *Gnamptogenys* must represent the last major radiative burst of the epigaeic ectatommines, already replaced in its center of origin, and unable to expand in the direction of Australia because of the powerfully-developed *Rhytidoponera* stock already present in that country.

Of the two predominantly cryptobiotic genera, *Proceratium* and *Discothyrea,* the former tends to have a more northerly range, while the latter is found more to the south. Both genera occur in the tropics, often in the same areas, and there are broad overlaps in range in both northern and southern temperate areas. *Discothyrea* is best developed and most abundant in tropical America and southward to Argentina, in the Australian region, and in central and southern Africa. *Proceratium* reaches a peak of abundance and diversity in the warmer parts of the Holarctic Region, wherever sufficient moisture exists, and this genus is well represented in the East Indies. In Central America there are three rare species, and two species have reached into the eastern tropical forest belt of Australia as far south as Brisbane. Another species has colonized Fiji. Two species are known from tropical Africa. This apparent tendency of the two genera to have complementary ranges outside the tropics is very interesting, but we know so little about the habits, particularly the food habits, of these ants that it is not now possible to say whether the tendency is adaptive in promoting avoidance of competition between the groups.

The presence of two endemic ectatommine species of different stocks (*Heteroponera* and *Discothyrea*) in New Zealand (out of a total of at most ten ant species endemic in New Zealand), and of moderately to highly diverse native representations of the tribe in southern South America, southern Australia, the Solomons, Fiji and New Caledonia, speaks for the age of the group. Few ant tribes can match this ''extralimital'' range, and of those that do, the Amblyoponini share an archaic aspect and a poverty of representation in the Ethiopian and other ''central'' land masses. Bearing in mind the Oligocene fossil traces and the lack of good ant fossils in earlier levels, it seems likely that the Ectatommini go back to or slightly beyond the beginning of the Tertiary. It may be guessed that the present peripheral contraction of the Ectatommini is due, at least in part, to the pressure of the rising Myrmicinae. The beginnings of a diversified myrmicine fauna are seen in the Baltic Amber, as well as in the Florissant Shales, but true members of the most potent myrmicine genera, *Pheidole* and *Crematogaster*, do not appear in these formations, nor even in later (Miocene) strata.

Treatment of Species-Level Taxonomy

The primary purpose of this section is to revise the generic classification of the Ectatommini, but in the course of the necessary review of the literature and authentic material of nearly all of the named forms, many species-level situations were found to require synonymy, adjustment or amplification. Also, among a number of previously undescribed species seen, certain ones were found to affect generic concepts by broadening them or by bridging what were formerly thought to be natural gaps. For these reasons, descriptions of a few new species were necessary to the primary purposes of this work; descriptions of still other species that do not affect generic concepts as significantly have been omitted here, though it is hoped that these can be treated elsewhere.

The compilation of a work of this sort also inevitably includes a miscellany of new or under-appreciated data referring to morphology, distribution, behavior, ecology, and variation, of a kind lacking in the literature for most of the forms in this tribe. In order that the required documentation backing the present major conclusions, and also the subsidiary information, should neither clutter the presentation of the generic data nor become a lost by-product, I have relegated most of this matter to an appendix, where the items are listed consecutively against boldface numbers corresponding to the indicator numbers placed in brackets in the text.

After synonymy and general remarks, there are listed for each genus the currently recognized species as far as known to me. Synonyms listed as such in Emery (1911) are omitted here. Each species is followed by author, date and page of original reference; the sources are listed more fully at the end of the paper.

Of the many forms treated until now as varieties or subspecies, some are rather obviously synonyms, and are treated as such with a minimum of discussion. Varieties and subspecies of unclear status are listed arbitrarily as species, since I feel that these names will eventually stand or fall as species or as infraspecific variants not worthy of formal nomenclatorial recognition (Wilson and Brown, 1953; Brown and Wilson, 1955). I should perhaps emphasize that the listing of former infraspecies names as species here implies no real conviction on my part that these entities are really worth the distinction; actually, I feel that most of such names will be revealed as synonyms when the proper study of their types has been made.

The capital letters placed in parentheses before each specific name indicate the kind of evidence upon which the present generic placement is directly based.

(T) indicates that type material, nidotypes, reliably type-compared material, or similarly authentic specimens have been examined, in most cases by myself; rarely, examination has been made by other myrmecologists.

(P) means that material identified from reasonably good descriptions, or from other satisfactory evidence, has been examined and is thought to be correctly determined.

In cases where the species is not seriously questioned, but no specimens referable to it have been seen, or if specimens seen cannot be satisfactorily verified as to identity, no entry has been made before the species name.

(?) signifies that, in my opinion, the species is inadequately described for purposes of distinction and that its taxonomic status is doubtful.

The species lists have been based on various myrmecological compendia and basic papers, and were checked against Emery's Genera Insectorum list and the Zoological Record, 1908 through 1953. References through 1957 are included so far as I am aware of them. I shall consider it a great favor if readers will send me notice of the inevitable omissions for inclusion in a corrective supplement.

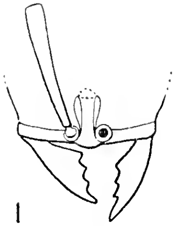
Key to the genera of Ectatommini, based on the workers

1. Size very large, head width across eyes over 3.6 mm.; hypopygium with an upwardly-directed comb of fine teeth on each side (Neotropical) *Paraponera* Fr. Smith

   Size much smaller, head width across eyes under 3.6 mm.; hypopygium without lateral combs . . . . 2.

2. Lobes of frontal carinae more or less sharply raised (sometimes vertical and fused together), leaving the condylar bulbs of the antennae completely or nearly completely open to dorsal full-face view (Figs. 1, 23-25,

46, 48). Small, compact chiefly cryptobiotic forms, usually ferruginous in color and with reduced eyes (Figs. 45, 47) . . . . 3.
Lobes of frontal carinae horizontal or at most feebly raised, covering or nearly covering the condylar bulbs of the antennae (Figs. 12, 36, 41, 43, 44). Mostly epigaeic foragers, but a few species are cryptobionts with characters to match . . . . 4.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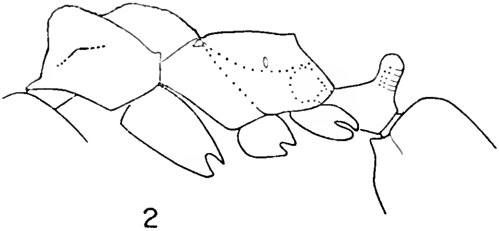
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Figure 1. *Proceratium arnoldi* Forel, syntype worker, dorsal view of anterior part of head, from a sketch by Dr. G. Arnold. Figure 2. *Ectatomma ?confine* Mayr, worker (Lancetilla, Tela, Honduras), side view of alitrunk and petiole.

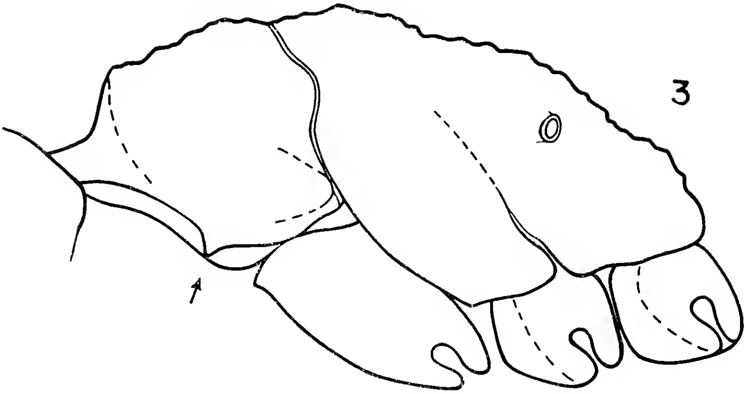


Figure 3. *Rhytidoponera laciniosa* Viehmeyer, worker, side view of alitrunk. Inferior pronotal tooth indicated by arrow.

3. Apical antennomere strongly bulbous, its length subequal to or > the combined lengths of the second through penultimate funicular segments (Fig. 48); mandibles small, edentate (though frequently with a masticatory comb of short setae), largely or completely overhung by clypeus (Widespread in tropical and warm temperate regions) . . . . . *Discothyrea* Roger

Apical antennomere at most moderately enlarged, much shorter than combined lengths of second through penultimate funicular segments; mandibles larger, armed with 3 or more teeth or denticulae, not or only in very small part overhung by clypeus (Figs. 1, 23-35, 45, 46) (Widespread except S. America) ....*Proceratium* Roger

4. Inferior pronotal margins just in front of each anterior coxa with a distinct, usually acute tooth, best seen from an oblique dorsolateral view (Fig. 3) (rarely missing on one or both sides in individual specimens); posterior tarsal claws always with a distinct median tooth; posterior coxae unarmed above (Australia; N. Guinea, to N. Caledonia, s. Philippines) *Rhytidoponera* Mayr

   Inferior pronotal angles unarmed or forming an obtuse angle, or, in the rare cases where the angle is present and more nearly toothlike, then the posterior tarsal claws lack a median tooth, or else the posterior coxae are toothed above ....5.

5. Mesonotum rounded and prominent, surrounded by deeply impressed sutural lines; it and the propodeum forming distinct convexities separated by the deep transverse fissure of the metanotal remnant (Fig. 2); posterior coxae always unarmed (Neotropical) ...... *Ectatomma* Fr. Smith

   Mesonotum and propodeum part of one continuous or near-continuous profile, interrupted at most by a suture-like groove at the position of the metanotum (rarely deep), or by an ill-defined impression in this region; posterior coxae armed above, or unarmed ....6.

6. Clypeus much modified, the median portion raised and produced as a short, blunt triangular point forward from the antennal insertions somewhat over the mandibles; antennal scrobes lateral, long and very deep (Russian Armenia, rare) .... *Aulacopone* Arnoldi

   Clypeus of normal form, broad and in one piece, not or only to a small extent covering the mandibles (Figs. 12, 41, 43, 44); antennal scrobes distinct and deep in only a few species ....7.

7. Dorsum of head without a median costa as distinct from other sculpture, or, if with a costa, it is short or not fully continuous (Figs. 41, 43, 44), and either the posterior coxae are toothed above (Figs. 17-20), or else the alitrunk and petiole are predominantly smooth and shining (Neotropical, Indo-Australian) ....*Gnamptogenys* Roger

   Dorsum of head with a distinct median costa from clypeus to vertex, continuous across frontal triangle (Fig. 12); posterior coxae unarmed above (Fig. 13); head and alitrunk thickly sculptured, usually hairy and pubescent and in large part opaque ....8.

8. Tarsal claws each with a prominent basal lobe and a large submedian tooth; propodeum with paired long teeth and petiole produced posterapically as a single long spiniform tooth (Figs. 7-11); palpal formula

6, 4. (Neotropical) .... *Acanthoponera* Mayr
Tarsal claws without prominent basal lobes, submedian tooth often absent, particularly on claws of posterior legs; propodeum and petiolar summit unarmed or with short teeth (Fig. 13); palpal formula 4, 3 or less (S. and C. America to Mexico; Australia, N. Zealand) .. *Heteroponera* Mayr

THE GENERA

ACANTHOPONERA MAYR

≤ *Ectatomma* subgenus *Acanthoponera* Mayr, 1862:732. Type: *Ectatomma* (*Acanthoponera*) *mucronatum* = *Ponera mucronata* Roger, 1860, by designation of Emery, 1911.

< *Acanthoponera*, Emery, 1911, p. 35; *nec* male.

= *Acanthoponera* subgenus *Acanthoponera*, Wheeler, 1932b:190.

It has already been shown (Brown, 1952c) that *Heteroponera* Mayr is the prior name for a group of species included by Emery in *Acanthoponera*, and ranked as subgenus *Anacanthoponera* by Wheeler (see below). *Heteroponera* deserves to be regarded as a separate genus on present evidence.

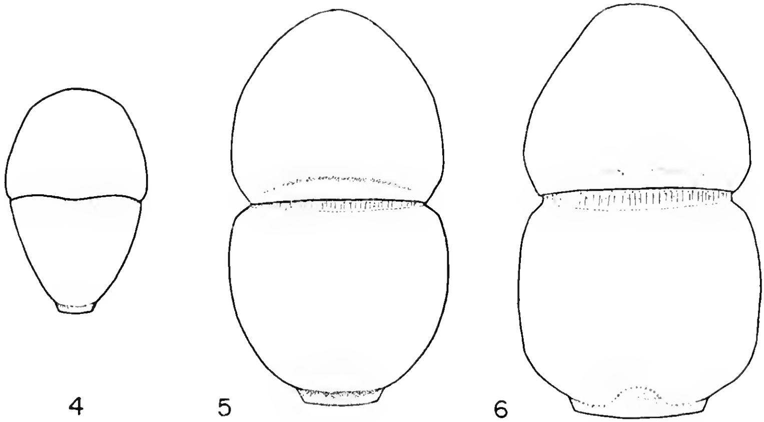
The species remaining in *Acanthoponera* as defined here are medium-sized ants (workers ranging from 5 to 10 mm. in outstretched length), generally of a yellowish or tan color, with large, convex eyes and shallow antennal scrobes. The propodeum bears a pair of teeth or spines (long and slender in worker), and the apex of the petiolar node is produced dorsocaudad as a slender subconical spine with a more or less acute tip. The tarsal claws are very well developed, and each has not only a strong submedian tooth, but also a prominent, narrow lobe resembling a third tooth. The palpi of the female and worker are segmented maxillary 6, labial 4 (this seems to be the formula in the single male available, although the basalmost segment in each of the palps of this specimen is not properly visible under the partly-retracted maxillae and labrum); this formula is the primitive one for the Formicidae, and it is not known to hold in any other ectatommine genus. The palpi are long and slender as compared to those of other ectatommines. The characters above are those expected of an epigaeic, nocturnal forager that climbs trees or other vegetation, habits now confirmed by observations of Weber (1939) and Wilson (personal communication) on *A. minor*.

The females of *Acanthoponera*, where known, are winged, slightly larger than workers from the same nest, and differ from the workers in the same ways that ponerines most often do. The female propodeal teeth are usually less well developed than in the worker. The color is the same or nearly the same as in the corresponding workers. The forewings have "complete" venation of the type of *Ectatomma*, but the hind wings differ from those of *Ectatomma* in that they lack the anal lobe. In the single *Acanthoponera* female available with wings, there is no trace of the first radial crossvein remaining, although such traces are present in the male specimen seen.

The male of this genus is known to me only from a single specimen sent by Father Borgmeier; I believe that this is the first true *Acanthoponera* male to be recorded. It will suffice here to describe this male as like a larger, more slender *Heteroponera* with tarsal claws as in worker-female *Acanthoponera*. A further notable character is the very extensive ventral excavation of the gaster; the cavity involves large parts of the second and following segments, and even the posteroventral border of the postpetiole. No such conformation exists in the few *Heteroponera* males I have seen, nor does it occur in other genera of ectatommines. More species must be examined in the male sex before we know whether or not this is a generic, or only a specific, character. The general color of this male is ferruginous yellow. The eyes are large, convex, and medially emarginate; the ocelli are large and clear. As already mentioned above, the male specimen seen has traces remaining of the first radial crossvein, visible in good light as tenuous veinlets extending downward from R toward Rs, but not reaching Rs before they fade out.

Acanthoponera is a rarely collected genus, less than a score of separate collections having reached myrmecologists to my knowledge. Nothing is known of its nesting habits or food, and the larva has never been seen, so far as I can learn. The genus is restricted to the New World, where it is known to range from Veracruz south into northwestern Argentina. Apparently it is restricted to forested country, although information on this is scanty. Probably an increase in night collecting in the tropics will give us more insight into the biology of this most interesting generalized ectatommine.

Eight names have been proposed for forms in the genus *Acanthoponera,* each based on one or two type specimens only. Material, whether determined or undetermined, is very scarce in collections, and the wide scattering of type depositions adds to the difficulty of revision at species level. Among the 21 worker and female specimens I have seen from 15 nests or individual collections, there appear to be only five distinct entities, each of which may represent a distinct species. It should be emphasized, however, that no real idea of species variability or species limits can be securely gained from such limited material. It is possible that all 21 specimens actually belong to one or two species only.



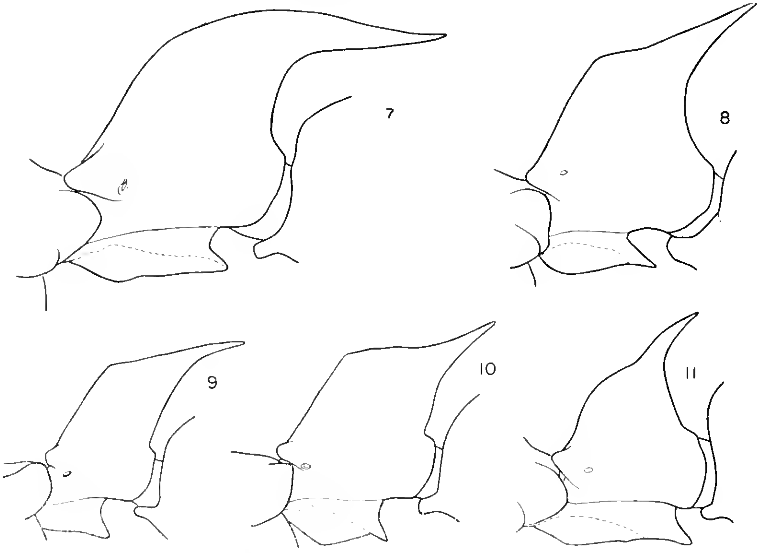
Figures 4-6. *Acanthoponera* spp., workers, dorsal views of first two gastric segments. Fig. 4, *A. minor.* Fig. 5, *A. mucronata.* Fig. 6, *A. peruviana* sp. nov., holotype. All drawn to same scale.

Of the five kinds, two have the "unconstricted" type of gaster, in which the second gastric segment is narrower than the postpetiolar segment in which it is based, and from which it issues without notable constriction, tapering from this point toward the apex, as shown in Figure 4. Of the two kinds with unconstricted gaster, one averages a little smaller and has a petiole shaped as in Figure 9; to this kind belong the holotype of *schwarzi,* the cotypes of *spininodis,* and a specimen taken in Veracruz by Wilson. The type of *spininodis* before me has the head distinctly broader than in the Guatemalan or Mexican specimens, but the difference is not great enough to warrant continuing *spininodis* as a species apart from *minor*, which name I think should apply to the first unconstricted-gaster kind. In applying this name, I am relying on Forel's statement concerning the small size of *minor*, and also the fact that his type locality is Teapa, Tabasco, near the known localities for this species in Mexico and Guatemala from which my specimens have come. Forel also states that the spine of the petiolar node in *minor* is less strongly elevated and forms less of an angle with the node, which, if I interpret the statement correctly, applies well enough to the specimens here assigned to *minor*.

The second kind with unconstricted gaster is represented in my collection by a worker from Hamburg Farm, Santa Clara Prov., Costa Rica (F. Nevermann), and by three workers from 6 miles west of Santo Domingo de los Colorados, Pichincha, Ecuador (leg. E. I. Schlinger and E. S. Ross). The average size is a little larger than in *minor* (average head width, without eyes, ca. 1.04 mm., as against a head width of 1.00 mm. or less in *minor*), and the node is thicker from front to rear, with the spine elevated a bit more strongly (Fig. 10). The Costa Rican specimen is light yellowish ferruginous in color (teneral ?), and the Ecuadorian workers are considerably darker, yellowish-brown. The metanotal groove is represented by a distinct impressed line, averaging more distinct than in *minor*. I doubt whether these specimens belong to *minor*, and their correspondence with other described species seems doubtful also; perhaps they represent an undescribed species, and it seems best to describe and name them formally, in view of the probabilities, as *Acanthoponera crassa* sp. nov. **[2]**.

Among the three kinds with constricted gaster, the smallest is represented by a single, winged female taken at Agudos, São Paulo State, Brazil (December 15, 1955), at light by W. W. Kempf. This specimen has a peculiarly-formed petiolar node (Fig 11), and the gastric dorsum is shining, with small, separated punctulae. The gastric constriction is distinct, but not especially strong. I cannot match this female with any known species, but it seems best to wait for material in which workers are associated before deciding whether it should be named.

Of the kinds with constricted gaster, one of intermediate-to-large size corresponds well to the types examined of *mucronata, wagneri* and *goyana* (Figs. 5, 8), and is undoubtedly the form described by Donisthorpe as *plaumanni.* This, the commonest form in collections, is known from Rio de Janeiro and Goias State in Brazil southward into northwestern Argentina and Bolivia. Through the kindness of Dr. G. Steinbach, of the Zoologisches Museum, Humboldt Universität, Berlin, I have been able to see Roger's *mucronata* type. Roger called the dorsa of postpetiole and succeeding segment, "dicht runzlig punktirt," which fits the next species discussed below better than it does this one. There is some size variation among different samples: *wagneri* type worker and three workers from Rurrenabaque, Beni, Bolivia (Mann leg.) average rather smaller (HW without eyes, 1.37-1.44



Figures 7-11. *Acanthoponera* spp., side views of petiolar node. Fig. 7, *A. peruviana* sp. nov., holotype worker. Fig. 8, *A. nucronata* worker from Beni R., Bolivia. Fig. 9, *A. minor* worker from Trinidad (syntype of *A. spinnodis* Weber). Fig. 10, *A. crassa* sp. nov., paratype worker from Ecuador. Fig. 11, *A.* sp. indet., female from Agudos, Sao Paulo, Brazil. All drawn to same scale.

mm.) than those from the vicinity of Rio, where HW may reach 1.63 mm. in the worker. Cephalic indices are much the same in all of these samples, ranging from 90-94. Donisthorpe cited directly only larger size as a distinction for his *plaumanni*, but, although he stated that he had checked previous descriptions, it seems that he did not realize that there was no significant difference between his measurement and the one given originally by Roger. The *plaumanni* type is thus probably only an average specimen of *mucronata*.

The third kind of *Acanthoponera* with constricted gaster is near the previous kind (*mucronata*) in size; its HW without eyes is about 1.55 mm., and its cephalic index is similar (93), but its gaster is even broader and more depressed, particularly the second segment (Fig. 6). The second segment is also distinctive in having a semicircular impression extending from the impressed band along the posterior border forward into the raised portion of the tergite (Fig. 6). The petiole is of a particular conformation (Fig. 7), and the gastric dorsum is decidedly more coarsely, closely and irregularly punctured than in the preceding forms, perhaps conforming to Roger's "dicht runzlig punktirt," based, of course, on a female. We know that the female of *mucronata* has gastric punctation much like that of its worker, so the sculptural character is not just a caste or allometric difference. I have seen only a single worker of this last kind, from Tingo-Maria, Peru, but this is so distinct from the previously described species, including the closely related *mucronata*, that I have little hesitation in describing it as a new species, *A. peruviana* sp. nov. **[1]**.

There is one named form of the genus that we have yet to consider: *A. goeldii* Forel. Dr. Wilson has examined the *A. goeldii* type and has compared it directly with *A. minor*. He feels that the two are different species, although their size is about the same. His quick sketch of the profile of alitrunk, petiole and gastric dorsum as seen from the side, and his description of the coarse sculpture and pilosity, particularly the rough, contiguous punctation of the gastric dorsum, are reminiscent of these features in *peruviana*, just discussed above, although the latter would of course be much larger than *goeldii*. At present, we know nothing directly of the size variation of either *peruviana* or *goeldii*, but judging from the size variation known for *mucronata*, *minor* and *crassa*, it does not seem likely that *peruviana* and *goeldii* are large and small forms of one and the same species. The possible relationship of these two species should, however, be kept in mind in the future.

To summarize the present and provisional species-level taxonomy of *Acanthoponera*, we may recognize five reasonably distinct species at present named: *mucronata*, *peruviana*, *minor*, *crassa* and *goeldii*. A stray female seen cannot be referred with safety to any described species.

ACANTHOPONERA species

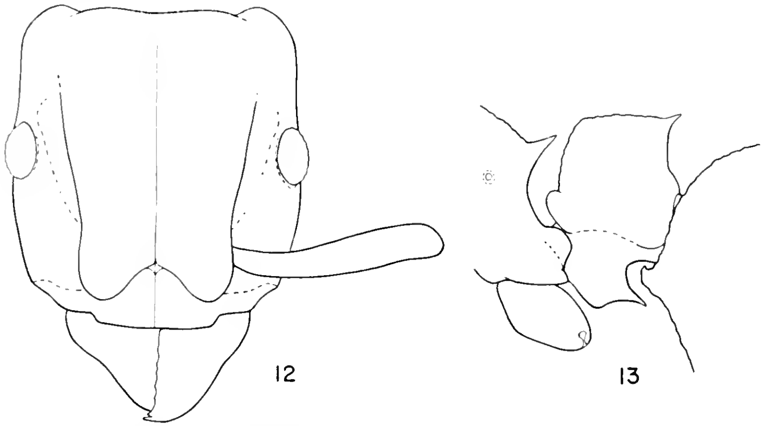
(T) *crassa* Brown, sp. nov. C. America, Ecuador [**2**, Fig. 10]
(T) *goeldii* Forel, 1912b:34. n. status c. Brazil
(P) *minor* Forel, 1899a:9. n. status s. Mexico to Trinidad [**2**, Figs. 4, 9]
(T) =*schwarzi* Wheeler, 1923b:188. n. syn.
(T) =*spininodis* Weber, 1939:97. n. syn.
(T) *mucronata* (Roger), 1860:299. s. Brazil, n. Argentina, Bolivia [**1**, Figs. 5, 8]
(T) =*wagneri* Santschi, 1921:84. n. syn.
(P) =*plaumanni* Donisthorpe, 1938:140. n. syn.
(T) =*goyana* Borgmeier, 1939:418. n. syn.
(T) *peruviana* Brown, sp. nov. e. Peru [**1**, Figs. 6, 7]

HETEROPONERA Mayr

> *Heteroponera* Mayr, 1887:532. Type: *Heteroponera carinifrons* Mayr, 1887, monobasic.
< *Acanthoponera* Mayr *et auct.*
> *Paranomopone* Wheeler, 1915b:117. Type: *Paranomopone relicta* Wheeler 1915, monobasic. n. syn.
> *Acanthoponera* subgenus *Anacanthoponera* Wheeler, 1923b:176. Type: *Ponera dolo* Roger, 1860, by original designation. Synonymy by Brown, 1952c.
> *Heteroponera* (reinstated), Brown, 1952c.

See discussion of synonymy under *Acanthoponera*, above. Wheeler's *Paranomopone* was set up for the sole aberrant species *relicta*, segregated chiefly because of its well-marked scrobes and its angulate humeri. But other *Heteroponera* show lesser development of the scrobes, varying with the species, so that the difference is reduced to one of degree. Angulate humeri are found also in *H. leae*.

Essential characters of the workers are given in the generic key. Most known females of *Heteroponera* (*brouni*, *carinifrons*, *dolo*, *imbellis*, *relicta*) are wingless and ergatoid, but those of *dentinodis* and *schwebeli* have normal wings before nuptial flight. The few known males of *Heteroponera* have the usual gastric shape of other ectatommines, with no excavation beneath. The *relicta* worker palpi are segmented 4, 3; *brouni* and *imbellis* both have 3, 3 (my dissections); Kusnezov (1954) claims that the worker of *H. dolo* has 3, 2. In general, the species of the genus are small in size and form small colonies in soil, rotten wood or epiphyte masses. The distribution is discontinuous, with four species in Australia and New Zealand and six or seven in the New World tropics south into Chile.



Figures 12 and 13. *Heteroponera inca*, sp. nov., paratype worker. Fig. 12, full-face view of head. Fig. 13, side view of petiolar node and adjacent structures.

HETEROPONERA species

(T) *brouni* (Forel), 1892:335. n. comb. N. Zealand: North I. **[5]**
(T) = *kirki* (Wheeler), 1923b:184. n. syn.
(P) *carinifrons* Mayr, 1887:533. Chile **[3]**
(P) *dentinodis* (Mayr), 1887:541. n. comb. s. Brazil, Bolivia **[3]**
(P) *dolo* (Roger), 1860:293. n. comb. se. Brazil to n. Argentina **[3]**
(P) = *aurea* (Forel), 1913c:203. n. syn.
(P) *imbellis* (Emery), 1895b:346. n. comb. sw. and e. Australia **[4]**

(P) =*hilaris* (Forel), 1895:421. n. syn.
(T) =*scabra* (Wheeler), 1923b:181. n. syn.
(T) =*occidentalis* (Clark), 1926:47. n. syn.
(P) =*nigra* (Clark), 1930:6. n. syn.
(T) *inca* Brown, sp. nov. sw. Colombia [**3**, Figs. 12, 13]
(?) *inermis* (Emery), 1894:143. n. comb. se. Brazil [**3**]
(T) *leae* (Wheeler), 1923b:181. n. comb. N. S. Wales
(T) *microps* Borgmeier, 1957:112. se. Brazil, Colombia [**3**]
(?) *panamensis* (Forel), 1899a:9. n. comb. Panama [**3**]
(T) *relicta* (Wheeler), 1915b:118. n. comb. n. Queensland
(T) *schwebeli* (Luederwaldt), 1918:54. n. comb. se. Brazil [**3**]

Note: Among the new combinations, *relicta* is transferred from *Paranomopone*, and the rest from *Acanthoponera*. Santschi's *Acanthoponera* (*Anacanthoponera*) *reichenspergeri* is now put in *Gnamptogenys* [**74**]. *Heteroponera minuta* Kusnezov (1954:34) is a *nomen nudum* so far as I can determine at present.

Key to known Australian-New Zealand species of Heteroponera Mayr — workers

1. Petiole tapering dorsally to an acute upwardly-directed tooth (e. N. S. Wales) .... *leae* (Wheeler)
Petiole rounded or subtruncate above, without an acute tooth at the summit 2

2. Humeri angulate as seen from above; antennal scrobes distinct and deep, each surrounded by a fine, sharp carina and divided for much of its length by another (n. Queensland, rainforest) .... *relicta* (Wheeler)
Humeri evenly and gently rounded as seen from above; antennal scrobes at most shallow, not distinctly bounded or divided 3

3. Petiolar node seen in lateral view profile fully erect, both anterior and posterior faces sloping very slightly inward toward the apical face, which is horizontal (e., s., sw. Australia) .... *imbellis* (Emery)
Petiolar node seen in lateral view profile slightly inclined posteriad; the anterior nodal face sloping posteriad, apical face sloping upwards toward the rear; posterior face feebly concave, overhung by the posterodorsal angle, which projects slightly posteriad (N. Z.) .... *brouni* (Forel)

Key to known New World species of Heteroponera Mayr — workers

1. Eyes minute, with only a very few facets; body size small, color ferruginous yellow, petiolar node thick scale-like, unarmed above (se. Brazil, Colombia) .... *microps* Borgmeier
Eyes large, with many distinct facets 2

2. Full adult color black or dark piceous; petiolar node unarmed above (Chile) . . . . *carinifrons* Mayr
Full adult color testaceous to dark reddish-brown, but not black; petiolar node with or without a posterodorsal tooth-like process or angle . . . . . . 3.

3. Propodeal teeth well developed and acute, longer than half the distance between the centers of their bases and longer than broad at base; occipital angles each forming a prominent subtruncate lobe (best seen from side) (Figs. 12, 13); posterodorsal petiolar tooth present and acute; color deep reddish-brown. (sw. Colombia) . . . . *inca* sp. nov.
Propodeal teeth reduced or obsolete, never half as long as the distance between the centers of their bases . . . . 4.

4. Large ferruginous yellow species, HL 1.20 mm. or more, with well developed but blunt tooth on apex of petiolar node; small but distinct extra (submedian) teeth on all tarsal claws (se. Brazil to n. Argentina) . . *dolo* (Roger)
Smaller species, HL 1.15 mm. or less; full adult color yellowish to reddish-brown; tarsal claws without distinct submedian teeth, at least on posterior legs . . . . 5.

5. Head relatively narrow (CI < 85); petiole in all sizes of workers terminating in a bluntly rounded posterodorsal border, without tooth or pointed process, petiolar node nearly or quite as long as high and as long as broad (se. Brazil) . . . . *schwebeli* (Luederwaldt)
Head broader (CI > 85); larger workers with a small, acute tooth on the posterodorsal petiolar border, this tooth vestigial in many smaller workers; petiolar node compressed from front to rear, distinctly higher than long and much broader than long (s. Brazil, Bolivia) . . . . *dentinodis* (Mayr)

Judging from the original description, Emery's *inermis* would key to couplet 5, and it is probably the same as either *schwebeli* or *dentinodis*. It is possible, but perhaps not likely, that the large and small workers of *dentinodis* represent different species. [3] *H. panamensis* apparently runs to couplet 5, but we do not know enough about it to key it further.

Rhytidoponera Mayr

≷ *Ectatomma* subgenus *Rhytidoponera* Mayr, 1862:731. Type: *Rhytidoponera araneoides* = *Ponera araneoides* Le Guillou, by designation of Emery, 1911.

> *Rhytidoponera* subgenus *Chalcoponera* Emery, 1897a:548. Type: *Chalcoponera metallica* = *Ponera metallica* Fred. Smith, by designation of Emery, 1911. Synonymy by Brown, 1953b:2.

= *Rhytidoponera,* Emery, 1911:36-39, including subgenera *Rhytidoponera* + *Chalcoponera.* 1914:397.

= *Rhytidoponera* + *Chalcoponera,* Wheeler, 1922:643-644. Clark, 1936:14-15. 1941:71.

This genus is distinguished by means of its dentiform inferior pronotal angles, each of which is situated, pointing downward, just in front of the fore coxa (Figure 3). These teeth are somewhat variable in shape, and at times their apices are blunt, but the sides are usually more or less concave, so that in basic form, the whole tooth is acute. Viehmeyer (1912) claims that the teeth are occasionally absent from some of his New Guinea examples, but it may be that he merely overlooked them in specimens that had the sternal plate of the prothorax in the dropped position, masking the silhouette. In such specimens, the tooth can be seen, with difficulty, only if the alitrunk is viewed from above and to one side. obliquely. Out of several thousand specimens of this genus, representing nearly all of the species from all over the range, I have seen only two specimens in which the inferior pronotal angles were absent or so reduced as to hardly deserve the term "tooth," and in one of the two cases this condition occurred on only one side of the insect. Clearly, absence of the pronotal teeth is an extremely rare occurrence of secondary nature, and perhaps represents a pathological condition.

Other characters of importance in generic diagnosis: well developed tooth present near midlength on all tarsal claws; posterior coxae unarmed above; promesonotal suture complete, apparently not ankylosed; eyes always present and well developed. Palpal segments, worker and female, appear to be constant at 3 maxillary, 2 labial, as based on dissections of several specimens each of *aurata, incisa, spoliata, taurus, impressa, metallica.* Males dissected (*impressa, mayri*) had 5 maxillary, 3 labial. The basal maxillary segment is very short in both sexes. Wing venation of both sexes as in *Ectatomma,* but anal lobe of hind wing absent.

A few species in related genera (e.g. *Heteroponera*) may bear a more or less angulate projection of the lower pronotal border corresponding to that of *Rhytidoponera*, but never so well marked as it usually is in the latter; furthermore, these species differ in one or more of the other characters, i.e., the posterior tarsal claws lack a distinct median tooth, or there is a tooth on the dorsal surface of the coxa, etc. In a few of the medium-sized and smaller species of *Rhytidoponera*, presumably closest to the generalized stock, normal winged males and females occur together in a proportion of nests in the same season at a given locality, and apparently nuptial flight and nest-founding occur much as in other generalized ponerines. In most species, however, true females become very scarce or absent, and their place is taken in whole or in part by fertile workers or by very worker-like ergatoids (Brown, 1953b; C. P. Haskins, *in litt.*); the males are produced over a wide season, which may in some cases last virtually the year around, and mating is accomplished when the males fly to another nest singly. Details of mating, reproduction and nest-founding in these forms remain to be clarified.

Larval morphology is discussed by the Wheelers (1952a: 124-127). Pupae are enclosed in rather dark-colored cocoons in the nests I have seen; the color approaches black in some arid-land Australian species. The male genitalia, at least in dissections of *R. impressa*, *R. metallica* and *R. mayri*, show only slight interspecific variation, and there appear to be no significant variations in these organs from the general plan as seen in other ectatommines. In particular, the volsella is very similar in outline to those of *Ectatomma* and the myrmicine genus *Myrmica*. The hypopygium shows differences in outline of the posterior border, but these are slight and in no case approach spectacular aberrations such as the forked member of *Paraponera* males.

Rhytidoponera ranges in Australia and adjacent islands, New Guinea, New Caledonia and neighboring parts of Melanesia in the east (but misses Fiji and New Zealand); westward it ranges to Timor, the Moluccas, and even to the southern Philippines (as based on a single series of the widespread form *araneoides*, collected by J. W. Chapman near Dumaguete, Negros Oriental). Considerable adaptive radiation has affected the genus, resulting in around 100 known, validly-named species; the total will undoubtedly surpass 150 as collections become more complete. One large group of forms of increased size has taken up xeric niches in Australia (e.g., *mayri, punctata*), and has produced rain-forest-inhabiting species in Melanesia (e.g. *strigosa, laciniosa*); both of these ecological types tend to be dark, piceous or black in color. Members of the same group living in savannah or open-woodland areas of northern Australia are often reddish or ferruginous in color. Perhaps the most successful and abundant life-forms are represented by the smaller species of the *metallica* and *victoriae* groups, strongest in eastern and southern Australia. These are among the most plentiful and conspicuous of Australian ants in many localities, and they seem in many ways to take the place of general-feeding myrmicines, particularly *Myrmica,* in the northern countries; indeed, such species as the common greenhead ant, *R. metallica,* apparently play a role in the Australian environment that is relatively more important than that of the commonest of *Myrmica* species in most parts of the Northern Hemisphere. *R. metallica* and *R. victoriae* are common even in lawns and gardens in some Australian cities, and the former is respected for the potency of its sting, which produces a dull, lasting ache out of all proportion to the size of the insect.

There exists very little detailed information on foraging and feeding habits of this genus. The species vary greatly among themselves, and according to season, in diurnation of foraging. *R. metallica* is, in general, a predominantly daytime-foraging species, while *R. mayri* and other large deserticolous species forage mostly at night, at least during warm weather. Foraging is mostly limited to the ground and low plants, except in the rain-forest, where some species may normally live and forage in arboreal situations. Even in southern Australia, however, there are some species (*anceps, aspera*) that have been found running on tree trunks well above the ground, and perhaps most species do this to some extent. Food consists of insect remains, and probably in some cases honeydew is taken (Clark, 1936); what else, if anything, is gathered we do not know. Wilson will publish notes elsewhere on the foraging biology of the New Guinea species.

The nests of *Rhytidoponera* species are usually made in the soil, except in rain forest, where many species live in rotten logs, and a few even in the "peat" gathered in epiphytic masses on the trees. Soil nests may be with or without a stone or log as cover, and if without cover, a crater or masonry dome may be present or absent, according to species and habitat. Nests under stones are more frequent in cooler upland districts, and masonry domes with a very wide apical entrance (often "decorated" with pebbles or small lateritic concretions) are characteristic of some of the larger desert species. These desert nests are externally very similar to those built by certain arid-land *Camponotus* species.

The genus *Rhytidoponera* in the present broad sense has never been comprehensively revised, although Clark dealt with a majority of the larger Australian species in his review of 1936. Aside from its proposal of some fairly obvious synonymy, this work is largely unsatisfactory as a revision, the basic failure being a lack of proper emphasis on the constant differences separating species, where such differences exist. Apart from the inadequacies of this revision and of the material upon which it was based, however, the larger Australian species are particularly difficult taxonomically. Many of the entities (species or superspecies) have vast, but strikingly discontinuous ranges, with more or less distinctly different populations completely isolated one from the next by great stretches of inhospitable country. The related questions of just how continuous this isolation is, and whether and to what extent such populations should be formally named, require much more study than Clark gave them, or than I can give them here.

Emery (1912) offered a brief review and key covering the smaller "Chalcoponera" species that is useful, but far out of date. Some revision of this group was completed by Brown (1954b), but basic revisionary work needs to be extended to the entire Australian fauna of the genus before a workable key will be possible.

Wilson **[6]**, in his manuscript revision of the ants of Melanesia, has covered the *Rhytidoponera* species of that region and constructed a key to the species, so I shall for the most part avoid mention of Melanesian forms here. As a result of his cooperation during and after his trip to Melanesia and his subsequent tour of the European museums, I am able to list new synonymy confirmed by him, some of which is drawn from his manuscript study. I have revised and keyed the New Caledonian species in this work **[33]**.

At the time of his death in 1956, Clark had completed part of a manuscript dealing with the Australian *Rhytidoponera* and other ectatommines, but the status of this work at present is not clear. It is to be hoped that Australian and other interested specialists will soon be able to undertake a full revision of this difficult but very important continental fauna of the genus **[8]**.

Rhytidoponera species

Excluded from this list are names placed in synonymy by Clark (1936) and Brown (1954b); *Ponera ruginoda* Fr. Smith was placed in *Rhytidoponera* by Emery (1911), but is omitted here since the name was based on the male of *Myrmecia pilosula* Fr. Smith (Brown, 1953c).

(T) *abdominalis* Viehmeyer, 1912:4. n. status. N. Guinea **[6]**
(P) *acanthoponeroides* Viehmeyer, 1924:227. N. Caledonia **[33]**
(P) *aciculata* (Fr. Smith), 1858:104. e. Australia **[9, 20]**
(P) = *laevior* Stitz, 1911:352. n. syn.
(T) *aenescens* Emery, 1900:312. N. Guinea **[6]**
(T) *anceps* Emery, 1898:233. e. and sw. Australia **[12]**
(T) *araneoides* (Le Guillou), 1842:317. Melanesia, etc. **[6]**
(T) = *rugosa* (Fr. Smith), 1859:143. syn. Donisthorpe, 1932:454.
(T) = *froggatti* Forel, 1910:10. n. syn. Wilson
= *arcuata* Stitz, 1911:352. n. syn.
(P) = *impressinodis* Stitz, 1912:498, n. syn. Wilson
(P) = *ceramensis* Viehmeyer, 1914b:112. n. syn. Wilson
(P) *aspera* (Roger), 1860:308. se. Australia **[7]**
atropurpurea Emery, 1914:396. ne. N. Caledonia **[33]**
(P) *aurata* (Roger), 1861b:169. n. Australia
(T) *barnardi* Clark, 1936:54. n. Queensland
barretti Clark, 1941:81. e. Australia
(P) *borealis* Crawley, 1918:88. n. status. Australia: Darwin dist. **[11, 28]**
(P) = *brunnea* (Clark), 1941:86, n. syn.
(T) *carinata* Clark, 1936:54.
(T) *celtinodis* Wilson, ms. sp. nov. N. Guinea **[6]**
(T) *cerastes* Crawley, 1925:584. nw. Australia
(P) *chalybaea* Emery, 1901:51. se. Australia **[7]**
(T) *chnoopyx* Brown, sp. nov. n. Queensland **[16]**

(T) *clarki* Donisthorpe, 1943:115, nom. pro *hilli* (Clark) Queensland [**32**]
(P) = *obscura* Forel, 1900b:60, nec Emery, 1896. n. syn.
(T) = *hilli* (Clark), 1941:85, nec Crawley, 1915. n. syn.
(T) *convexa* (Mayr), 1876:92. e. Australia [**13, 19**]
(P) *cornuta* Emery, 1895b:347. n. Queensland
(P) *crassinodis* Forel, 1907:270. W. and e. Australia
(P) *cristata* (Mayr), 1876:91. N. S. Wales, s. Queensland
(P) *croesus* Emery, 1901:50. e. N. S. Wales, se. Queensland [**7**]
(T) *douglasi* Brown, 1952b:137, nom. pro *levior* Crawley sw. Australia [**17**]
dubia Crawley, 1915:132. Australia: Darwin dist.
(T) *eremita* Clark, 1936:78. c. Australia
(T) *ferruginea* Clark, 1936:48. nw. Queensland
flavicornis Clark, 1936:64. W. Australia
flavipes (Clark), 1941:84. S. Australia
(?) *flindersi* Clark, 1936:60. S. Australia [**17**]
(T) *foreli* Crawley, 1918:87. Australia: Darwin dist.
(T) *foveolata* Crawley, 1925:581. sw. Australia
(T) *fulgens* (Emery), 1883:148. N. Caledonia [**33**]
(T) = *socrula* Emery, 1914:395. n. syn.
fuliginosa Clark, 1936:47. ne. S. Australia
greavesi Clark, 1941:81. n. Queensland
gregoryi Clark, 1936:47. ne. S. Australia
(T) *haeckeli* Forel, 1910:15. Queensland: C. York [**30**]
hanieli Forel, 1913b:660. Timor
(T) *hilli* Crawley, 1915:131. Australia: Darwin dist. [**18, 32**]
(P) *impressa* (Mayr), 1876:92. e. Queensland [**7**]
(P) *incisa* Crawley, 1915:132. c. Australia [**17**]
(P) *inops* Emery, 1900:312. N. Guinea [**6**]
(T) = *striata* Donisthorpe, 1949b:744. n. syn. Wilson
(P) *inornata* Crawley, 1922:436. n. status sw. Australia [**14**]
(T) = *carbonaria* Wheeler, 1934:139. n. syn.
(T) *kurandensis* Brown, sp. nov. n. Queensland [**15**]
(T) *laciniosa* Viehmeyer, 1912:5. N. Guinea [**6**, Fig. 3]
(P) = *petiolata* Viehmeyer, 1912:5. n. syn. Wilson
(T) *lamellinodis* Santschi, 1919b:327. n. Queensland [**30**]
laticeps Forel, 1915b:12. n. Queensland [**25**]
(T) *maledicta* Forel, 1915b:15. n. status n. Queensland [**21, 31**]
(T) *maniae* Forel, 1900b:57. S. Australia, w. N. S. Wales [**18, 19**]
(T) = *spatiata* Forel, 1900b:58. n. syn.
(T) *mayri* (Emery), 1883:150. arid s. half of Australia [**20**]
(P) = *glabrior* Forel, 1907:268. n. syn.
(P) = *quadriceps* Clark, 1936:30. n. syn.
(T) = *stridulator* Clark, 1936:37. n. syn.

(P) = *occidentalis* Clark, 1936:39. n. syn.
(P) = *petiolata* Clark, 1936:41, nec Viehmeyer, 1912, n. syn.
(P) = *dixoni* Clark, 1936:46. n. syn.
(T) *metallica* (Fr. Smith), 1858:94. Australia, except far n. [**14, 21**]
(T) = *purpurascens* Wheeler, 1915c:805. n. syn.
(T) = *varians* Crawley, 1922:436. n. syn.
(T) = *caeciliae* Viehmeyer, 1924:227. n. syn.
= *pulchra* (Clark), 1941:86. n. syn.
(T) *micans* Clark, 1936:62. W. Australia
(T) *mirabilis* Clark, 1936:29. c. Australia [**20**]
(T) *nexa* Stitz, 1912:500. n. status N. Guinea [**6**]
(T) = *major* Stitz, 1912:501. n. syn. Wilson
= *gagates* Donisthorpe, 1941:51. n. syn. Wilson
(T) = *waigeuensis* Donisthorpe, 1942:703. n. syn. Wilson
(?) *nigra* Clark, 1936:81. S. Australia [**19**]
(T) *nitida* Clark, 1936:45. w. N. S. Wales
(T) *nodifera* Emery, 1895b:348. e. N. S. Wales, se. Queensland
(P) *nudata* (Mayr), 1876:91. Queensland
(T) *numeensis* E. André, 1889:221. N. Caledonia [**33**]
(T) = *acupuncta* Emery, 1914:396. n. syn.
(T) *peninsularis* Brown, sp. nov. C. York Peninsula [**27**]
(T) *pilosula* Clark, 1936:80. w. N. S. Wales
(T) *pulchella* (Emery), 1883:149. N. Caledonia [**33**]
punctata (Fr. Smith), 1858:104. S. (and W.?) Australia [**17**]
(T) *punctigera* Crawley, 1925:582. sw. Australia
(?) *punctiventris* Forel, 1900b:56. n. status N. S. Wales
(P) *purpurea* (Emery), 1887:444. N. Guinea, n. Queensland [**6, 7**]
(P) *reflexa* Clark, 1936:76. Australia: Darwin dist. [**22**]
(P) *reticulata* Forel, 1893:458. Australia: Darwin dist. [**23**]
(P) *rotundiceps* Viehmeyer, 1914a:28. n. N. Guinea [**6**]
(P) *rufescens* Forel, 1900b:58. n. status e. Queensland [**13**]
rufithorax Clark, 1941:82. n. Australia
(P) *rufiventris* Forel, 1915b:11. n. and W. Australia [**24**]
(T) *rufonigra* Clark, 1936:58. sw. Australia [**17**]
(P) *scaberrima* Emery, 1895b:347. n. Queensland [**10**]
(T) = *malandensis* Forel, 1915b:10. n. syn.
(T) *scabra* (Mayr), 1876:90. e. Queensland [**25**]
socrus Forel, 1894:236. w. N. S. Wales
(T) *spoliata* Emery, 1895b:348. n. Queensland [**25**]
(T) *strigosa* Emery, 1887:444. n. status N. Guinea, etc. [**6**]
(T) = *intricata* Emery, 1910:533. n. syn. Wilson
(T) = *curvata* Stitz, 1912:499. n. syn. Wilson
= *schlaginhaufeni* Viehmeyer, 1912:4. n. syn. Wilson

(T) = *nitens* Donisthorpe, 1949c:403. n. syn. Wilson
(T) *subcyanea* Emery, 1897a:548. N. Guinea, etc. [**6**]
(T) = *transversiruga* Emery, 1910:532. n. syn. Wilson
(P) = *aruana* Karawajew, 1925:78. n. syn. Wilson
(P) = *wallacei* Donisthorpe, 1932:474. n. syn. Wilson
(T) *tasmaniensis* Emery, 1898:232. n. status se. Australia [**21**]
(T) = *cristulata* Forel, 1900b:59, n. syn.
(P) *taurus* Forel, 1910:12. n. and c. Australia [**20, 28**]
(T) *tenuis* Forel, 1900b:58. coastal n. Queensland [**27**]
(T) *trachypyx* Brown, sp. nov. Australia: c. N. Territory [**28**]
(T) *turneri* Forel, 1910:14. Queensland: C. York [**30**]
(T) *tyloxys* Brown and Douglas, sp. nov. W. Australia [**29**, Figs. 36, 37]
(T) *versicolor* Brown, sp. nov. mts. of N. Caledonia [**33**]
(T) *victoriae* E. André, 1896:261. e. Australia [**15, 31**]
(T) = *modesta* Emery, 1895b:348. n. syn.
(T) = *scrobiculata* Forel, 1900b:59. n. syn.
(T) = *cedarensis* Forel, 1915b:15. n. syn.
(T) *violacea* Forel, 1907:269. n. status W. Australia [**13**]
(T) = *opacior* Crawley, 1925:583. n. syn.
(P) *viridis* (Clark), 1941:83. ne. S. Australia [**26**]
(T) *wilsoni* Brown, sp. nov. N. Caledonia [**33**]
yorkensis Forel, 1915b:12. Queensland: C. York

PARAPONERA Fr. Smith

= *Paraponera* Fr. Smith, 1858:110. Type: *Paraponera clavata* = *Formica clavata* Fabricius, monobasic.
= *Paraponera*, Emery, 1911:27.

This monotypic genus, exclusively neotropical, is well known and easily recognized from its giant size. Smith correctly noted the palpal segmentation: all castes of both sexes have a 5,3 formula. The female is winged, and both it and the worker have the hypopygium bordered on each side by an upwardly-directed comb of slender spinules. The male subgenital plate is in the form of a slender, upcurved biramous fork resembling that seen in the males of cerapachyines. The hind wings of both sexes have a well-developed anal lobe. Weber (1946) has discussed certain aspects of the morphology and habits, and has called attention to the resemblances *Paraponera* bears to *Ectatomma*. Larval morphology is covered by G. C. and J. Wheeler (1952a:117, pl. 2, figs. 1-9).

AULACOPONE Arnoldi

= *Aulacopone* Arnoldi, 1930a:139. Type: *Aulacopone relicta* Arnoldi, 1930a: 140, figs. 1-5, female, monobasic.

All that is known to me about the remarkable species *A. relicta* is contained in the original description, based on a single dealate female — still the sole specimen known. The genus, if correctly described and figured, is apparently closest to *Heteroponera*, but differs widely in the structure of the fronto-clypeal area (see key to genera, above). The type locality is in intermediate mountain forest at Alazapin, 40 km. southwest of Lenkoran in Russian Armenia.

ECTATOMMA Fr. Smith

< *Ectatomma* Fr. Smith, 1858:102. Type: *Ectatomma tuberculatum* = *Formica tuberculata* Olivier, by designation of Bingham, 1903.

= *Ectatomma* subgenus *Ectatomma*, Emery, 1911:42.

= *Ectatomma* subgenus *Ectatomma*, Wheeler, 1922:643.

In the Emery-Wheeler classification, *Ectatomma* included the nominate and three other subgenera: *Gnamptogenys*, *Poneracantha*, and *Parectatomma*. Mann (1922) and Borgmeier (1929) proposed the elevation of *Gnamptogenys* to generic rank. Santschi followed Emery and Wheeler, and even added two more subgenera in 1929, each subgenus to include a single species. These two names, *Tammoteca* and *Commateta*, never gained wide acceptance, and it seems clear that both should be placed in the synonymy of *Gnamptogenys* (see below). When all the species placed under *Ectatomma* in the sense of Emery and Wheeler are assembled, one finds that the assemblage is divided into two distinct groups on the basis of both adults and larvae. Concerning the larvae, the Wheelers (1952b) say, "*Emeryella*, *Stictoponera*, *Ectatomma* (*Poneracantha*), *E.* (*Parectatomma*), *E.* (*Gnamptogenys*) are so similar that they can be separated only by differences of a sort that distinguish species elsewhere. It is interesting to note that Emery in the Genera Insectorum regarded *Emeryella* as very close to *Gnamptogenys*." The Wheelers regard *Ectatomma sensu stricto* larvae as quite different from those of the genera and subgenera just listed (1952b: 657, 658).

My own studies, based on adult characters, are in good agreement with the larval findings. I find several good differences separating *Ectatomma* from its erstwhile sister subgenera, and when one gets used to the idea of separation, it is even a bit surprising that these two groups of species have been associated in one genus for so long. The workers of the true *Ectatomma* resemble in some ways those of the larger species of *Rhytidoponera* from Australia and New Guinea, and like *Rhytidoponera*, they always lack a tooth on the dorsal surface of the posterior coxa. The build of the worker alitrunk is distinctive, with its convex mesonotum (Fig. 2) set off on all sides by distinct sutural grooves, and its tendency (damped in two or three species) to develop three eminences on the pronotum; also, several of the species have evolved slit-shaped propodeal spiracles. The antennal insertions are covered by translucent bullae, very prominent and situated just within the frontal lobes, and the petiolar node is erect and more or less angular in the worker and female. The sexes have a well developed anal lobe on the hind wing, a character shared with *Paraponera*. All tarsal claws preserve the distinct submedian tooth.

Male genitalia are much like those of *Paraponera* (Weber, 1946), but the hypopygium is of the normal form. The wing venation of both sexes is of the "complete" type, the forewing having all of the primitive formicid elements except the first radial crossvein. The palpi are segmented 2, 2, in worker and female; the basal segment of the maxillary palp is broadened and strongly compressed, but is not very short like those of *Gnamptogenys* and *Rhytidoponera*. The apical segment of the maxillary palp is slender. In the male, the maxillary palp is normally 5-segmented, but occasionally the terminal segment is very short and fused to the preceding segment, so that there are only four movable segments. Relative lengths of segments variable, especially the last two. Male labial palpi 3-segmented.

The species of *Ectatomma* are mostly widespread and relatively successful insects, frequently common over wide areas of Mexico and Central and South America, southward into northern Argentina. Some species (*quadridens, ruidum*) are more usually encountered in forested areas, while others may occur in more open, even in arid areas (*opaciventre*). *E. tuberculatum* is found in rather arid districts as well as in rain forest. The genus is, however, rather strictly confined to those parts of the Americas with a tropical or warm subtropical climate. The biology of two of the common species (*tuberculatum* and *ruidum*) is reviewed in a full and informative account by Weber (1946). Among his more interesting observations, one may note that both he and Cook found that the eggs laid by the females became very dark in color, whereas worker-laid eggs may in some cases remain light in color, as is usual for other ants; also, the larvae are capable of some limited locomotion by crawling.

The species-level taxonomy of *Ectatomma* has been more or less confused, partly by mixups involving *muticum* and *edentatum*, also *ruidum* and *morgani*, and partly because of excessive accumulation of infraspecific names. Most of this confusion is rather simply dissipated when sufficient material of all the variable species is considered at one time. However, there remain a number of problems that can be settled only when more material from critical areas reaches the proper collections. Outstanding among these problems are the status of *confine* and *aztecum*, and the two north-south species pairs in South America, *lugens-permagnum* and *edentatum-morgani*. Weber (*op. cit.*) has already suggested synonymy for the variants of *E. tuberculatum*, and his suggestions are mostly formally adopted here.

Ectatomma species

(P) *acrista* Forel, 1909:254. n. status. Paraguay **[42]**
(T) *aztecum* Emery, 1901:50. s.w. Mexico **[34]**
(?) *confine* Mayr, 1870a:397. ''New Granada;'' C. America? **[35, Fig. 2]**
(P) *edentatum* Roger, 1863:173. s. Brazil, n. Argentina **[36, 41]**
(P) = *iris* Forel, 1909:253. n. syn.
(P) = *densestriata* Forel, 1912b:31. n. syn.
(P) = *inversa* Santschi, 1912b:521. n. syn.
(T) *lugens* Emery, 1894:144. n. status. Amazon-Orinoco basins **[37]**
(?) *macdonaghi* Forel, 1915a:351. n. status. n. Argentina **[36]**
(P) *morgani* Forel, 1912b:31. Amazon-Orinoco basins **[38]**
(P) *muticum* Mayr, 1870b:962. n.e. Brazil: Ceara, etc.; Mexico? **[41]**
(P) = *lobulifera* Forel, 1909:254. n. syn.
(P) *opaciventre* Roger, 1861b:169. s. Brazil, n. Argentina **[39]**
(P) = *concolor* Santschi, 1919a:37. n. syn.
(T) *permagnum* Forel, 1908:342. n. status. c. Brazil to Bolivia and n. Argentina **[37]**

(P) = *strigosum* Emery, 1894:144, nec Emery, 1887. n. syn.
(P) = *confusa* Forel, 1909:266. n. syn.
(P) = *aerea* Forel, 1912b:32. n. syn.
(T) *planidens* Borgmeier, 1939:418. s. Brazil [**40**]
(P) *quadridens* (Fabricius), 1793:362. Panama to n. Argentina [**40**]
(P) *ruidum* Roger, 1860:306. s. Mexico to Amazon Basin [**34, 38**]
(P) *tuberculatum* (Olivier), 1791:498. Mexico to n. Argentina [**42**]
(P) = *punctigerum* Emery, 1890b:56. syn. after Weber, 1946.
(P) = *irregularis* Santschi, 1921:83. syn. after Weber, 1946.

A key to the species of Ectatomma, based primarily on the workers

Note: The postpetiole and first gastric segment are one and the same. Both first and second gastric segments usually bear coarse piligerous punctures in addition to the sculpture discussed in this key. See qualifications marked with an asterisk (*) at end of key.

1. Second gastric segment very finely, superficially and evenly punctulo-reticulate and opaque, the reticulation not forming striolae except possibly some very fine indistinct ones near the margins or sides, away from the center of the disc . . . 2
   Second gastric segment in large part distinctly striate or striolate over the center of the disc . . . 3

2. Fine punctulo-reticulation of first gastric segment unrelieved on the disc (but often forming fine striolation across vertical anterior face of the tergite) (n. Argentina, s. Brazil) . . . *opaciventre* Roger
   Fine sculpture of first gastric segment generally overlain loosely by fine, irregular rugulation, transversely arched in front (Amazon Basin to Venezuela) . . . *lugens* Emery*

3. First and second gastric segments, as well as head, alitrunk and petiole, very regularly and evenly striate, similarly finely throughout . . . 4
   The second gastric segment, and often also the posterior part of the first, with sculpture finer or otherwise contrasted to that of the anterior half of the first segment . . . 5

4. Individual costulae of sculpture all with rather smooth and even surfaces; color of full adults approaching black (Venezuela to n. Argentina and Bolivia) . . . *quadridens* (Fabricius)
   Individual costulae of sculpture on head and alitrunk, especially on the

pronotum, with eroded, rough surfaces, in extreme manifestation yielding a beaded effect at magnifications of 80× or more; usual full adult color dull yellowish-brown, with alitrunk and gaster patchily infuscated above (se Brazil) .... *planidens* Borgmeier

5. Eye moderate in size, its greatest diameter approximately equal to, or shorter than, the length of the apical antennal segment 6
Eye larger, its greatest diameter distinctly greater than the length of the apical antennal segment 8

6. Pronotum with an obtuse, but very high and prominent median eminence and small but distinct, subrectangular lateral (humeral) tubercles Fig. 2) (Colombia, C. America, rare) .... *confine* Mayr
Pronotum without, or with only a very indistinctly differentiated median eminence; lateral tubercles or angles obsolete 7

7. Full adult color ferruginous brown, with yellowish legs and antennae; sculpture rather coarse and irregular, wavy or vermiculate on first gastric segment (Peru to Trinidad; see text) .... *morgani* Forel*
Full adult color piceous to black, legs and antennae not or scarcely lighter; transversely arched striation of anterior dorsum of first gastric segment rather smooth and regular, not wavy (s. Brazil, n. Argentina) *edentatum* Roger*

8. Node of petiole seen from side high, narrow, distinctly constricted near the middle of its height; anterior half of first gastric segment coarsely vermiculate or ruggedly reticulate-rugose (c. Mexico to Trinidad and Ecuador) .... *ruidum* Roger
Node of petiole seen from side gradually increasing in thickness from apex to base; at least the anterior half of the first gastric segment with rather regular, parallel rugulation or costation, this not or only gently wavy 9

9. Median and lateral eminences of pronotum suppressed, usually quite obsolete, or the laterals represented by brief indistinct dorsolateral margination; second gastric segment superficially transversely striate, the striation spaced and partly effaced anteriorly, so that this much of the disc is distinctly shining (Ceara, etc., in ne Brazil; ?sw Mexico) ...... *muticum* Mayr
Median and (more particularly) lateral pronotal eminences developed as more or less salient eminences or angles; second gastric segment finely, densely and regularly striolate (except in some samples of *tuberculatum*, but in these, the lateral pronotal eminences are very well developed and acute) 10

10. All surfaces of body and appendages covered with very numerous short, erect hairs; in perfect full-face view, more than 15 erect hairs projecting beyond the straight outline of the cheek between eye and anterior corner of head (sw Mexico) . . . . *aztecum* Emery
Erect hairs present, but longer and much less abundant; in perfect full-face view, fewer than 10 hairs (often none at all) visibly projecting beyond the straight outline of the cheek between eye and anterior corner of head 11

11. In perfect full-face view, the occipital border straight to feebly convex, usually with more or less rectangular occipital angles; head coarsely reticulate-rugose, the rugae enclosing foveae with more or less shining bottoms; color ferruginous except in N. South America, where some populations are more brownish (Mexico to n. Argentina) . . . . *tuberculatum* (Olivier)*
In perfect full-face view, the occipital border broadly concave; occipital angles narrowly rounded; head finely longitudinally striate, with some V-like rugules across the vertex; color deep reddish to black (e. Brazil to n. Argentina and Bolivia) . . . . *permagnum* Forel*

*The form *acrista* Forel, from Paraguay and vicinity, is probably only a southern extreme geographic variant of *tuberculatum* and is not keyed. The species pairs *lugens-permagna* and *edentatum-morgani* may indicate merely the ends of respective clines of single species. In both cases, material from the crucial intermediate zone in the Amazon Basin is lacking or insufficient.

GNAMPTOGENYS Roger

> *Gnamptogenys* Roger, 1863:174. Type: *Ectatomma* (*Gnamptogenys*) *tornatum* = *Ponera tornata* Roger, 1861, by designation of Emery, 1911.

> *Ectatomma* subgenus *Stictoponera* Mayr, 1887:539. Type: *Ectatomma coxale* Roger, 1860, by designation of Bingham, 1903. n. syn.

> *Ectatomma* subgenus *Holcoponera* Mayr, 1887:540. Type: *Holcoponera striatula* = *Gnamptogenys striatula* Mayr, 1883, by designation of Emery, 1911. n. syn.

> *Alfaria* Emery, 1896:41. Type: *Alfaria simulans* Emery, 1896, monobasic. n. syn.

> *Ectatomma* subgenus *Poneracantha* Emery, 1897a:547. Type: *Ectatomma* (*Poneracantha*) *bispinosum* = *Ectatomma* (*Holcoponera?*) *bispinosum* Emery, 1890, monobasic. n. syn.

> *Rhopalopone* Emery, 1897a:549. Type: *Rhopalopone epinotalis* Emery, 1897, monobasic. n. syn.

> *Emeryella* Forel, 1901a:334. Type: *Emeryella schmitti* Forel, 1901, monobasic. n. syn.

> *Ectatomma* subgenus *Mictoponera* Forel, 1901a:372. Type: *Ectatomma* (*Mictoponera*) *diehli* Forel, 1901, monobasic. syn. Emery, 1911.

> *Ectatomma* subgenus *Parectatomma* Emery, 1911:44. Type: *Ectatomma triangulare* = *Ectatomma* (*Gnamptogenys*) *triangulare* Mayr, 1887, by original designation. n. syn.

> *Spaniopone* Wheeler and Mann, 1914:11. Type: *Spaniopone haytiana* Wheeler and Mann, 1914, monobasic. n. syn.

> *Wheeleripone* Mann, 1919:282. Type: *Wheeleripone albiclava* Mann, 1919, by original designation. n. syn.

> *Opisthoscyphus* Mann, 1922:4. Type: *Opisthoscyphus scabrosus* Mann, 1922, monobasic. n. syn.

> *Ectatomma* subgenus *Commateta* Santschi, 1929c:476. Type: *Ectatomma* (*Parectatomma*) *bruchi* Santschi, 1922, by original designation, monobasic. n. syn.

> *Ectatomma* subgenus *Tammoteca* Santschi, 1929c:476. Type: *Ectatomma concinnum* = *Ectatomma concinna* Fred. Smith, 1858, by original designation, monobasic. n. syn.

> *Emeryella* subgenus *Barbourella* Wheeler, 1930:10. Type: *Emeryella* (*Barbourella*) *banksi* Wheeler, 1930, by original designation, monobasic. n. syn.

The genera and subgenera here placed in synonymy have been the subjects of long and painstaking inquiry. It was clear from the beginning of the study that the old association of *Gnamptogenys* with *Ectatomma* (*q.v.*) within one genus was incorrect, as Mann (1922) and Borgmeier (1929) already had indicated by their use of *Gnamptogenys* as a separate generic name. It now seems clear that *Ectatomma* (*sensu stricto*) is a phyletically "lower" ectatommine genus, whereas *Gnamptogenys* and the synonyms listed above constitute the "upper" ectatommines. As the present study progressed, the "upper" genera fell into four groups, as follows:

GNAMPTOGENYS Group (New World)

Gnamptogenys, *Poneracantha*, *Emeryella*, *Parectatomma*, *Commateta*, *Tammoteca*, *Barbourella*.

HOLCOPONERA Group (New World)

Holcoponera, *Spaniopone*.

STICTOPONERA Group (Old World)

Stictoponera, *Rhopalopone*, *Mictoponera*, *Wheeleripone*.

ALFARIA Group (New World)

Alfaria, Opisthoscyphus.

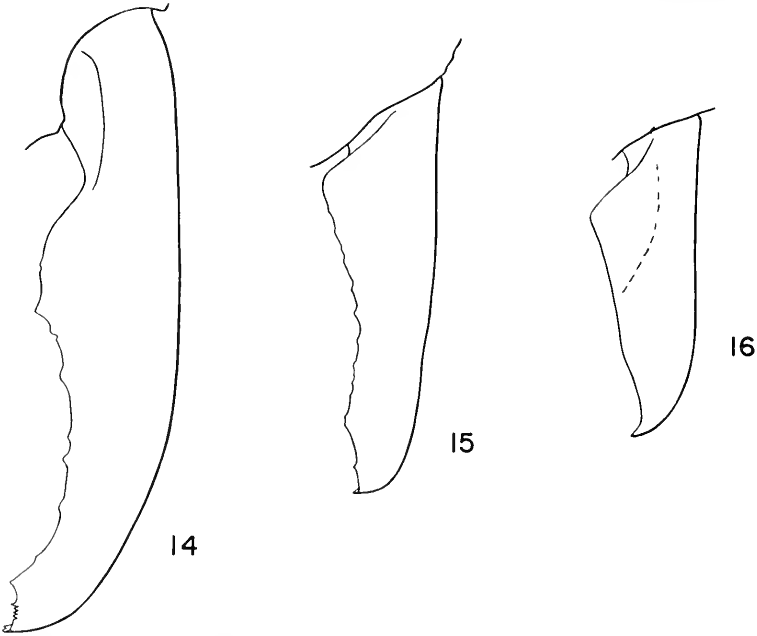
Within each group, it is now safe to consider the genera synonymous. The justification for this synonymy is now offered for each group in turn.

GNAMPTOGENYS Group

The genera and subgenera in this group have been separated primarily on the basis of mandibular structure, and secondarily on alitruncal suturation, plus propodeal armament. The mandibular forms represented grade through from the extremes by way of a remarkably finely stepped array of intermediate species, assembled for the first time during the course of this study. This series of species can be divided only by the drawing of arbitrary lines, with no natural gaps to help in the drawing of these lines. The other characters that have been used to divide this assemblage of species prove useless because they are not in concordance with the more conspicuous mandibular tendencies. Of course, it is possible to eliminate the troublesome "intermediate" species, those carrying "diagnostic" characters discordantly, by relegating them to monotypic subgenera, as Santschi did with *Tammoteca* and *Commateta*. But Santschi's approach, whether cynical or extremely naive, seems justly to have been shunned by other specialists in the Formicidae.

Everything considered, it makes better biological sense to drop the artificial generic assortment of these species. This done, it becomes easier to recognize and describe the very interesting phylogenetic trends in development of the mandibles within the group, considered as one radiating unit. The primitive mandibular form apparently is the triangular type more or less characteristic of the *Parectatomma* species, and also found more or less faithfully copied in *Poneracantha* and in the species of the *Holcoponera*, *Stictoponera*, and *Alfaria* groups. In this type, apical and basal borders are approximately perpendicular to one another (Figs. 41, 43, 44), but, contrary to the impression given by some older writings, these two borders most often meet through a distinct curve, even considering that this curve can in some cases be rather sharply rounded.

In the *Gnamptogenys* group, variation away from the triangular condition follows a double morphocline (*sensu* Maslin 1952). One of the two series of variants, expressed approximately in the consecutive arrangement *aculeaticoxae* → *hartmani* → *nigrifrons* → *bruchi* → *haenschi* → *concinna* → *alfaroi* → *tornata* → *mordax*, shows a tendency toward broadening the curve of the basal angle until, in extreme cases such as *mordax*, the basal and apical borders have become continuous, and the mandible has achieved a linear shape. Accompanying this change of shape, the blade of the mandible is becoming more and strongly deflected ventrad in its apical half, so that the mandibles as seen from the side are strongly arched, while the dentition transforms into a vaguely double-ranked set of blunt tubercles.



Figures 14-16. *Gnamptogenys* spp., dorsal views of left mandibles. Fig. 14, *G. semiferox*, sp. nov., paratype worker. Fig. 15, *G. mediatrix* sp. nov., holotype worker. Fig. 16, *G. rastrata* (Mayr), holotype female. All drawn to same scale.

If we follow the other morphocline outward from *aculeaticoxae* in the series represented roughly by *aculeaticoxae* → *triangularis* → *rastrata* → *mediatrix* → *semiferox* → *Emeryella schmitti*, we see the blade first lengthen without losing its triangular shape, and then, beginning with *rastrata* and *mediatrix*, it becomes concave along the masticatory margin and more convex along the outer margin, with further increase in length (Figs. 14-16), until an extreme falciform shape is attained in *schmitti*. The mandible of *E.* (*Barbourella*) *banksi* belongs with the group just discussed, but it is slightly aberrant in its own right; the difference is not great enough to support the separation of *banksi* in a monotypic genus or subgenus. The morphocline that obliterates the distinction between *Gnamptogenys* and *Emeryella* as genera also brings *Barbourella* into the fold. It should be noted that this morphocline has been completed by the two new species described in this contribution — *G. mediatrix* and *G. semiferox* **[78, 77]**.

The other character previously utilized in making subgeneric and generic splits in this group, the alitruncal suturation, consists in its generalized condition of a weakly impressed, but fully ankylosed, semicircular line marking the promesonotal suture, and a straight, deeply cut transverse line at the site of the metanotum (metanotal groove; most *aculeaticoxae* → *schmitti* morphocline members). In the *aculeaticoxae* → *mordax* morphocline, effacement of one or both of these lines is erratic in its expression among species and species-groups, and intermediate stages exist in all possible combinations. There seems to be no practicable means of using this suturation for the definition of groupings worthy of formal generic or subgeneric names, and convergence here makes even the plotting of informal species-groups a more or less arbitrary matter.

In this group, there remains one aberrant species, *G. bispinosa* (Emery), that has previously been assigned to a separate subgenus, *Poneracantha*. *G. bispinosa* has very long propodeal spines, but *G. aculeaticoxae* has small, acute teeth in the same position, and in this and other ways, *aculeaticoxae* and the new species, *mecotyle*, are intermediate between *bispinosa* and the other *Gnamptogenys*. There remains the somewhat different form of the head in *bispinosa*; however, to anticipate the findings of synonymy among the four generic groups for which evidence is offered below, the cephalic difference cannot well stand as a generic character when such a diverse group of other species is included in *Gnamptogenys.* In this, I only follow the evidence of the larvae, dealt with farther below.

HOLCOPONERA Group

Holcoponera has seemed like a compact and well-defined genus up to the time of this study, and I treated it as a genus in early drafts of this revision. The workers and females are similar to those of *Gnamptogenys* in their widespread and uniform costulate sculpture, but the workers have a more compact, dorsally convex alitrunk, crossed by a single suture (the promesonotal suture) which is deeply cut, and, at least to external appearances, completely separates the alitrunk into two parts. No such complete suturation is found in *Gnamptogenys sensu stricto.* The node of the petiole in worker and female is erect or inclined posteriad, usually more or less cupuliform to thick disciform. Added to the seemingly clearcut alitruncal difference in the worker there has previously been stressed a character in the forewing of the male, namely, the absence of the second and third abscissae of Rs; but this character is now known to occur in some species of undoubted *Gnamptogenys* as well. G. C. and J. Wheeler found the larvae of *Holcoponera* distinct from the related genera in that the head hairs were branched or bifurcate, whereas those of the related genera examined had simple head hairs. This character may eventually prove useful in segregating a generic group that could bear the name *Holcoponera*, but at the present time, its usefulness is greatly restricted by the fact that only a very few species of "higher ectatommines" have been examined in the larval stage. Of these few species, none are particularly "critical" in problems involving generic limits, and among them are none of the species that seem to be intermediate between *Holcoponera* and the other "higher" genera. Such species do exist, as I found to my great inconvenience at a time when I thought I had this revision just about completed, except for minor details.

In speaking of the connections I have discovered between *Holcoponera* and other groups, it should first be emphasized that

Holcoponera is not as large a genus in number of species, races and varieties as Santschi and others have considered it to be, nor is it quite as homogeneous a group as some, including myself, have thought. The first steps toward this realization were made in a recent paper (Brown, 1957) in which several forms were synonymized, two new species were described, and a species formerly placed in *Rhopalopone* (*relicta* Mann) was transferred into *Holcoponera*. Of the two new species added, one, *H. acuta*, was merely somewhat bizarre in possessing a petiole toothed at the summit; the other, *H. mina*, was seen to form a bridge between the more "typical" *Holcoponera* members (specifically, *H. strigata*) and *relicta*, hence the generic transfer. The species *relicta* was not transferred from *Rhopalopone* just because it fitted so very badly there, but because I felt that it was a little closer to *Holcoponera*, especially considering the fact that all other known *Rhopalopone* (synonym of *Stictoponera*, and therefore of *Gnamptogenys*, see below) species were Indo-Melanesian in distribution. It can be seen from this that the separation of *Holcoponera* from *Stictoponera* was more a matter of geography and convenience than morphological distinctness, but so long as no further difficulties arose, it seemed best to me to preserve the old and familiar generic arrangement for practical reasons. But further difficulties *have* arisen.

The species *reichenspergeri*, described by Santschi in *Acanthoponera*, was viewed belatedly, and proved not to belong to the genus in which Santschi had placed it. Instead, it was found to have characters allying it with *Holcoponera*, with the "*Rhopalopone*" group of *Stictoponera*, and with *Spaniopone*. The gastric sculpture **[74]** does not have the regular costulation of the other New World species, and all in all, I think we must realize that *reichenspergeri* is the last straw to be piled on the already considerable weight of evidence against the separation of the three major generic groups centered around *Gnamptogenys*, *Holcoponera* and *Stictoponera*. We can add to this evidence farther below in discussing the characters of new species in the *Stictoponera* Group, but before we leave the *Holcoponera* Group, it seems well to discuss briefly the monotypic genus *Spaniopone*.

Wheeler and Mann described *Spaniopone haytiana* as a proceratiine because of superficial resemblances to *Proceratium*, but Emery (1919, p. 107) soon pointed out the characters that allied *S. haytiana* with what I now call the "higher" ectatommines. Although Emery's comments were ignored by Wheeler in his 1922 classification, it is clear that Emery was correct in stating the relationships of *Spaniopone*. Among former *Holcoponera*, two species, *mina* and *relicta*, make approaches to *Spaniopone* in several respects, as does the omniparent *reichenspergeri*. If *haytiana* had been discovered in New Guinea or Java, rather than in Haiti, the chances are that it would have been placed in *Rhopalopone* from the beginning; certainly, there is nothing striking to separate it from the described "*Rhopalopone*" we already know from the Old World. Instead of a monotypic genus, it seems we have here just another moderately modified descendant of an old faunal element that was neither *Holcoponera* nor *Stictoponera*, but was ancestral to both stocks — in short, we have another intergradient species.

In view of the above facts and interpretations placed on them, it can be seen that we have in *Holcoponera* a stock that has been born and has radiated within the New World tropics, and that has attained a certain degree of adaptive success while evolving along a certain morphological pathway. There are some species, among them the common species, that we can point to and say, "There is *Holcoponera*." But we must not forget that there are other species of which we must say, "That could be *Holcoponera*, or it could be *Stictoponera*." Now, the question arises, should we recognize the new adaptive penetration that the *Holcoponera* stock has apparently made, and upon which its radiation is based, by granting the group generic status? Or should we emphasize instead the continuing existence of intergradient species, albeit frequently exceedingly rare and local ones, that still link the *Holcoponera* stock with other, independently radiating sister groups? I take the second choice because I believe that it is the most practical one. If we separate *Holcoponera* by drawing an arbitrary line around it, we shall never rest easy about distinguishing, or keying, or making biological statements about, the groups sundered in this way. The claim is often made that genera with many species become "unwieldy" — although it is never stated just how one gains by splitting such a genus on arbitrary lines into two or more genera, or, worse, into subgenera. We have only to look at the generic classification of the birds, or, within the ants, at the subgeneric classification of *Camponotus*, to see where such arbitrary splitting leads.

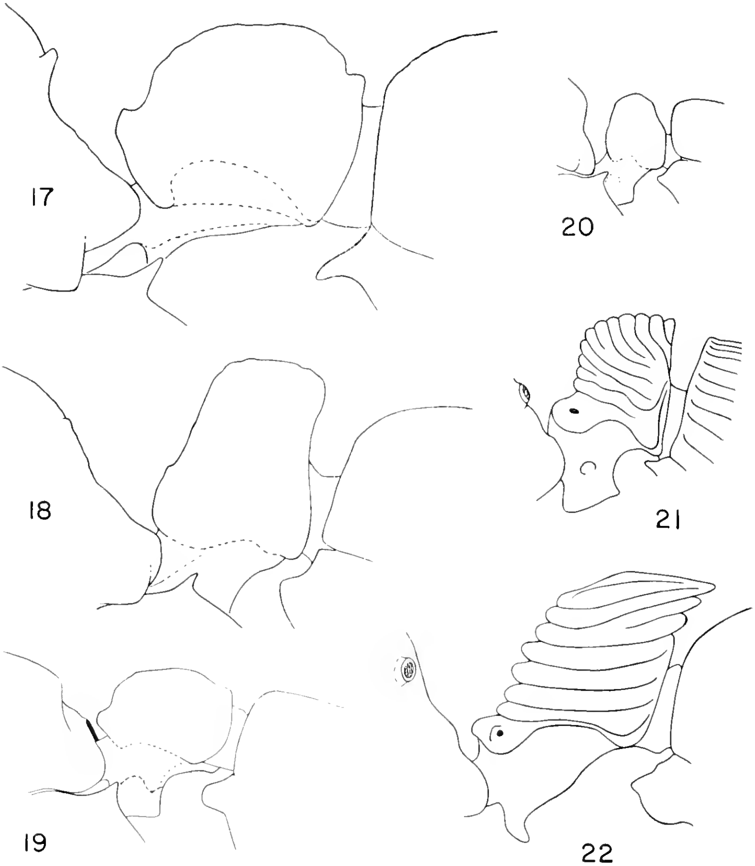
I feel that it is best to recognize now, while there are still few enough species known in the ectatommine tribe for one man to see and assimilate in one revisionary effort, that the old generic limits are mostly fading under the accession of new species, rather than the reverse. There is every reason to believe that many more species exist, unknown, and it is from the ranks of these rare and local forms that so many of our intergradient species come. We shall do the future discoverers of these forms a service if we give them a reasonably clear choice among a few large- and medium-sized genera instead of presenting them with a welter of small genera, none of which are sharply defined. And, just as important on the theoretical level, we shall be defining our genera in the way that is closest to objectivity, by stressing the gaps left when the intergrades die out. This is not, however, meant to discourage the search for new characters that may lead to new phylogenetic concepts and to new and more objective generic splits.

STICTOPONERA GROUP

The genus *Rhopalopone*, already discussed under the *Holcoponera* Group, above, is clearly a key group in ectatommine classification. Due to an extraordinary series of oversights, Emery, Forel, Wheeler and Mann all missed the extra tooth on the tarsal claws of (most) *Rhopalopone* species, and therefore continued to classify this genus in subtribe Typhlomyrmicini (see introductory section), apart from *Stictoponera* and *Wheeleripone* — the genera with which it is actually so closely allied as to be inseparable on any rigorous basis.

Another character supposedly distinguishing *Rhopalopone* was its possession of a fairly well defined funicular club; but this character is rendered worthless by the fact that club distinctness grades through without regard for the old generic limits between

Rhopalopone and *Stictoponera.* Mann's diagnosis of *Wheeleripone* and Wheeler's 1922 key to the ectatommine genera grant unwarranted value to the state of the alitruncal suturation and



Figures 17-22. *Gnamptogenys* spp., workers, side views of petioles and adjoining structures. Fig. 17, *G. biroi* (Emery) from near Sogeri, Papua (ex *Stictoponera*). Fig. 18, *G. panda* (Brown) from near Muping, Sikang Prov., western China (ex *Stictoponera*). Fig. 19, *G. chapmani* sp. nov., holotype. Fig. 20, *G. epinotalis* (Emery) from the Huon Peninsula, New Guinea, Wilson No. 931 (ex *Rhopalopone*). Fig. 21, *G. mina* (Brown), paratype (ex *Holcoponera*). Fig. 22, *G. acuta* (Brown), paratype (ex *Holcoponera*). Figs. 17-20 are all drawn to the same scale; Figs. 21 and 22 drawn to a very slightly larger scale.

to the degree of undercurvature of the gaster; actually, these traits are graded in degree, and differ by species rather than by genera. A review of almost all the Old World species shows clearly that the characters so far employed will not separate *Rhopalopone*, *Stictoponera* and *Wheeleripone* as generic entities. If we look at all the species of this group together, we can see better whether a division is necessary.

The first thing one notes is that there are two extremes of nodal form among the species. In *coxalis* and relatives, the petiolar node is low and paniform (Figs. 17, 19), while in all the former *Rhopalopone* species examined, the node is erect and more or less anteroposteriorly compressed, even unto the form of a thick, blunt scale (Fig. 20). In addition, the *Rhopalopone* species are quite small, and the *Stictoponera* species described up to now have been considerably larger. However, we must note the following exceptions.

The species *taivanensis* and *panda* combine *Rhopalopone* nodes (Fig. 18) with *Stictoponera* size. The new species *chapmani* (Fig. 19) is typically *Stictoponera* in form of node, but is in the *Rhopalopone* size range. In *Wheeleripone*, *albiclava* would fall into *Stictoponera* in all characters, *crenaticeps* and *aterrima* fit best in *Rhopalopone*, and *lucida* is in between. I think this summary of the status of the diagnostic characters should serve as convincing proof of the futility of trying to separate the *Stictoponera* Group species as genera or subgenera. It is an equally difficult matter to separate these Old World forms from the New World ones. In the matter of sculpture, for instance, one finds that the new species of the *Stictoponera* Group from New Guinea (*G. grammodes*, and certain of the *Rhopalopone* species) approach, in the extent of their costulate or striate sculpture, the New World *Gnamptogenys*. Then, how does one separate *Spaniopone haytiana* from the smaller *Rhopalopone?* Or the latter from Mann's *relicta* of Brazil? Or Borgmeier's *Alfaria striolata* (Brazil) from the Old World *Stictoponera?* I think that the answer must be that we cannot separate these species or groups of species into genera or subgenera on the presently recognized characters.

ALFARIA Group

As I shall show in my species-level treatment of this group **[65]**, Mann's genus *Opisthoscyphus* was founded on an artist's misrepresentation of the species formerly known as *Alfaria minuta* Emery. It is easier to eliminate this name than to account for the position of *Alfaria* as a genus. Of the nine species described in *Alfaria*, only four appear to stand at present. *A. simulans*, *A. bufonis* and *A. minuta* share as a characteristic the extremely inflated second gastric segment, but *A. striolata* has a less strongly developed second gastric segment, in this respect coming much closer to some species of the former genera *Stictoponera*, *Rhopalopone* and *Parectatomma*. In its sculpture also, *A. striolata* is more typical of *Stictoponera*, and, in fact, *striolata* connects the other three valid *Alfaria* species so broadly to *Gnamptogenys* that I am forced to still another generic synonymy. This is the way generic revisions in the ants seem often to end; when I began this section, I would have bet on *Alfaria* as the most firmly founded and most distinct of the ectatommine genera, and I gave up the idea of generic distinctness for the group only when I first saw Father Borgmeier's *striolata*.

This completes the survey of the four groups of higher ectatommine genera. I think I have made a reasonable case for the synonymy of the genera and subgenera within each group, and it also now seems plain that no clear distinction exists among the groups, at least so far as we now know. Following the evidence as I see it, I have assigned all of these generic and subgeneric names to the synonymy of *Gnamptogenys*. This synonymy is set down with the greatest reluctance, and with the hope that some future study based on better material may establish a clear division of the species.

The species now falling in *Gnamptogenys* are very various, as might be expected by the former large number of genera and subgenera now included in the concept; however, there are as many features of homogeneity among these species as there are of heterogeneity. The *Gnamptogenys* species run for the most part to compact, heavily sclerotized forms. The size is small to medium-large, and the eyes of the workers range from minute to large. The shapes of the head and body are rather conservative, and never really bizarre, although the elongate mandibles of the *schmitti* and *mordax* groups are unusual modifications of the triangular type found in most species. No distinct scrobes are formed to receive the antennae, and the clypeus is present and distinct as a broad, convex shield extending across the front of the head over the mandibles. Frontal carinae horizontal and with distinct, horizontal lobes roofing to some extent the antennal insertions. The eyes are usually placed near or behind the middle of the sides of the head, rarely absent. Antennae 12-segmented, with or without a club at the apex of the funiculus. Palpi of worker and female segmented 3,2 or 2,2. The 3,2 formula has been found in workers or females of *aculeaticoxae, alfaroi, annulata, bispinosa, chapmani, concinna, coxalis, menadensis* and *schmitti*, although the basal segment is short and very easily missed. A few species, notably *mordax* and close relatives, have lost one maxillary segment (perhaps the basal and second segments have fused), so that they now have a formula of 2,2. The former *Holcoponera* species, including *relicta, porcata* and forms of the *striatula* complex, all actually dissected, have formulae of 2,2, with the basal segment of the maxillary palp compressed and triangular, the free angle bearing a stout sensillum; the apical segment is long, slender and weakly curved. *G. minuta* (formerly *Alfaria m.*) has a formula of 1,2, *teste* Borgmeier, 1957:117.

The alitrunk is compact, and usually has a simple dorsal outline seen in profile, either convex or straight, rarely with a deeply impressed metanotal groove. Either the promesonotal suture or the metanotal groove, or more rarely both, may be developed to varying degrees, but the promesonotal suture, even when apparently completely separating the alitrunk into two parts (as in many former *Holcoponera*), seems to confer little or no flexibility upon the alitrunk. The propodeum may have a distinct declivity, or it may merge into the dorsal surface. The propodeum usually is unarmed, but small paired teeth are present in a few species, and these reach large size in *bispinosa*. A character of importance occurs on the dorsal face of the posterior coxae, each of these having a distinct tooth, spine or tubercle. This armament of the hind coxae is exclusive to the genus *Gnamptogenys*, and is lacking in only a few species scattered through different groups, so that it seems very likely that it is a primitive trait secondarily lost in these species. The tarsal claws of each leg usually bear each a median or subbasal tooth, which may be difficult to detect except at very high magnifications in ideal silhouette against a brightly lighted background; in *epinotalis*, the extra tooth appears to be absent from the middle and hind tarsi, but is present on each fore tarsal claw. The extra tooth is well developed in the larger species, but tends to be inconspicuous in the smaller, cryptobiotic forms.

The petiolar node varies in form (Figs. 17-21, 42) from low paniform to thick disciform; a few species have the summit produced posterodorsally as a blunt tooth (Fig. 22). The form of the gaster varies with the species group; usually the postpetiole is separated from the succeeding (second gastric) segment by a very distinct constriction, and the latter segment is more or less distinctly undercurved. The remaining apical segments are reduced and more or less retractile within the second gastric segment. A functional sting is always present in the castes of the female sex.

Sculpture in *Gnamptogenys* species is based on a thick, heavy integument, so that figures can be and often are deeply cut and bizarre. The New World species are mostly covered with costulate or striate sculpture of a very regular and striking kind, whereas in the Indo-Melanesian species, striate and costulate sculpture is either absent or present over only limited areas of the body, and deep-set, umbilicate foveolae are often substituted. In the smaller, cryptobiotic species of both continents, the sculpture tends to become shallower and finer, and punctation may become mixed with striation or rugulation on the same surfaces.

Pilosity is normally simple and fine, the hairs being of uneven lengths, erect or suberect, and usually fairly abundant but not overly conspicuous. Smaller hairs may form a pubescence of the subappressed kind over parts of the appendages or other limited areas of the body.

Color of the worker and female castes varies from jet black, sometimes with contrasting light-colored appendages or sections of appendages, to testaceous in some small cryptobiotic species. The adults take a long while to develop full pigmentation, so that a full range of yellow and reddish examples may occur in the nest of a species that is definitively black. This color problem has been the cause of considerable synonymy at the species level.

It is perhaps risky to generalize concerning the sexual castes, since these are known for only a fraction of the species; females are known for more species than are males, since the nests are frequently small and the females therefore not difficult to find and take. Most females are either known in the winged state or from apparently normally dealate queens, but a few species, particularly among the smaller ones, have ergatoid queens without wings or fully developed flight sclerites in the thorax.

The males are quite distinct from the female castes, and are always winged. The size is usually slightly smaller than the workers of the same nest, and the head is much modified from the female-worker plan. The eyes are very large, occupying often a major portion of the sides of the head. Mandibles usually remaining fairly well developed, triangular and with serial dentition, but possibly not importantly functional. The palpi usually have more segments than in the worker, and perhaps this is invariably true. The basic formula in the male is maxillary 5, labial 3, but in some species or individuals there may be variable reduction. Thus, the fourth and fifth maxillary palp segments are fused in *concinna*, but are still distinguishable, and Kusnezov (1954:34) claims that the *triangularis* male has a formula of 4, 2. The notauli and parapsidal furrows are well developed (so far as known), and the scape is shorter, usually very much shorter, than the funiculus, appearing much the same as one of the longer funicular segments. The genitalia are retractile, or largely so, but the genital capsule is usually extruded in the available material. The parts are heavily sclerotized and rather simple, resembling the corresponding pieces of *Myrmica* so far as investigation has gone. The subgenital plate is unremarkable, being usually narrowly rounded and pubescent at its apex. However, very few species have been given more than a very superficial examination.

Wings similar in male and female, usually of the "complete" type, with all basic formicid elements in the forewing except the first radial crossvein. In some species (e.g., *G. mordax*, Brown and Nutting, 1950: pl. 8, fig. 5) Mf2 is completely contracted, and in quite a few others (*Holcoponera* Group), Rsf2·3 has disappeared as well.

The male sculpture is usually much reduced as compared to that of the corresponding workers, and is often largely effaced to give smooth, shining areas of wide extent, particularly over alitrunk and gaster. Otherwise, the sculpture is often a feeble and much less regular version of the corresponding worker's. The pilosity is little different from that of the female castes, but the color is often darker. Males are often taken separately at light, and in this case, it is usually impossible to determine to what worker-based species they belong, unless previous association has been made from nest material. Furthermore, we know very little about variation in the males, either individual or geographic, and it seems from the present evidence that this sex is not going to play a very important role in the taxonomy of the group. Final judgment on this matter, however, will have to rest on closer examination of a much more nearly representative sample of the species.

The larvae of species now included in *Gnamptogenys* are described by G. C. and J. Wheeler in their ''Ant larvae of the subfamily Ponerinae'' (1952a, pp. 121-124, 127-128, 132-134, pls. 3-5), and the generic affinities discussed in Part II of the same work (1952b, pp. 657-660).

As limited here, *Gnamptogenys* is known from two areas: one in the Old World, from Ceylon and western China to Fiji; and the other in the New World, from Texas to Tucumán and Buenos Aires, including Hispaniola in the Antilles. It seems safe to consider the genus a part of the ''Old Endemic'' fauna of South America, present there at the beginning of the Tertiary. Some of the imperfectly known fossils of the Tertiary (Oligocene) in Europe and North America are close to *Gnamptogenys,* and at least one does actually belong to the genus. Like *Heteroponera,* the Old and New World branches of *Gnamptogenys* show some separate radiation, but without loss of the linking species, particularly the small ''*Rhopalopone*'' forms.

We know very little about the biology of *Gnamptogenys* species, since many of them are rare and secretive in habits. Most of the species are restricted to moist tropical forests, where they nest mostly in rotten wood or in the soil; a few are semi-arboreal nesters in epiphyte ''peat,'' at least facultatively so. Usually, the colonies consist of only a few individuals, probably in most cases under 100, and frequently under 50. The queen is usually a dealate, more rarely an ergatogyne, and some colonies may have several reproductive females. The food probably consists mostly of small arthropods; Mann (1934:177-178, pl. 6) found *schmitti*, a long-mandibulate species, preying on millipeds in Haiti, and it seems likely that other specialized types of mandibles in the genus reflect prey preferences as yet unknown.

GNAMPTOGENYS species

Only new synonymy is listed here. Old synonyms can be found in Emery, 1911; Santschi, 1929c; Brown, 1954c, 1957. The new combinations are marked with an asterisk (*). Following the grand list, the trivial names are listed again in the genera or subgenera in which they stood prior to this publication; the order is that of the grand list, and all names are listed, whether synonyms or not.

(P) *aculeaticoxae* (Santschi), 1921:81. * Panama to Bolivia [**45, 73**]
(P) *acuminata* Emery, 1896:50. Amazon-Orinoco drainage [**43**]
(T) *acuta* (Brown), 1957:491. * Bolivia, Peru [**46**, Fig. 22]
(T) *albiclara* (Mann), 1919:283. * Solomons: Ysabel I.
(P) *alfaroi* Emery, 1894:145. Costa Rica [**50**]
(P) *annulata* Mayr, 1887:543. se. Brazil, Bolivia n. to C. Amer. [**44**]
(P) *arcuata* (Santschi), 1929c:457. * se. Brazil [**79**]
= *regularis* (Santschi), 1929c:457, nec Mayr, 1870. * n. syn.
(T) *aterrima* (Mann), 1921:411. * Fiji
(T) *banksi* (Wheeler), 1930:10. * Panama
(P) *bicolor* (Emery), 1889:493. * se. Asia [**47**]
(P) *binghami* (Forel), 1900a:317. * Burma, Borneo, Philippines [**47**]
(P) *bispinosa* (Emery), 1890a:40. * Panama, Costa Rica [**49**]
(P) *biroi* (Emery), 1902b:154. * N. Guinea [**47**, fig. 17]
(T) *bruchi* (Santschi), 1922:241. * n. Argentina
(T) *bufonis* (Mann), 1926:101. * s. Mexico [**65**]
(T) *chapmani* Brown, sp. nov. Philippines [**58**, Figs. 19, 44]
(P) *concinna* (Fr. Smith), 1858:103. Bolivia to C. America [**57**]
= *romani* Wheeler, 1923a:2. n. syn.
(T) = *semicircularis* Borgmeier, 1929:195. n. syn.
(P) = *conica* Borgmeier, 1929:196. n. syn.
(T) *continua* Mayr, 1887:544. s. Mexico to s. Brazil [**56**]
(P) = *panamensis* Santschi, 1931:265. n. syn.
(P) *costata* (Emery), 1889:494. * Tenasserim to Sumatra, Philippines [**47**]

(T) *coxalis* (Roger), 1860:308. * Ceylon [**47**]
crassicornis (Forel), 1912a:51. * Sumatra [**47**]
(T) *crenaticeps* (Mann), 1919:285. * Solomons: Ysabel I.
(T) *cribrata* (Emery), 1900:311. * N. Guinea [**53**]
(P) *curtula* (Emery), 1896:44, 47. * s. Mexico, C. America [**70, 79**]
(P) = *stolli* (Forel), 1899a:7. * n. syn.
(T) *dammermani* (Wheeler), 1924:2. * E. Indies, Philippines [**53**]
(T) *diehli* (Forel), 1901a:372. * Borneo [**53**]
(T) *epinotalis* (Emery), 1897a:550. * N. Guinea [**53**, Fig. 20]
(T) *exarata* Emery, 1901:50. Amazon-Orinoco drainage [**54**]
(T) *gracilis* (Santschi), 1929e:468. * British Guiana
(T) *grammodes* Brown, sp. nov. Papua [**60**, Fig. 41]
(T) *haenschi* Emery, 1902a:27. Bolivia, Peru, Ecuador [**51**]
(T) *hartmani* (Wheeler), 1915a:390. * Texas [**52**]
(T) *haytiana* (Wheeler and Mann), 1914:11. * Haiti [**63**]
(T) *horni* Santschi, 1929e:475. n. status Panama to Bolivia [**62**]
(T) *interrupta* Mayr, 1887:543. C. America, ?S. America [**55**]
(T) *kalabit* Brown, sp. nov. n. Borneo [**59**, Fig. 43]
(P) *laevior* (Forel), 1905:7. * Java [**47**]
lucida (Mann), 1919:285. * Solomons: Malaita I.
(T) *luzonensis* (Wheeler), 1929:30. * Philippines [**53**]
(T) *macretes* Brown, sp. nov. Papua [**61**]
(?) *magnifica* (Santschi), 1921:81. * sw. Brazil [**71**]
(T) *major* (Emery), 1902b:154. * N. Guinea [**53**]
(T) *malaensis* (Mann), 1919:281. * Solomons: Malaita I. [**53**]
(T) *mecotyle* Brown, sp. nov. Bolivia [**66**, Fig. 42]
(T) *mediatrix* Brown, sp. nov. Brazil [**78**, Fig. 15]
(P) *menadensis* (Mayr), 1887:539. * E. Indies, Philippines [**47**]
(T) *menozzii* (Borgmeier), 1928a:32. * se. Brazil [**64, 73**]
(T) *mina* (Brown), 1957:494. * Bolivia, Peru [**46, 73**, Fig. 21]
(T) *minuta* (Emery), 1896:106. * S. and C. America [**65**]
(T) = *emeryi* (Forel), 1901b:326. * n. syn.
(T) = *scabrosus* (Mann), 1922:5. * n. syn.
(P) = *mus* (Santschi), 1931:265. * n. syn.
(T) = *panamensis* (Weber), 1940:80, nec Santschi, 1931. * n. syn.
(T) = *carinata* (Weber), 1940:82. * n. syn.
(P) *moelleri* (Forel), 1912b:34. * se. Brazil [**81**]
= *splendens* (Santschi), 1929e:450. * n. syn.
(T) *mordax* (Fr. Smith), 1858:98. C. and S. America [**69**]
(P) = *nodosa* (Latreille), 1802:217. n. syn.
(P) = *parensis* Forel, 1912b:33. n. syn.
(T) = *sebastiani* Borgmeier, 1937:220. n. syn.
(T) *nigrifrons* Borgmeier, 1948:199. Peru
(T) *panda* (Brown), 1948a:263. * w. China [**48**, Fig. 18]

(P) *pleurodon* (Emery), 1896:47. * Amazon drainage [**71, 72**]
(P) = *emeryi* (Santschi), 1929c:463, nec Forel, 1901. * n. syn.
(P) = *recta* (Santschi), 1929c:465. * n. syn.
(P) = *vidua* (Santschi), 1929c:467. * n. syn.
(P) *porcata* (Emery), 1896:48. * Costa Rica [**71**]
(T) *posteropsis* (R. Gregg), 1951:77. * Sumatra, Philippines [**47**]
(T) *rastrata* (Mayr), 1866:890. * se. Brazil [**73**, Fig. 16]
(T) *regularis* Mayr, 1870b:965. s. Mexico to Paraguay [**68**]
(P) = *splendida* Pergande, 1895:871. n. syn.
(P) = *fiebrigi* Forel, 1909:253. n. syn.
(T) *reichenspergeri* (Santschi), 1929b:274. * se. Brazil [**74**]
(T) *relicta* (Mann), 1916:403. * Matto Grosso [**46**]
(P) *rimulosa* (Roger), 1861a:18. se. Brazil [**75**]
(?) *rustica* (Santschi), 1929c:446. * Paraguay [**79**]
(P) *schmitti* (Forel), 1901a:334. * Haiti [**83**]
(T) = *minor* (Wheeler), 1936:195, nec Forel, 1900. * n. syn.
(T) *schubarti* (Borgmeier), 1948:198. * se. Brazil [**64, 73**]
(T) *semiferox* Brown, sp. nov. Dominican Republic [**77**, Fig. 14]
(P) *simplex* (Emery), 1896:48. * C. America [**46**]
(?) *simplicoides* (Forel), 1908:341. * se. Brazil [**79**]
(T) *simulans* (Emery), 1896:42. * C. America [**65**]
(?) *spiralis* (Karawajew), 1925:79. * Java [**47**]
(P) *striatula* Mayr, 1883:32. S. America, Jamaica, etc. [**79, 46**]
(P) = *brasiliensis* (Emery), 1902c:181. * n. syn.
(P) = *angustiloba* (Forel), 1908:341. * n. syn.
(P) = *angustipleura* (Forel), 1908:342. * n. syn.
(P) = *paulina* (Forel), 1908:342. * n. syn.
(T) = *pernambucana* (Santschi), 1929c:452. * n. syn.
= *calcarata* (Santschi), 1929c:452. * n. syn.
= *hybrida* (Santschi), 1929c:455. * n. syn.
(P) *strigata* (Norton), 1868:4. * s. Mexico to Honduras [**70, 80**]
(T) *striolata* (Borgmeier), 1957:116. * se. Brazil [**65**]
(P) *sulcata* (Fr. Smith), 1858:99. C. America to e. Brazil [**82**]
(P) = *lineata* Mayr, 1870b:965. n. syn.
(P) = *cearensis* Forel, 1912b:33. n. syn.
(T) = *nitens* Mann, 1916:407. n. syn.
(T) = *ypirangensis* Borgmeier, 1928b:60. n. syn.
(T) = *bufonum* Weber, 1938:208, nec *bufonis* Mann, 1926. n. syn.
(T) *taivanensis* (Wheeler), 1929:32. * Formosa [**48**]
(T) *teffensis* (Santschi), 1929c:449.* Amazon-Orinoco drainage [**81**]
(T) = *concinna* Santschi, 1929c:450, nec Fr. Smith, 1858. * n. syn.
(P) *tornata* (Roger), 1861:15. s. Mexico to Colombia [**67**]
(P) = *ericae* Forel, 1912b:33. n. syn.

(P) *tortuolosa* (Fr. Smith), 1858:99. Amazon-Orinoco to Ecuador **[76]**
(P) = *quitensis* Forel, 1920:133. n. syn.
(P) *triangularis* Mayr, 1887:544. n. Argentina to se. Brazil **[73]**
= *richteri* (Forel), 1913c:203. * n. syn.
(?) *trigona* Emery, 1905:114. * se. Brazil **[73]**
wasmanni (Santschi), 1929c:466. * Pará, Panamá **[79]**
(T) = *isthmica* (Santschi), 1929c:467. * n. syn.
(T) *wheeleri* (Santschi), 1929c:488. * Costa Rica **[79]**
(P) = *mayri* (Santschi), 1929c:453. * n. syn.

*New Combinations in Gnamptogenys

From *Stictoponera: bicolor, binghami, biroi, costata, coxalis, crassicornis, laevior, menadensis, panda, posteropsis, spiralis, taivanensis.*

From *Rhopalopone: cribrata, dammermani, diehli, epinotalis, luzonensis, major, malaensis.* Note: *R. relicta* Mann was transferred to *Holcoponera* by Brown, 1957:491. *R. simillima* (Fr. Smith) *sensu* Emery has been transferred to *Prionopelta* (Amblyoponini) by Brown, 1953b:12.

From *Wheeleripone: albiclava, aterrima, crenaticeps, lucida.*

From *Ectatomma* (*Poneracantha*): *aculeaticoxae, bispinosa.*

From *Acanthoponera* (*Anacanthoponera*): *reichenspergeri.*

From *Spaniopone: haytiana.*

From *Emeryella s. str.: schmitti, minor* Wheeler, nec Forel.

From *Emeryella* (*Barbourella*): *banksi.*

From *Holcoponera: acuta, arcuata, regularis* Santschi, nec Mayr, *curtula, stolli, gracilis, magnifica, mina, moelleri, splendens, pleurodon, emeryi* Santschi, nec Forel, *recta, vidua, porcata, relicta, rustica, simplex, simplicoides, brasiliensis, angustiloba, angustipleura, paulina, pernambucana, calcarata, hybrida, strigata, teffensis, concinna* Santschi, nec Fr. Smith, *wasmanni, isthmica, wheeleri, mayri. H. striatula* Mayr was originally described in *Gnamptogenys.*

From *Alfaria: bufonis, minuta, emeryi, mus, panamensis* Weber, nec Santschi, *carinata, simulans, striolata.*

From *Opisthoscyphus: scabrosus.*

From *Ectatomma* (*Parectatomma*): *hartmani, menozzii, rastrata, schubarti, richteri, trigona.* The species *triangularis* was originally described as a *Gnamptogenys.*

From *Commateta: bruchi.*

From *Tammoteca: concinna* (Fr. Smith), placed here only by Santschi.

Key to New World species of Gnamptogenys — workers

1. Propodeum armed with a pair of long, slender spines, normally at least as long as the distance between the inner sides of their bases (C. America) .... *bispinosa* (Emery)
Propodeum unarmed, or with a much smaller pair of teeth ....2.

2. Second postpetiolar (second gastric) segment very strongly vaulted in the manner of *Proceratium*, and much inflated, its maximum cross-section diameter much greater than that of postpetiole . . . . 3.
Second postpetiolar segment usually (but not always) less strongly vaulted; its maximum cross-section diameter subequal to, or smaller than, that of postpetiole . . . . 5.

3. Size smaller, head width < 1.0 mm., length of alitrunk (WL) < 1.6 mm.; superficial sculpture consisting of extremely fine, opaque, amorphous or subgranulose roughening (C. and tropical S. America) . . . . . . *minuta* (Emery)
Size larger, head width > 1.0 mm., WL > 1.6 mm.; superficial sculpture consisting of extremely fine, even striolation, giving a silky luster to the integument . . . . 4.

4. Alitrunk with a well-defined and distinctly impressed metanotal groove (s. Mexico) . . . . *bufonis* (Mann)
Metanotal groove obliterated on dorsum of alitrunk (C. America) . . . . *simulans* (Emery)

5. Postpetiole completely transversely striolate both above and below; very small, yellowish *Proceratium*-like species with minute eyes (Haiti) . . *haytiana* (Wheeler and Mann)
Postpetiole predominantly longitudinally costulate or striate over the dorsum, or at least with some longitudinal striation or costulation in the central or posteromedian part of the disc . . . . 6.

6. Pronotum separated from remainder of alitrunk by a very distinct suture, completely breaking the sculpture . . . . 7.
Promesonotal suture absent across the dorsum, or indicated by an impressed line that does not break the sculpture 18

7. Alitrunk with sculpture on dorsum partly replaced by extensive smooth, shining areas . . . . 8.
Dorsum of alitrunk sculptured (usually costulate or striate) throughout 9.

8. Postpetiolar dorsum (and that of succeeding segment) coarsely and regularly costulate in a longitudinal direction; color (of types) red-brown (w. Brazil) . . . . *relicta* (Mann)
Postpetiolar dorsum (and that of succeeding segment) with irregular striation arching over a shining, obscurely longitudinally striate posteromedian area; color deep piceous to black (se. Brazil) *reichenspergeri* (Santschi)

9. Compound eye small, its maximum diameter < the greatest thickness of the apical funicular segment; postpetiole truncate at base, the smooth anterior face separated from the costulate dorsal surface by a rim or margin (Fig. 21) (Bolivia, Peru) .... *mina* (Brown)
Compound eye larger, its maximum diameter equalling or exceeding the greatest thickness of the apical funicular segment; postpetiole with anterior face costulate and curving directly into dorsal surface (Fig. 22) .... 10.

10. Petiolar node terminating in a distinct flattened posterapical tooth or process, grossly acute, especially in lateral view; ventral process of petiole triangular, tapering to a narrow, slightly recurved lobe or tooth (Fig. 22) (Bolivia, Peru) .... *acuta* (Brown)
Petiolar node not terminating in a distinct posterapical tooth or process, though the posterior apex may project slightly backwards; ventral process of petiole differently shaped (not as in Fig. 22) .... 11.

11. Ventral surface of postpetiole predominantly transversely costulate (C. America) .... *simplex* (Emery)
Ventral surface of postpetiole predominantly longitudinally or obliquely costulate ... . 12.

12. Funicular segment I (basal segment) as long as or slightly longer than II and III taken together; small species (s. Mexico, C. America) ..
strigata (Norton)
Funicular segments II and III relatively longer (II particularly); II and III together longer than I .... 13.

13. Larger species, with long antennae, scape length (excluding basal neck) normally > 1.08 mm. .... 14.
Smaller species, with shorter antennae, scape length normally < 1.08 mm. .... 17.

14. Petiolar node more or less tilted posteriad in side view, the posterodorsal angle sharply rounded and slightly overhanging the posterior face; ventral process triangular or rounded, unilobed .... 15.
Petiolar node erect, in side view the posterodorsal angle not very much more sharply rounded than anterodorsal angle, and not overhanging posterior face; ventral process bilobed, or at least tending to form a posterior heel or corner .. .. 16.

15. Sculpture fine, more than 30 costulae between eyes; anterior ⅓ to ½ of postpetiolar dorsum transversely-arched costulate; head narrow, especially across occiput, occipital angle as seen from side sharply rounded, subauriculate (Guianas) .... *gracilis* (Santschi)
Sculpture coarser, less than 30 costulae between eyes; at most a very

narrow band of transverse costulae along the anterior margin of postpetiole; head broader, occipital angle as seen from side gently rounded, not auriculate

(Costa Rica) .... *porcata* (Emery)
(sw. Brazil) .... *magnifica* (Santschi)

16. Antennae (and individual segments) more slender, the penultimate segment distinctly longer than broad (se. Brazil) .... *moelleri* (Forel)
Antennae (and individual segments) thicker, the penultimate segment as thick as or thicker than long (Amazon-Orinoco drainage) .... *teffensis* (Santschi)

17. Petiolar node and ventral process usually more or less as described in first lug of couplet 14, ventral process usually a tapered triangle (Panama to Bolivia) .... *pleurodon* (Emery)
wasmanni (Santschi)
Petiolar node usually as described in second lug of couplet 14: ventral process bilobed, square-cut, or with a single rounded lobe .... group of *striatula* (Emery)
(The *striatula* group includes six nominal species: *arcuata*, *curtula*, *rustica*, *simplicoides*, *striatula* and *wheeleri*, of which perhaps two to four are good species. One extreme of variation is "typical" *striatula*, with fine costulation and a square-cut or emarginate ventral petiolar process [S. America, Antilles]; another fairly well-marked form is *curtula*, with posterior lobe of ventral process reduced to a broad convexity [s. Mexico, C. America]. These and other forms are linked by intergrades; apparently character displacement is involved.)

18. Mandibles elongate and falcate or subfalcate, their inner margins in large part very distinctly concave, only their apical portions meeting or crossing when mandibles are closed (Figs. 14, 15) .... 19.
Mandibles triangular, with distinct apical and basal angles separated by a rounded basal angle, and the apical margin straight or very feebly concave (Fig. 16), or else the apical and basal margins continuous with each other in one broad convexity bearing low, vaguely double-ranked tubercles .... 22.

19. Mandibles exceedingly long and slender, each with an exposed straightline length > length of head proper (HL) (Haiti) ...*schmitti* (Forel)
Mandibles shorter and relatively broader, straightline length of each mandible < HL .... 20.

20. Inner borders of mandibles each with only a short triangular tooth to represent the basal angle (Panama) .... *banksi* (Wheeler)
Inner borders of mandibles each retaining the basal angle as a low, broadly rounded lobe or flange lying basad of midlength (Figs. 14, 15) .... 21.

21. Mandibles longer (Fig. 14); propodeum unarmed, its declivity transversely costulate; sternum of postpetiole predominantly smooth and shining (Dominican Republic) .... *semiferox* sp. nov.
Mandibles shorter (Fig. 15); propodeum with a pair of short teeth, its declivity longitudinally costulate; sternum of postpetiole transversely to obliquely costulate throughout (se. Brazil, Pará) .. *mediatrix* sp. nov.

22. When head is seen in perfect full-face (dorsal) view, and the antennal scapes are laid back as straight as possible from their insertions, they either fail to reach, or just barely reach, but do not distinctly surpass, the part of the occipital border nearest to which they fall ....23.
In same view, the antennal scapes when laid straight back from their insertions do distinctly surpass the posterior occipital border nearest to where they fall ....33.

23. Dorsal surfaces of mandibles distinctly and continuously striate over the basal third or more of their length ....24.
Dorsal surfaces of mandibles smooth and shining to the base, though sometimes with scattered punctures .... 25.

24. Larger species, head width across eyes > 1.2 mm.; mandibular striation extending from insertions to apices (Bolivia, Ecuador) .... *haenschi* Emery
Smaller species, head width across eyes < 1.0 mm.; apical half of mandibles smooth and shining (Texas) .... *hartmani* (Wheeler)

25. Dorsal face of propodeum predominantly or wholly transversely striate, although the anteriormost portion may sometimes bear sharply diverging oblique striation ....26.
Dorsal face of propodeum predominantly longitudinally costulate or striate, continuing the longitudinal promesonotal sculpture straight back to at least the propodeal midlength, and usually beyond ..... 27.

26. Large, long-headed species, head length (HL) > 1.7 mm.; when head is seen in perfect full-face view, occipital border evenly convex; blunt but distinct vestiges of paired teeth on the propodeal declivity (Costa Rica) ....*alfaroi* Emery
Smaller, more short-headed species, HL < 1.5 mm.; when head is seen in perfect full-face view, occipital border straight or feebly concave in the middle; propodeum absolutely unarmed (C. America to s. Brazil and Bolivia) ....*annulata* Mayr

27. Anterior margin of narrow anterior apron of clypeus (not to be confused with underlying labral outline) distinctly concave in the middle, and the lateral corners rounded ....28.
Anterior margin of anterior apron of clypeus straight, or if shallowly concave, then terminating laterally in sharply rectangular corners ...31.

28. Compound eye of worker large, its greatest diameter > the maximum width of antennal scape .... 29.
Compound eye of worker small, usually consisting of only about 6-15 pigmented facets; greatest diameter less than, or at least not exceeding, maximum width of antennal scape .... 30.

29. Larger species, size and sculpture very variable, width of head across and including compound eyes > 1.0 mm. (C. America, tropical S. America) .... *mordax* (Fr. Smith)
Smaller species, width of head across and including eyes < 1.0 mm. (Peru, Guianas) .... *exarata* Emery

30. Medium-sized species, width of head across and including compound eyes > 0.7 mm. (C. America) ....*interrupta* Mayr
Very small species, width of head across eyes < 0.7 mm. (s. Mexico to se. Brazil, Jamaica) .... *continua* Mayr

31. Metanotal groove distinct and impressed, visible in all lights; sculpture fine, 38 or more costulae between compound eyes, 19 or more between frontal carinae (se. Brazil) ....*rimulosa* (Roger)
Metanotal groove absent or very indistinct, at best visible only in certain lights and views; sculpture coarser, < 38 costulae between eyes, < 19 between frontal carinae ....32.

32. Larger species (usually HW > 0.73, WL > 1.25 mm.); petiolar node longitudinally costulate, at most only the lower part of the anterior face transversely costulate (s. Mexico to Paraguay) ... . *regularis* Mayr
Smaller species (usually HW < 0.73, WL < 1.25 mm.); petiolar node with costulae arching transversely across entire anterior face, from top to bottom (Panama, Trinidad, Amazon-Orinoco drainage to Bolivia) *horni* Santschi

33. Large species, head width without eyes > 2.0 mm.; color usually ferruginous; sculpture fine; petiolar node produced to a blunt posterapical point or tooth (C. into tropical S. America) ......*concinna* (Fr. Smith)
Small and medium species, head width without eyes < 2.0 mm. .....34.

34. Postpetiolar tergum with parallel chains of coarse punctures separated by irregular rugulae arranged in a pattern arching over a posteromedian area of finer longitudinal costulation; succeeding segment strongly recurved and longitudinally costulate; eyes reduced (se. Brazil) *striolata* (Borgmeier)
Tergum of postpetiole (and of succeeding segment) evenly costulate, nearly always in a longitudinal direction; second postpetiolar segment more weakly downcurved ....35.

35. Mandibles predominantly smooth and shining, with scattered punctures; striae or costulae, if present, restricted to basal third or less of length; transverse dorsal sutures of alitrunk obliterated, except in *G. nigrifrons* .... 36.
Mandibles predominantly longitudinally costulate or striate; metanotal groove represented by a distinct narrow impressed line .... 41.

36. Size larger, head width without eyes > 1.3 mm. (Amazon-Orinoco drainage to Ecuador) .... *tortuolosa* (Fr. Smith)
Size smaller, head width without eyes < 1.3 mm. .... 37.

37. Anterior clypeal apron with sharply angular free corners; mandibles sublinear, sharply downcurved, their basal and apical margins meeting through a single continuous convexity; petiolar node longer than broad to (rarely) very slightly broader than long .... 38.
Anterior clypeal apron with rounded free corners; mandibles more or less triangular, the basal and apical margins distinct and separated by a distinct but rounded basal angle; petiolar node always distinctly broader than long .... 40.

38. Node of petiole seen from the side ending in a blunt point distinctly overhanging the posterior face (Amazon-Orinoco drainage) ...
acuminata Emery
Node of petiole seen from the side without a distinctly projecting posterodorsal point .... 39.

39. Head in back of antennal insertions black or nearly so; mandibles straw yellow, contrasting sharply with black of cranium; alitrunk, node and gaster varying from black to yellowish-ferruginous; costulae of propodeal declivity longitudinal (C. and tropical S. America) ....
sulcata (Fr. Smith)
Head yellowish to brown in color; mandibles dull yellow to brownish, usually lighter than cranial color, but not markedly contrasting with it; head and rest of body nearly concolorous; many workers from Central America and Mexico with costulae transverse across propodeal declivity (s. Mexico to Colombia) .... *tornata* (Roger)
(*G. acuminata*, *G. sulcata* and *G. tornata* are often difficult to distinguish, and further material could well show them to be just variants of a single plastic species.)

40. Transverse sutural lines effaced on alitrunk dorsum, so that the surface forms one unbroken, very gentle convexity from pronotum to propodeal declivity; propodeal angles evenly rounded as seen from the side (n. Argentina) .... *bruchi* (Santschi)
Metanotal groove impressed and distinct, separating propodeal dorsum into a convexity distinct from promesonotum; propodeal angles salient and more nearly rectangular as seen from side (Peru) ....
nigrifrons Borgmeier

41. Petiolar node markedly longer than broad (Fig. 42); anterior pronotum covered by a broad band of transversely arching costulae (Bolivia) . . . . . *mecotyle* sp. nov.
Petiolar node broader than long, as broad as long, or very slightly longer than broad; costulae longitudinal over the full pronotal length, only occasionally with one or two obscure transverse costulae at the junction of pronotum and cervix . . . . 42.

42. Size smaller, head width without compound eyes < 1.0 mm. (se. Brazil)
rastrata (Mayr)
?*trigona* Emery
Size larger, head width without compound eyes > 1.0 mm. . . . . 43.

43. Sculpture finer, usually > 26 costulae between compound eyes; size smaller, head width without eyes 1.25 mm. or less . . . . 44.
Sculpture coarse, usually 26 or less costulae between compound eyes; size larger, head width without eyes > 1.25 mm. . . . . 45.

44. Sculpture finer, petiolar node with 13-16 transverse costulae visible from above; node usually wider than long (s. Brazil to n. Argentina) . . . . .
triangularis Mayr
Sculpture coarser, petiolar node with 11-13 transverse costulae visible from above; node usually not distinctly broader than long (Panama to Bolivia) . . . . *aculeaticoxae* (Santschi)
(*G. triangularis* and *G. aculeaticoxae* have mutually exclusive ranges so far as known; they are both variable in the diagnostic characters, and may possibly be mere geographical variants of a single species.)

45. Ventral process of petiole with a blunt or rounded anterior free angle and a salient, dentiform or subdentiform posterior free angle (Rio Grande do Sul, Paraná) . . . . *menozzii* (Borgmeier)
Ventral process of petiole with only the rounded anterior free angle or lobe developed; posterior angle absent or reduced to a simple low, broad convexity (S. Paulo, Rio de Janeiro) . . . . *schubarti* (Borgmeier)
(*G. menozzii* and *G. schubarti* may be part of the geographical variation of a single species.)

Key to Old World species of Gnamptogenys — workers

1. Second postpetiolar (second gastric) segment with tergum predominantly (usually longitudinally) costate or striate, this sculpture extending over the basal third or more of the exposed portion of the segment. 2.
Second postpetiolar segment smooth, punctate, or otherwise sculptured; remnants of costation or striation, if present, peripherally distributed, and if found at base of segment, not extending beyond basal quarter 7.

2. Compound eyes placed within the posterior quarter of the sides of the head, nearly at the posterior angles (Sumatra, Mindanao) .... *posteropsis* (R. Gregg)

   Centers of compound eyes placed anterior to posterior quarter of sides of head ....3.

3. Eyes small, each composed of 20 or less facets; petiolar node antero-posteriorly compressed, in the form of a thick scale, rounded above; body size smaller, head width (without eyes) < 0.80 mm. (N. Guinea) .. *major* (Emery)

   Eyes larger, each composed of many more than 20 facets; petiolar node low, rounded, paniform; body size larger, head width (without eyes) > 0.80 mm. ....4.

4. Eyes very large, occupying fully ⅓ length of sides of head, their greatest diameter approximately = combined length of penultimate and antepenultimate antennal segments (N. Guinea) .... *biroi* (Emery)

   Eyes not so large, occupying distinctly < ⅓ length of sides of head, their greatest diameter distinctly < combined length of penultimate and antepenultimate antennal segments ....5.

5. Occipital angles as seen from the side each produced as a small, simple, narrowly rounded, lamellate lobe or margin, much narrower than compound eye; petiolar node distinctly transversely costulate its length; second postpetiolar tergum longitudinally finely costulate (or striate) over basal half to third, remainder smooth and shining (N. Guinea) ... *macretes* sp. nov.

   Occipital angle as seen from the side produced as a large, more or less fan-like lobe or "ear" with a narrow translucent margin, usually angled at both ends, lobe as wide as or wider than compound eye; petiolar node not transversely costulate, or with a few costules near posterior end; second postpetiolar tergum coarsely longitudinally costate (or fluted) for nearly its entire length ....6.

6. Sculpture finer, denser and more opaque, with noticeable development of longitudinal striation or costulation between punctures over head and alitrunk; costulae of postpetiole fine, close and distinct; funiculi slender, its segments III through VI longer than thick (Ceylon) .... *coxalis* (Roger)

   Sculpture coarser, striation absent or suppressed in favor of the coarse foveolae over head and alitrunk; costulae of postpetiole coarse and often indistinct, sometimes consisting merely of elongate welts between foveolae; funicular segments III through VI as thick as or thicker than long (Sumatra, Tenasserim to Mindanao) .... *costata* (Emery)

7\. Postpetiole coarsely and very distinctly striate over tergum, intercostular punctures reduced in center of disc, larger on sides (N. Guinea) ..... *grammodes* sp. nov.
Postpetiole smooth, or punctate, or indefinitely rugulose; striation, if present, fine, indistinct and interrupted, subordinate to coarser punctures or other sculpture .... 8.

8\. Length of antennal scape (excluding basal neck) 0.87 mm. or more ... 9.
Length of antennal scape (excluding basal neck) < 0.87 mm. ...... 14.

9\. Petiolar node anteroposteriorly compressed, excluding ventral process, higher than long, with steep, high anterior and posterior faces (Fig. 18) .... 10.
Petiolar node low, paniform, gently rounded above, longer than high, excluding ventral process (Fig. 19) .... 11.

10\. Gastric dorsum with fine, irregular interpunctural sculpture developed (rendering the surface more opaque) and reaching even to the center of the second postpetiolar tergum; color red-brown; posterior occipital corner as seen from the side terminating in a distinct (but variable) point or lobe (w. China) .... *panda* (Brown)
Gastric dorsum with interpunctural spaces smoother, more shining, especially the disc of the second tergum; color blackish-brown; posterior occipital corner as seen from the side evenly rounded, without lobe or point (Formosa) .... *taivanensis* (Wheeler)

11\. Alitrunk almost completely smooth and shining, with scattered inconspicuous punctures; mesonotum coarsely and evenly longitudinally costate; four apical antennomeres ivory white, contrasting with rest of funiculus, which is ferruginous in color (Solomons) .. *albiclava* (Mann)
Alitrunk coarsely foveolate, including mesonotum; antennal club not white .... 12.

12\. Greatest diameter of eye subequal to greatest thickness of apical antennomere; body usually more or less concolorous brownish-red (Burma, Sumatra to Philippines) .... *binghami* (Forel)
(*G. crassicornis* Forel and *G. spiralis* Karawajew probably would run to *binghami*, but in these, the eye is placed in front of the middle of the side of the head. They may both be only variants of *binghami*, in which eye position varies.)
Greatest diameter of eye markedly $>$ greatest thickness of apical antennomere; full adult color usually blackish or bicolored .... 13.

13\. Full adult color piceous to black over body; a narrow median strip on mesonotum smooth and shining (Sumatra to Celebes and Philippines) *menadensis* (Mayr)

Full adult color with gaster (and often the head) piceous, alitrunk much lighter, orange-ferruginous; median strip of mesonotum finely, indefinitely, longitudinally rugulose, more or less opaque (se. Asia to Java) . *bicolor* (Emery)

14. Alitrunk smooth and shining dorsally (when clean), with separated punctures or foveolae . . . . 15.
Alitrunk dorsally in large part (at least the pronotum) densely sculptured and more or less opaque, with or without definite punctures or foveolae . . . . 19.

15. Head with straight, parallel sides and rectangular occipital corners; eyes large and only gently convex, occupying about ¼ length of sides of head (Figs. 43, 44); antennal scapes short and thick, surpassing occipital margin by much less than their apical thickness . . . . 16.
Head with sides more or less convex, occipital corners rounded; eyes smaller, occupying 1/5 or less of length of sides of head; antennal scapes longer and more slender, surpassing occipital margin by their apical width or more . . . . 17.

16. Size larger, head width (without eyes) > 0.70 mm. (Java) . . . . *laevior* (Forel)
Size smaller, head width (without eyes) < 0.70 mm. (Philippines) . . . . *chapmani* sp. nov.

17. Antennal funiculus bicolored, the four apical segments whitish in color, contrasting with the ferruginous color of the rest of the antenna (Solomons: Malaita I.) . . . . *lucida* (Mann)
Antennae concolorous ferruginous . . . . 18.

18. Dorsum of head with coarse contiguous punctures, the median strip longitudinally costulate and subopaque (Fijis) *aterrima* (Mann)
Dorsum of head with punctures mostly separated by smooth, shining intervals; median strip almost free of punctures, smooth and shining (Solomons: Ysabel I.) . . . . *crenaticeps* (Mann)

19. Eyes large, occupying about ¼ length of sides of head; their greatest diameter > greatest thickness of antennal scape (Fig. 43) (n. Borneo) *kalabit* sp. nov.
Eyes small, occupying much < ¼ length of sides of head; their greatest diameter < greatest thickness of antennal scape . . . . 20.

20. Second tergum of gaster (second postpetiolar segment) densely punctate, subopaque, the coarse punctures subcontiguous and separated only by vague longitudinal costulae (Solomons: Malaita I.) . . *malaensis* (Mann)
Second tergum of gaster with separated small punctures, the broad intervals smooth and shining . . . . 21.

21. A broad median area extending over the anterior half or more of the propodeum smooth and shining (N. Guinea) . . . . . . 22.
Propodeum completely sculptured, or at most with a very narrow, indefinite smoothed area limited to the anterior third of the dorsum (E. Indies, Philippines) . . . . 23.

22. Punctures of postpetiole large and deep, relatively few in number, separated by broad shining spaces; full adult color of body deep brownish-red . . . . *cribrata* (Emery)
Punctures of postpetiole small, superficial and densely arranged, separated by narrow shining spaces, the total surface subopaque; full adult body color ferruginous yellow . . . . *epinotalis* (Emery)

23. Size larger, maximum pronotal width 0.38 mm. or more; full adult body color deep brownish-red, postpetiolar punctures large and deep . . *dammermani* (Wheeler)
Size smaller, maximum pronotal width < 0.38 mm., full adult color yellowish-ferruginous; postpetiolar punctures smaller and shallow . . *luzonensis* (Wheeler)
(According to the original description, *diehli* (Forel) would run to couplet 23; Wilson has seen the type and finds it to differ from *dammermani*. Differences from *luzonensis* unclear.)

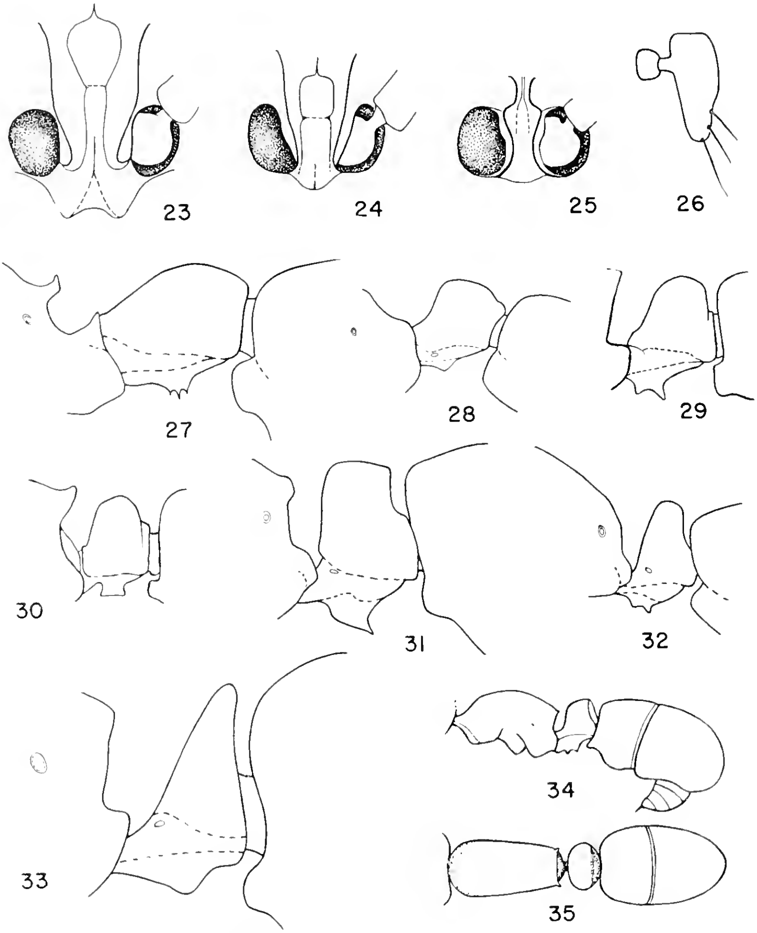
PROCERATIUM Roger

> *Proceratium* Roger, 1863:171. Type: *Proceratium silaceum* Roger, 1863, monobasic.
> *Sysphingta* Roger, 1863:175. Type: *Sysphingta micrommata* Roger, 1863, monobasic. Synonymy after Dalla Torre, 1893:18.
> *Sysphincta* (!) Mayr, 1865:12, and most subsequent authors; emendation of *Sysphingta* Roger.
> *Proceratium* subgenus *Sysphincta*, Forel, 1913a:212.

The genera *Proceratium* and *Sysphincta* have been relatively well known to specialists of the northern countries. Taking separately the Nearctic, European and Japanese representations of these two genera, it has previously been considered possible to separate them on the Emery-Wheeler key characters, thus:

Clypeus with an anterior median projection; petiole more or less nodiform . . . . *Sysphincta.*
Clypeus without an anterior median projection; petiole in the form of a thick erect scale . . . . *Proceratium.*

However, it seems that the protests of Forel (1913a) against this generic distinction have been overlooked. Forel stated that



Figures 23-35. *Proceratium* spp., workers, dorsal views of anteromedian part of head, all drawn to same scale. Fig. 23, *P. pergandei* (Missouri). Fig. 24, *P. melinum* (Italy). Fig. 25, *P. toschii* (holotype, Kenya). Figure 26, *P. croceum* (Alabama), detail of maxillary palpus, female. Figures 27-32. *Proceratium* spp., workers, side views of petioles and adjoining structures, all drawn to same scale. Fig. 27, *P. stictum*, sp. nov. (holotype, n. Queensland). Fig. 28, *P. micrommatum* (Veracruz). Fig. 29, *P. melinum* (n. Italy). Fig. 30, *P. toschii* (holotype). Fig. 31, *P. croceum* (Alabama). Fig. 32, *P. papuanum* (Malanda, n. Queensland). Fig. 33, *P. relictum*, female syntype (Fiji). Figures 34, 35. *P. arnoldi*, body, from sketches by Dr. G. Arnold, worker syntype (S. Rhodesia). Fig. 34, side view. Fig. 35.

for both the clypeal projection and nodal form characters there existed "all possible intergrades." Since that time, the number of species described has doubled, and some of the forms added are further intermediates in the two crucial characters. Other forms show extreme development of characters of either genus; *stictum* (Fig. 27, 45, 46) is a "super-*Sysphincta*," while *relictum* is a "super-*Proceratium*" (Fig. 33). It has been possible to assemble a representative series of species showing the gradualness of change from "super-*Sysphincta*" to "super-*Proceratium*" in nodal form (Figs. 27-35), and also illustrating nicely the loss of the median projection of the clypeus. Figure 46 shows the broad median clypeal lobe, apparently the generalized condition, still preserved in *stictum*. Figures 23 to 25 show the degeneration of the lobe into a bicarinate median projection in *pergandei* and allies (Fig. 23), then through the stage of fusion of the carinae to a unipartite projection in the *melinum* group (Fig. 24), and finally to the low vestigial flange of the African species *toschii* (Fig. 24) and *arnoldi* (Fig. 1), after which, in the remainder of the species, there is left no trace of the projection.

Other characters have been studied in the search for separatory features to distinguish two or more genera among the full array of species, but so far all characters appear to show gradation from one extreme to the other.

In mandibular dentition, one begins with a distinctly four-dentate masticatory border in *stictum* and follows the gradation through a number of species to the condition where two strong apical teeth remain, followed basad by an indefinite number of low, irregular denticles or else a relatively smooth margin. In some of the *Sysphincta* species, the undercurving of the principal (second) gastric segment is extreme, but this character again grades over by easy steps to a less extreme condition. The same applies to the palpal segmentation, as far as known **[84]**. Too few larvae are yet known for these to be of any help with the classification, and this goes also for male genitalic characters.

The workers of *Proceratium* are small to medium-small in size, generally ferruginous to reddish-brown in color, with greatly reduced eyes. The general habitus is distinctive (see Fig. 45) because of the under-turned gastric apex, which is a consequence of the large, vaulted second segment of the gaster. The reduced apical segments bear a stout sting and are retractile to some extent within the second segment. The first gastric segment (postpetiole) is very variable in size with the species, and in some of the "*Sysphincta*" species it is reduced almost to the status of the myrmicine postpetiolar node (e.g., in *P. watasei*). In fact, these variations in the gastric proportions, and especially in the ratio of postpetiole to the succeeding segment, are of the type that must have led to the myrmicine gastric configuration from an ectatommine stock not far distant from *Proceratium* beginnings.

Most of the remaining characteristics of the genus are, like the reduced eyes and depigmented coloration, connected with the cryptobiotic life led by the species. The antennae are well developed, and their insertions have migrated anteromedially in order to give freer play to the funiculi straight ahead. The clypeus and "frontal" area are constricted by this migration of the antennal sockets, and the lobes of the frontal carinae are narrowed and tilted on edge so as not to hamper the movement of the scapes. The alitrunk is welded into one compact piece, with little or no trace left of the transverse dorsal sutures.

The antennae are 12-segmented in worker and female, and 13-segmented in the male. The maxillary palpi are 2-, 3-, or 4-segmented in the workers and females so far dissected, while in these same specimens, the labial palpi are either 2- or 3-segmented (known palpal formulae are 2,2; 3,2 and 4,3) **[84]**.

Sculpture in the worker and female usually consists of fine, dense reticulo-punctation, with sometimes a little superimposed rugulation, but in *stictum* the punctures are coarser and the entire sculpture rougher. The gaster is usually predominantly smooth and shining, with fine piligerous punctulation. The pilosity normally consists of abundant fine, short hairs, subappressed to inclined-erect, forming a kind of pile over large areas of trunk and appendages. Occasional longer fine hairs are more scattered. There is often a definite fine carina running down the middle of the cephalic dorsum, probably homologous to the similar feature of *Acanthoponera* and *Heteroponera*.

In the female, the compound eyes are much larger than the minute ones of the worker, and are similarly situated near the middle of the sides of the head. The female and male often (particularly in the North American species) have the metanotum produced into an acute median tooth or bladelike carina.

The female may be either fully winged (and later dealate) as usual for ants, or she may appear in ergatoid form, intergrading to the worker form. Both normal and ergatoid females may occur in the same nest.

The wings in both sexes are a somewhat reduced version of the basic ponerine type; in those I have seen of *Proceratium*, the forewing vein (Rsf2·3) formed of the second and third free abscissae of the radial sector is missing, leaving a single large polygonal cubital cell; occasionally, the distal part of this vein, equivalent to Rsf3, is retained, as in some *Myrmica*. The cross-vein m-cu is often lacking, too.

Details of morphology are dealt with by Kennedy and Talbot (1939, all castes), by Kratochvíl (1944, all castes) and by M. R. Smith (1943, male) for different species. The larvae, at least during later stages of development, develop large, smooth bosses that are arranged symmetrically over the body and are unlike those of any other ant genus. However, the larvae are known for only the North American species, and even then from very few specimens (G. C. and J. Wheeler, 1952a: 134-137, pl. 5, figs. 17-27). The male genitalia are figured by Kennedy and Talbot (*loc. cit.*), but I can find no close correspondence between my dissections of males of the same species (*silaceum*) and their drawings of these organs. The genitalia need to be restudied.

Proceratium is widely distributed in the warmer half of the North Temperate Zone in areas with sufficient moisture in the soil, being found from Spain to Japan, and it ranges through southeastern Asia, the Malay Archipelago to New Guinea, reaching southeastern Queensland in Australia **[96]** and having a representative (*relictum*) in Fiji in the east. In eastern North America, three species range widely in the forested areas from the Gulf of Mexico northwards, two of them reaching New England and the Great Lakes region **[97, 98]**. Another three species range widely in southern Mexico and Central America, and one of these has been taken on Cuba, to which country it may have been historically introduced. In addition to the North African species, which are part of the southern Palaearctic fauna, there are two species, *arnoldi* (Southern Rhodesia) and *toschii* (Kenya), known from the African Continent.

We have only fragmentary, and often contradictory, information on the biology of *Proceratium* species. The nests are small, usually consisting of from 10-50 workers and one dealate female, though sometimes supernumerary queens, either dealate or ergatoid, are present in one nest. The nest consists of small rounded chambers hollowed out of soft rotten wood or in the soil; toward the cooler limits of the range, particularly in North America, nests and foraging workers are found under deepset rocks instead of in rotten wood. The nest site is usually in forest shade, in old moist gardens, or similar habitats that are constantly moist.

In the artificial nest, *Proceratium* species have been offered various foods. Fiala (in Kratochvíl, 1944) states that his *melinum* (=*fialai*) took bee honey; Haskins (1930) found that his *croceum* would not take honey, but that both adults and larvae would feed on the larvae, and sometimes on the pupae, of various genera of ants. Haskins also reported his *croceum* feeding on "meat" after long hesitation. L. G. and R. G. Wesson (1940) studied *pergandei* in Ohio, and noted that this species refused the brood of *Camponotus* and *Formica* as food, and also avoided all other insects offered, both living and dead. The *pergandei* did, however, appear to feed on the gastric contents of several *Formica* and *Camponotus* worker adults.

Observations made more recently by Wilson and myself and others (to be published elsewhere) on *silaceum* and *pergandei* indicate that these species may be specialized egg predators, eating the eggs of various other arthropods, especially of spiders. This may be the explanation also for the Wessons' observation of *pergandei* feeding on the gastric contents of dead worker ants, for these ants may well have been carrying eggs in their ovaries. Just how far egg predation extends as a general habit among *Proceratium* species is not known.

Males and females are produced in small numbers, usually toward the end of the summer in the North Temperate Zone, where the nuptial flight occurs normally during the last half of August in many places. The flight takes place during afternoon (*melinum*), and both sexes climb to a distance from the nest entrance before taking flight. Workers issue from the nest also during the nuptial flight, as is often the case with otherwise cryptobiotic ants. The flight has been observed by Fiala, (in Kratochvíl, 1944) for *melinum*.

Haskins (1930) mentions the curious habit in *croceum* workers of backing up to the brood of other ants to employ the sting. What, if any, function can be ascribed to this action is a matter for future observation to settle. The general activity of *Proceratium* species is rather sluggish, although they can move quickly on occasion. The antennae are held porrect in front of the head and during foraging are vibrated ceaselessly, much in the manner of cerapachyines and dorylines.

On the basis of external morphology, the species of *Proceratium* can be grouped conveniently in series from thick-noded ("*Sysphincta*") to "super-*Proceratium*" with a scalelike petiole. One can see seven vague groups:

Stictum Group: *stictum*. Pergandei Group: *algiricum* **[85]**, *mayri, pergandei, watasei*. Melinum Group: *itoi, melinum* **[94]**, Micrommatum Group: *convexiceps, micrommatum*. Arnoldi Group: *arnoldi, toschii*. Silaceum Group: *carinifrons, croceum, japonicum, lombokense, longigaster, mancum, normandi, numidicum, papuanum, silaceum*. Relictum Group: *relictum*. Unassigned: *californicum*.

PROCERATIUM species

The species marked with an asterisk (*) have previously been placed in *Sysphincta* by most authors, although those names not marked "n. comb." were either placed in *Proceratium* when originally described, or were transferred to *Proceratium* by some author (Mayr, Dalla Torre) subsequently. The names marked "n. comb." were all originally described in *Sysphincta*.

(?) *algiricum* Forel, 1899b:305. * n. Africa [**85**]
(T) *arnoldi* Forel, 1913a:210. * S. Rhodesia [**86**, Figs. 1, 34, 35]
(?) *californicum* T. W. Cook, 1953:45. California [**87**]
(P) *carinifrons* Menozzi, 1939:175. Sumatra, Philippines [**88**, **91**]
(T) *convexiceps* Borgmeier, 1957:120. Costa Rica [**89**]
(P) *croceum* (Roger), 1860:288. se. N. America [Figs. 26, 31]
(P) *itoi* (Forel), 1917:717. n. comb. * Japan [**90**]
(P) *japonicum* Santschi, 1937:362. Japan

(T) *lombokense* Emery, 1897b:593. Lombok [**91**]
longigaster Karawajew, 1935:59. Indo-China [**88**]
(P) *mancum* Mann, 1922:6. C. America, s. Mexico [**92**]
(P) *mayri* Forel, 1899b:306. * s. Europe [**85**]
(P) *melinum* (Roger), 1860:291. * s. and c. Europe [**94**, **84**, Figs. 24, 29]
(P) = *europaea* Forel, 1886:clxiii. * n. syn.
= *rossica* Arnoldi, 1930b:144. * n. syn.
(T) = *fialai* Kratochvíl, 1944:54, 86. * n. syn.
(P) *micrommatum* (Roger), 1863:176. * Panama, s. Mexico, Cuba [**93**, Fig. 28]
(P) = *cavernicola* Borgmeier, 1937:221. * synonymy by Borgmeier, 1957:118.
(?) *normandi* Santschi, 1929a:138. n. Africa [**95**]
(P) *numidicum* Santschi, 1912a:172. n. Africa, Balkan Pen. [**95**]
(T) *papuanum* Emery, 1897b:592. N. Guinea, ?e. Australia [**96**, Fig. 32]
(T) = *Ponera caeca* Donisthorpe, 1949a:491. n. syn.
(P) *pergandei* (Emery), 1895a:264. n. comb. * se. N. America [**97**, Fig. 23]
(T) *relictum* Mann, 1921:413. Fiji. [Fig. 33]
(P) *silaceum* Roger, 1863:172. se. N. America [**98**]
= *crassicorne* Emery, *rugulosum* Wheeler and *vestitum* Emery, synonymy by Creighton, 1950:36-40.
(T) *stictum* Brown sp. nov. n. Queensland [**99**, **84**, Figs. 27, 45, 46]
(T) *toschii* (Consani), 1951:167. n. comb. * Kenya [**100**, Figs. 25, 30]
(P) *watasei* (Wheeler), 1906:303. n. comb. * Japan

DISCOTHYREA Roger

> *Discothyrea* Roger, 1863:176. Type: *Discothyrea testacea* Roger, 1863, monobasic.

> *Pseudosysphincta* Arnold, 1916:161. Type: *Pseudosysphincta poweri* Arnold, 1916, by original designation, monobasic. n. syn.

> *Prodiscothyrea* Wheeler, 1916:33. Type: *Prodiscothyrea velutina* Wheeler, 1916, monobasic. n. syn.

> *Pseudosphincta* Wheeler, 1922:645, 762. Variant spelling of *Pseudosysphincta*. n. syn.

The genus *Discothyrea* includes a modest number of small to minute species, very compact in form and extreme in the development of the "proceratiine traits," and especially notable for the exaggerated enlargement of the apical antennal segment. The raised median portion of the clypeus between the frontal lobes is fused with the frontal lobes and elevated with them to form, in some species, a flat-topped platform (Fig. 47, 48) between the antennal insertions; in other species, the width of this structure is decreased, and finally, in several species, it is reduced to a simple vertical plate or flange that separates the now very closely approximated antennal insertions. The lower part of the clypeus is reduced to a strongly projecting apron covering the middle parts of the mandibles (Fig. 48) and serving as the front rim of the platform upon which the antennae are inserted. The clypeal apron may be rounded or truncate as seen from above.

With the enlargement of the apical antennal segment, the segments between it and the first funicular segment (pedicel) become axially compressed and tend to fuse one to another to reduce the number of segments. This fusion and reduction renders determination of segment numbers virtually impossible in some species, even when one uses cleared specimens under the higher powers of a compound microscope. Furthermore, it is clear that fusion is irregular in some species, and differs in degree among individuals, and even on different sides of the same specimen.

In spite of this difficulty, the antennal segmentation has been granted value as a generic character. *Discothyrea* has been considered to be ''normally'' nine-segmented, including the scape, although actually there are a number of species in Africa, the New World, and Australia with lesser counts: eight, seven, and even as few as six antennal segments, including the scape; for a discussion of this situation, see Borgmeier, 1954:191.

Prodiscothyrea is distinguished primarily on the basis of its ten-segmented antennae; the other characters of cephalic structure cited by Wheeler as diagnostic are all found well developed in one or more nine-segmented species of *Discothyrea* (e.g., *clavicornis*, *oculata*, *mixta*), and therefore are useless as generic characters. We therefore have the anomalous situation in which one genus is distinguished by its having ten antennal segments, from another genus that has six, seven, eight, or nine. Clearly, the ten-segmented species belong in *Discothyrea*. But the same character does not rest its variation at ten segments, for the new species *mixta* **[105]**, otherwise exceedingly similar to certain *Discothyrea* and *Prodiscothyrea* species, turns out to have eleven segments. And there is *Pseudosysphincta poweri* to be considered; essentially, this last is a *Discothyrea,* but with twelve antennal segments. Now that we have an unbroken series of species with all possible segmentations from six to twelve, it is plainly not advantageous to recognize more than one genus for this group, at least until some better character can be found on which to base the separation. Except for the segmentation, *Discothyrea* in this new, collective sense is an exceptionally homogeneous and well-marked genus.

Some other characters of the *Discothyrea* worker may be reviewed. Eyes small to minute, placed near or anterior to the middle of the sides of the head. Mandibles rather small, apex acute, followed by a usually edentate masticatory margin that is straight to concave and lined with a very even, close rank of minute peg-like bristles; the masticatory border is terminated basally by a rounded or bluntly toothlike basal angle. The palpi of maxilla and labium are variously segmented, according to species; Wheeler (1916:33 and pl. 4, fig. 3) found a formula of 4,4 in *velutina*, whereas Borgmeier counted 1,3 in *sexarticulata* (1954:193, figs. 8, 9). A comparative study of the maxillary palpi, very difficult in these small insects, remains to be made by the first reviser of the genus. (But see the recent study by Borgmeier, 1957:122-125.) The mouthparts are altogether peculiar in their reduction, and it would be interesting to know what the food is.

The alitrunk is short, usually vaulted and sutureless dorsally, and terminates posteriorly in a declivity that is more or less distinctly set off from the dorsal surface by paired propodeal angles or vestigial teeth. Petiole reduced, anteroposteriorly compressed and not very high, usually in the form of a thick disc or scale, bluntly pointed above or with one or two low rims running around its free margin from one side to the other. The node is normally attached over a large proportion of its posterior surface to the postpetiole. Postpetiole and succeeding gastric segments are arranged much as in *Proceratium* (Fig. 47). Legs stout; spur of posterior leg pectinate, spur of middle leg very small, perhaps absent in some species. Tarsal claws small, simple.

Basic sculpture consisting of minute piligerous or tuberculate punctures, in most species crowded densely over most of the body, rendering it opaque or subopaque; rarely, however, the punctures are much smaller, spaced, and the surface generally shining. Usually, the sculpture tends to thin out more toward the gastric apex, so that shining interspaces appear in the species with this type of sculpture. Entire, or nearly the entire, body covered by a very dense, fine erect pubescence or pile, helping to render the surface more opaque, or else the pubescence reduced to virtually invisible pruinescence. Longer hairs are scarce or absent. Integument color ranges from testaceous to dark brown or mahogany, or combinations of these.

The female is like the worker, but slightly to distinctly larger; usually with well developed ocelli and flight sclerites of the thorax, and with larger compound eyes. Ergatoid females may occur in some species, as workerlike individuals with rather large compound eyes and a trace of one or more alitruncal sutures remaining on the dorsum. Wing venation is of the *Myrmecina* type (see M. R. Smith, 1943: fig. 5C), with Rs+M, Rsf2·3, and Rsf 4·5 lined up to form a single strong unit joining the anterior margin of the wing near its apex (i.e., "radial cell closed"). Mf2 is present, but not r-m, Mf3 or beyond, or m-cu. Of course, wings are known for only a few of the species so far.

The male is smaller and more slender than the female, with a subglobose head, large compound eyes, small ocelli, and well developed, triangular mandibles shaped much as in the worker. Antennal insertions very close together, separated by a vertical carina representing the fused clypeus and frontal lobes in the female castes; a more or less distinct vestige of the horizontal clypeal apron is also present. The antennae are composed of a short scape, approximately equalling in length the succeeding three segments, and twelve funicular segments, all but the first of which (pedicel) are longer than broad. The first segment of the funiculus is globular or subglobular and broader than long to slightly longer than broad, according to species. The funiculus as a whole is slender, with slight incrassation toward the apex.

Mesonotum with or without notauli. Wings as in the female. Petiole as in female, but usually longer and lower. Gaster variable in shape and proportions, the postpetiole either larger than or smaller than the succeeding segment; apical segments only slightly deflected ventrad. Sculpture of fore part of body much as in the corresponding workers, densely punctulate, in the species so far known; gaster more smooth and shining. Color dark brown or black. Genitalia as yet remaining unstudied; hypopygial border rounded.

Larva remaining undescribed.

The range of *Discothyrea* lies predominantly within the tropics and warm temperate parts of the Southern Hemisphere, although we have records for the southeastern United States and for Hainan Island, southern China, and Formosa. The genus is represented by one (and possibly more) species on New Caledonia, one on New Zealand, two or three in the southern Brazil-northern Argentina area, and two or so in South Africa. It is restricted to the moister nest sites, though it can be carried about by commerce in plant roots and humus, and therefore often turns up in gardens. It should be expected in greenhouses and plant propagating beds wherever the temperature and moisture are held sufficiently high. Considering the relative abundance of colonies as measured by number of collections to date, it seems that by and large, *Proceratium* and *Discothyrea* tend to have complementary distributions outside the tropics.

Due to its chiefly tropical and south temperate distribution, as well as to its small size, inconspicuous nests, death-feigning habits and cryptobiotic tendencies, *Discothyrea* is relatively rarely collected, and little is known concerning its habits. Nests are found in rotten wood, rotting nuts, etc., in the leaf litter, and in large rotting logs. In the hilly parts of southeastern Australia, I have found them under stones rather frequently, especially in the galleries of other species of ants. Individual workers have been recovered from plant roots and similar situations in the soil, and in moss covering logs and rocks in wet areas. It is probable that the colonies are more frequent than they seem to be to a collector working in the usual way to search for ants.

The food is unknown; from the aberrant nature of the mouthparts, it must be something rather special. Several authors have thought that it "is almost a certainty that they are carnivorous," and Moore (1940:308) gave it as his opinion that the food of *Discothyrea* in New Zealand might consist of mites taken in ant nests. Since the similarly specialized *Proceratium* is now thought to be an arthropod egg predator, in part at least, a similar feeding habit could possibly be followed by *Discothyrea;* at any rate, it is worth checking in the field. Colonies of *Discothyrea* thus far examined held ten or twenty workers plus a female and brood; winged forms can be produced in equal or even greater numbers, and both sexes are normally produced in the same nest.

DISCOTHYREA species

New combinations are marked with an asterisk (*). *D. bryanti* and *D. velutina* are transferred from *Prodiscothyrea*, *D. poweri* from *Pseudosysphincta*.

(P) *antarctica* Emery, 1895a:266. N. Zealand: North I.
(T) *bidens* Clark, 1928:38. Australia: s. e. Victoria [**101**]
(T) *bryanti* (Wheeler), 1917:29. * Malaya, Java, Hainan I.
(P) *clavicornis* Emery, 1897b:593. Melanesia
(T) *crassicornis* Clark, 1926:46. sw. Australia [**101**]
denticulata Weber, 1939:100. British Guiana [**103**]
(P) *globus* Forel, 1905:4. Java
(?) *hewitti* Arnold, 1916:160. S. Africa [**102**]
horni Menozzi, 1927:270. Costa Rica [**103**]
humilis Weber, 1939:100. Panama [**103**]
icta Weber, 1939:101. Trinidad [**103**]
(?) *isthmica* Weber, 1940:78. Panama [**103**]
(T) *leae* Clark, 1934a:29. S. Australia: Lofty Range [**101**]
(T) *mixta* Brown, sp. nov. Liberia [**105**, Figs. 47, 48]
(P) *neotropica* Bruch, 1919:400. [**103**]
(P) *oculata* Emery, 1901:52. w. and e. Africa [**102**]
(?) *patrizii* Weber (emended from "patrizzii"), 1949:2. [**102**]
poweri (Arnold), 1916:162. * S. Rhodesia [**102**]
(T) *remingtoni* Brown, 1948b:38. N. Caledonia [**104**]
sauteri Forel, 1912:47. n. status Formosa
(?) *sculptior* Santschi, 1913:302. n. status French Congo [**102**]
(T) *sexarticulata* Borgmeier, 1954:191. Brazil: S. Cat., S. Paulo [**103**]
(P) *testacea* Roger, 1863:177. se. United States [**103**]
(P) *traegaordhi* Santschi, 1914:3. w., e., s. Africa [**102**],
(T) *turtoni* Clark, 1934b:53. Australia: Victoria [**101**]
(T) *velutina* (Wheeler), 1916:34. * n. Queensland

APPENDIX

The pages of this appendix are reserved for notes and descriptions dealing chiefly with species-level taxonomy and biology. In the descriptions, the abbreviations for measurements and indices are as follows: TL, total outstretched length of head and body, including mandibles. In ectatommines, many species have recurved gasters, and in these, the length measurement is made to the posteriormost point of the gaster in its normal position, this point usually falling on the curved tergital surface of the vaulted second gastric segment. HL, maximum measurable length of head, including clypeus but not mandibles, as seen from full-face (dorsal) view. The occipital angles are normally included if these project. HW, maximum measurable width of head as seen from full-face view, eyes are usually excluded. CI, or cephalic index, is HW/HL × 100.

In cases where places of deposition, often cited in brackets, are abbreviated, [MCZ] stands for the Museum of Comparative Zoology at Harvard College, Cambridge, Massachusetts; [USNM] stands for the United States National Museum at Washington; [CAS] stands for the California Academy of Sciences, San Francisco; [NM Vienna] stands for the Naturhistorisches Museum at Vienna.

[1] ACANTHOPONERA PERUVIANA sp. nov.

(Figures 6, 7)

Holotype worker: TL 8.7, HL 1.73, HW excluding eyes 1.56 (CI 90), greatest diameter of eye 0.43, scape L 1.07, WL 2.60 mm.

Similar to *A. mucronata,* but differing as follows: Head with sides more nearly straight and parallel, occipital angles rectangular. Eyes larger. Sculpture of head looser, with wider, more shining spaces between the rugae, especially along both sides of median carina and in antennal scrobes. Propodeal spines heavier and longer, approaching 0.7 mm. in L (ca. 0.4-0.5 mm. in *mucronata* workers), gently divergent; when viewed from the side, more definitely arched in their basal halves and less strongly elevated than in *mucronata.*

Shape of petiole shown in Figure 7; note the continuous curve formed by anterior nodal face and dorsal outline of spine. Gaster markedly depressed and somewhat broadened (Fig. 6), with a deep constriction between postpetiole and second segment, the latter slightly broader and with a conspicuous posterior impression extending forward into the main tergital surface from the depressed apical band. Second segment only feebly downcurved, and the exposed sternum correspondingly longer than in *mucronata*. Apical segments retracted in this specimen, but the slender sting exserted.

Gastric sculpture much coarser, denser and more opaque than in *mucronata*, consisting of abundant, uneven-sized punctures, slightly larger on the postpetiole than on the second segment, forming a dense irregular rugoreticulum on the sides, less dense in the middle, where narrow, shining interspaces exist on the second segment.

Erect hairs abundant, though fewer than in *mucronata*, but thicker, stiffer and longer. Body color bright ferruginous yellow.

Holotype a unique worker [CAS] from Monson Valley, Tingo Maria, Peru, October 26, 1954 (E. S. Ross and E. I. Schlinger leg.).

[2] ACANTHOPONERA CRASSA sp. nov.

(Figure 10)

Holotype worker: TL 6.2, HL 1.24, HW excluding eyes 1.07 (CI 86), greatest diameter of eye 0.30, scape L 0.85, WL 1.82 mm.

Similar to *A. minor*, but a little larger. Head narrowing from a point in front of eyes toward occiput, narrowest, and sides sloping inward, behind eyes near the much-rounded occipital corners; occipital margin short, median section straight, or even feebly convex. Median pronotal eminence low, but better developed than in other species of the genus. Metanotal groove distinct, broad and rather deep. Propodeal spines (L ca. 0.35 mm.) straight and obliquely elevated as seen from the side; diverging, with tips feebly curved mesad as seen from above. Petiolar node (Fig. 10) thicker than in minor (Fig. 9), its posterapical tooth deflected more or less dorsad. Gaster very much like that of *minor* (Fig. 4) in general form, but slightly larger.

Sculpture in general a little coarser on head, alitrunk and node than in *minor*, the interspaces larger and shining. Pronotal rugules forming a V around the median eminence. Gaster smooth, shining, with abundant fine, separated punctulae, giving rise to dense, reclinate golden-brown pubescence. Longer fine erect hairs abundant.

Body color orange-brown, legs more yellowish.

Holotype [CAS] one of a series of 4 workers taken 6 miles west of Santo Domingo de los Colorados, Pichincha, Ecuador, February 23, 1955 (E. S. Ross and E. I. Schlinger leg.). The remaining three workers are paratypes [CAS, MCZ]. HL 1.22-1.25 mm., CI 87-89.

Considered as belonging to *A. crassa* is a short series of workers [USNM, MCZ] from Hamburg Farm, Santa Clara Prov., Costa Rica, February 26, 1925 (F. Nevermann leg.). The MCZ specimen measures HL 1.19, HW excluding eyes 1.03 mm. (CI 87). The color is much lighter than in the type series, being bright ferruginous yellow, and the occipital angles are somewhat more abruptly rounded; transverse part of occipital border broader than in type, concave in middle. Eyes a little larger, propodeal teeth shorter and feebly bent in side view, and the posterapical petiolar teeth flattened and only slightly deflected dorsad.

In color and head shape, the Costa Rican samples are somewhat intermediate, tending toward *minor*, but in the characters of total size, metanotal groove and petiolar thickness and form, they are clearly related to *crassa*. The differences from *minor* could possibly represent geographical variation, but the known distribution of *minor* and *crassa* does not support this very well.

[3] The taxonomy of the New World *Heteroponera*, like that of *Acanthoponera*, remains in a very unsatisfactory state, due primarily to the lack of sufficient material and to the inadequacy of some of the descriptions of forms undoubtedly belonging here. There are a few firm points, however. There is not much doubt about what *dolo* is; Roger's description fits reasonably well this large, yellowish species, the commonest one in collections, and distributed widely from Rio de Janeiro south to Uruguay and Misiones (the westward extent of its range is unknown). I have

seen quite a few series and strays from within this area, and the species is reasonably constant: the worker head length (HL) runs from about 1.20 to about 1.50 mm., and the cephalic index from 85 to 91. The occiput seen full-face is slightly concave in outline. Judging from the original description, Forel's var. *aurea* is apparently a semicallow worker of *dolo*.

H. carinifrons is a distinct species, easily recognized by its small size, blackish color and unarmed node; it is now known from various localities in Chile, and the variation from one series to the next is slight. *H. microps* Borgmeier is very small, has minute eyes and an unarmed, rather scale-like petiolar node, and is light ferruginous in color. In addition to the types, from southeastern Brazil, I have seen specimens of *microps* taken at Venecia, near Medellin, Colombia (S. Flanders leg.), a rather surprising extension of the range. The Colombian sample was taken near a sample of *Typhlomyrmex pusillus* Emery in the soil; *T. pusillus* is also an ant usually thought of as having a much more southerly distribution in South America.

With the *dentinodis* complex, we come to the serious confusion in *Heteroponera*. Up to now, there have been named in this group *dentinodis* itself, plus three varieties: *panamensis, inermis* and *schwebeli*. Mayr described *dentinodis* from southern Brazilian examples with a short tooth on the posterior apex of the node in larger workers, but said that this tooth was obsolete on the nodes of smaller workers. However, there is no definite statement that Mayr's large and small workers come from the same nest series, so we cannot be sure that they represent the same species. The few specimens I have seen from the southern part of Brazil are strays, and so we still have no assurance that the two types of workers represented in collections are conspecific, though this does seem likely. Emery complicated the situation by describing var. *inermis* from a female without developed posterapical nodal tooth; this female indicates either that the tooth character does not vary in correlation with size (i.e., is not markedly allometric, as Mayr implied), or, more likely, that another species exists with poorly developed tooth in all sizes of workers and females as well. We now know, in fact, that such a species exists in Lüderwaldt's var. *schwebeli*, but *schwebeli* seems too large to be the same as *inermis*. It may be that Emery's measurement was too low, but we shall not be sure of the identity of *inermis* until the type can be reviewed.

Referred to *dentinodis* provisionally are the following: a larger worker from Parecy Novo, Rio Grande do Sul; HL 1.02, HW without eyes 0.90, WL 1.35 mm., CI 88. One smaller worker each from Nova Teutonia, Santa Catarina (F. Plaumann leg.), and Agudos, S. Paulo (W. W. Kempf leg.), measure HL 0.78-0.79, HW 0.70-0.71, WL in both examples 1.04 mm.; a winged female from Petropolis, Rio de Janeiro (Coll. Borgmeier): HL 0.97, HW 0.85, WL 1.32, forewing L about 3.5 mm. The cephalic index for these three large and small workers and one female ranges from 88 to 90. The female has a well developed and acute posterapical nodal tooth. An anteroposteriorly compressed node is characteristic for all of these specimens.

The holotype of var. *schwebeli*, from Estacão Alto da Serra, S. Paulo, has HL 1.12, HW 0.92, WL 1.51 mm.; CI 82. A similar, but slightly smaller specimen from Jaguara, Paraná, in Coll. Borgmeier, has HL 0.98, HW 0.78, WL 1.21 mm.; CI 78. Both of these, as well as a dealate female from S. Teresa, Espiritu Santo (O. Conde leg.), have dense, irregularly punctate sculpture, opaque for the most part; interpunctural spaces of postpetiole narrow and finely reticulate or coriaceous. A similar specimen from Agudos, S. Paulo (R. Müller leg.), Coll. Kempf, measures HL 1.07, HW 0.87, WL 1.43 mm.; CI 81. This last example is more shining, especially on the gaster, where the interpunctural spaces are largely smooth and shining on postpetiole as well as on the succeeding segment. So far as I can see, *schwebeli* is distinct from the sympatric *dentinodis* in shape of petiolar node (see key) as well as in the narrower head. The female node, however, is more anteroposteriorly compressed than in the worker. Total size averages larger than in the few *dentinodis* I have seen, but worker size even here overlaps slightly. For the time being, it seems best to recognize *schwebeli* as a species in its own right, though it may later prove to be the same as *inermis*, as mentioned above.

Two workers in the Borgmeier Collection (Nr. JBV 47) from Campinas, Goiás, Brazil, resemble large *dentinodis* in size and general appearance, but are light yellowish-ferruginous in color and have thicker nodes (not as thick from front to rear as in worker *schwebeli*, however) with the posterior apex continued backward as a stout subconical projection or tooth. Whether these specimens represent a different species, or mere geographical variation in *dentinodis*, cannot be decided without material from intervening areas in Brazil.

Concerning var. *panamensis*, I have asked some questions about the type in the British Museum, kindly answered by Mr. G. E. J. Nixon, who made comparison for me with a paratype worker of the species I describe below as *H. inca* sp. nov. Mr. Nixon's remarks are adapted in part and follow in the next three paragraphs.

H. panamensis type is slightly smaller than *inca*, and more slender. Outstretched length (the small apical gastric segments are hidden and not included in length) of *panamensis* type about 3.8 mm. Color virtually the same as in *inca*. Head distinctly longer than broad and decidedly narrower than in *inca*, less convex dorsally and without the occipital lobes of *inca;* occipital margin straight.

Propodeal teeth very short, forming angular projections not longer than wide at base. The second gastric segment is much less strongly differentiated from the first than in *inca*, and is nearly the same width as the first segment (postpetiole). Left mandible with 7 teeth, the seventh tooth forming the basal angle; the three teeth next to the seventh tooth very weak.

Sculpture much finer than in *inca;* surface of head between the frontal area and occiput and between the scrobes quite dull, very finely longitudinally striate and with the median carina in full relief. Between scrobes and eyes the surface finely rugose, not easily defined at 40×; toward the occipital angles the sculpture thickens slightly.

From this characterization, it appears that *panamensis* is much closer to *dentinodis* than to *inca*, and it is not impossible that *panamensis* and *dentinodis* are synonymous. However, the distributional facts and the darker color of *panamensis* are, it seems to me, sufficient cause to hold up synonymy until a direct comparison of the type with other material can be made. For the time being, *panamensis* is raised to nominal species status.

HETEROPONERA INCA sp. nov.

(Figures 12, 13)

Holotype worker: TL to apex of second gastric segment 4.8, HL 1.14, HW including eyes 1.10, HW excluding eyes 1.06 (CI

93), exposed scape L 0.76, greatest diameter of compound eye 0.24, WL 1.44 mm.

General habitus that of *H. dentinodis*, but more robust in build, darker in color, with a differently shaped head, longer propodeal teeth, thick petiolar node with calcarate ventral process, and with a proportionately larger postpetiole.

Head in full-face view as in Figure 12; note especially the somewhat depressed and lobiform occipital angles. Seen from the side, head strongly convex across vertex and central occiput; occipital lobes auriculate, broad, obliquely subtruncate, with narrowly rounded corners above and below, much as in *Gnamptogenys costata* and *G. menadensis*. Antennal scrobes weakly defined curving above the eyes and terminating indefinitely some distance behind toward the occipital angles. Eyes strongly convex, each with a circummarginal sulcus. Mandibles triangular, basal angles blunt; apical tooth and a smaller preapical tooth strong, acute, remainder of margin with coarse, shallow crenulation. Clypeus convex in the middle and with narrow, depressed anterior apron, the margin of which is feebly convex seen in outline from dorsal view. Scapes short, incrassate toward apices; when laid straight back or nearly so from their insertions, falling slightly short of the occipital margin. Funiculi gradually thickened toward their apices; the last three segments could be considered as forming an indistinct club; penultimate and antepenultimate segments about as long as thick, segments II-VIII thicker than long.

Alitrunk robust, pronotum rounded above, separated from the narrower mesonotum by a deep-cut (possibly mobile) suture; inferior pronotal margin obtusely angled on each side. Mesonotum forming a single gentle convexity with propodeal dorsum; metanotal groove marked by a very indistinct transverse line or sulcus. Propodeal teeth well developed and acute, larger than in any other *Heteroponera* so far described; seen from above divergent, slightly longer than the distance between the inner sides of their bases. Petiole as in Figure 13; seen from above, the node is slightly broader than long, excluding posterapical tooth, which in this view is broad at the base, tapering to a narrowly rounded point.

Postpetiole large, semiglobose, broader than long, slightly narrowed around its apical border. Succeeding segment as long as postpetiole, but narrower (about as broad as long seen from above), weakly downcurved and tapering toward apex. Apical segments tapered rapidly apicad, at least partially retractile. Legs robust; each middle and posterior tibia with a single large pectinate spur; all tarsal claws slender and simple (without submedian teeth or denticles).

Mandibles smooth and shining (when clean), with scattered punctures. Antennae, gula, gastric apex and legs with very fine indistinct punctulation or reticulation, subopaque to opaque. Head, alitrunk, node and gaster irregularly reticulo-rugulose over an extremely fine microsculpture, opaque, with inconspicuous coarse punctures crowded on head and alitrunk, but becoming fewer and still less conspicuous posteriorly. Upper scrobes with fine transverse rugulae.

Normally exposed surfaces of body covered with an abundant and mostly decumbent, fine, light-colored pubescence, sparse only on the mandibles, gula and retractile segments of gaster. Body and appendages also with an abundant pilosity of fine, tapered erect hairs, uneven in length, the longest about twice the length of the propodeal teeth. Body color deep brownish-red, legs more reddish.

Holotype, one of a long series of workers taken about 6 miles west of Cali, Valle, Colombia, at an altitude of 1630 m., March 20, 1955 (E. I. Schlinger and E. S. Ross leg.), deposited in California Academy of Sciences. The paratypes have the same data as the type. TL 4.7-5.0, HL 1.11-1.20, HW 1.00-1.11, CI 91-93. Propodeal teeth vary slightly in length and thickness, but in general are longer than broad at base. Posterapical tooth of petiolar node varies considerably in length, sometimes being markedly shorter than as shown in Figure 13, and sometimes more slender and acute, but not much longer. Color ranging from that of the holotype to very dark reddish-brown. Paratypes in CAS, Coll. Borgmeier, USNM, MCZ.

[4] *Heteroponera imbellis* (Emery). This little species is widespread in eastern, southeastern and southwestern Australia, where it makes small nests under stones or woody fragments, or

directly in the soil without cover. It forages at least partly during the daytime, and solitary workers can be seen leaving the tiny, inconspicuous nest entrance to move slowly about in the open and among the leaves and debris of the soil cover. Although Wheeler (1934, p. 140) thought it hypogaeic in habits, I have not found it so. One worker was seen carrying unidentifiable remains of a very small insect into the nest.

H. imbellis does not seem to be very conspicuous anywhere, but it is not rare. I have found as many as four nests in a single day's collecting at one locality. One nest contained over 70 workers and several ergatoid females. The ecological tolerance of this ant is surprisingly wide; it occurs in a great variety of vegetation zones, from the wet mountain forest of the Australian Alps (at least to 1300 m. altitude) and southeastern Queensland to dry savannah woodland in the southern Flinders Ranges of South Australia (Mt. Remarkable) and the treeless savannah west of Melbourne.

Considerable variation is seen in size, color, sculpture, length and abundance of pilosity, angularity of propodeum, and antero-posterior thickness of the petiolar node. A large part of the color variation is due merely to the long period of adult tenerality, which may cause whole broods of workers to appear very different from one nest to another. The color also affects the visibility of sculptural patterns. I have examined 21 nest samples, mostly in good series, from nearly as many scattered localities, including 6 cotypes of *occidentalis* and a type of var. *scabra*, and I believe that the forms listed in the synonymy can be defended at best only as local or nest variants of *imbellis*. All of the characters mentioned appear in varying combinations and degrees, and I find considerable intergradation connecting all series. The present material shows no obvious "racial" pattern on a broad geographical scale, even for single characters.

[5] Cotypes of *H. brouni* from the Canterbury Museum at Christchurch, N. Z., received through the kindness of Dr. R. R. Forster, were compared directly with the type series of subsp. *kirki* and found to be as closely identical as series from two different nests can be. Wheeler's diagnosis of *kirki* is not as representative as Forel's. I have followed Wheeler in recognizing the obvious lapsus or typographical error in Forel's original spelling, "*brownii,*" and in emending the name to *brouni*. The species is widely distributed in the North Island of New Zealand, but I have seen no specimens from the South Island.

[6] Justification of new synonymy and other systematic changes in *Rhytidoponera* attributed to Dr. E. O. Wilson are included in the manuscript he is preparing on the Ponerinae of Melanesia, amounting to a revision of the species of this region. Wilson collected extensively in Melanesia during 1954-1955, and on his return to the United States, he was able to make critical comparisons of MCZ material, including specimens forwarded to him out of his own Melanesian samples, with types in several of the principal European collections. This type-comparison work was important in establishing many of the new synonymies put forward here, both in his name and in my own.

[7] The *impressa* group, *R. aspera* and *R. croesus* were revised by Brown (1954b:1-11) and a number of names put into synonymy under these species. I have omitted these junior synonyms from the list.

[8] In his revision of the larger Australian *Rhytidoponera*, Clark (1936) placed a number of names proposed by earlier authors in the synonymy. Unfortunately, he failed to offer evidence for most of the synonymies, and it is possible that some of them are incorrect. In any case, they should all be reviewed. However, a spot check convinces me that most of his assignments in synonymy are probably correct. None of the synonyms from the 1936 work will be listed here.

[9] A previous guess (Brown 1952b:137) that *laevior* Stitz was based on part of the type series of *aciculata* (Fred. Smith) is strongly backed by an obscure reference of Roger (1860:307) that I had not noticed before. Roger here cites *aciculata* material in the Berlin Museum that was sent by Smith. There can be little doubt that this is part of the material used by Stitz to describe *laevior*. In order to clear up any doubt about this

synonymy, I here select Hunter River, New South Wales, as the type locality for *laevior*, since this is also the type locality cited by Smith for *aciculata*.

[10] *R. scaberrima* and *R. malandensis*, described from northern Queensland localities very close together, cannot be distinguished. Although *malandensis* was described as a subspecies of *R. laciniosa* Viehmeyer, from New Guinea, *laciniosa* clearly is not closely related to the Queensland form.

[11] I found this little species (*borealis*) fairly common everywhere in the open tall eucalypt woodland southeast of Darwin, at Berrimah, at Howard Springs, and along the edges of the Howard River gallery forest, in the Northern Territory of Australia. Foraging workers are often found abroad in bright sunlight. Nests are made directly in the soil, or under logs, at least during the dry season. I also have a worker from the Finniss R., N. T. (R. Parkinson leg.). Clark's description of *brunnea*, while failing to mention some details of sculpture, nevertheless fits this species passably well. It is the common representative of the *metallica* group in the Darwin area.

[12] *R. anceps* has been poorly known, due chiefly to its rarity and local distribution. Wilson has compared specimens from near Brisbane (W. M. Wheeler leg.) with Emery's type in Genoa, and he finds that they match well. In the Museum of Comparative Zoology are other samples from Tamborine Mt. (A. M. Lea) and National Park (H. Hacker), both localities also in southeastern Queensland near the New South Wales border. Very likely the species occurs in northeastern New South Wales. The most obvious character, and one Emery does not properly emphasize, is the very low, blocky petiolar node of the worker and female. Seen from the side, the worker node averages just about as long as high without the ventral process, the proportions varying slightly either way in different specimens. As seen from above, the node is as long as broad, or very nearly so. The dorsal surface is distinct, even subtruncately set off, but is always slightly convex and usually rises slightly from front to rear. The posterior face is vertical or slightly receding ventrad. The head is not quite so wide behind as in related *metallica*-complex forms, and there is a weak impression in the middle occipital region, best seen when the head is tilted slightly back from full-face view. The scapes are rather slender and, when laid straight back, they surpass the occipital border by distinctly more than their greatest width. Funicular segments all more or less distinctly longer than broad. Color brown or reddish-brown, the gaster often darker brown, without metallescence. Second gastric segment finely striate in a transverse arch, which passes posteriorly into a longitudinal, concentric ellipse; this posterior region somewhat more shining.

In addition to the Queensland samples, I have two workers and a headless male that I provisionally call *anceps*, collected at the Thomas River Station, east of Esperance, Western Australia, by E. O. Wilson and C. P. Haskins. The locality is a wooded depression in the heath-covered sandplain, the trees being mainly paperbark (*Melaleuca cuticularis*), yate (*Eucalyptus cornuta*) and wattles (phyllodineous *Acacia* spp.), the last-named contributing in places to the shrubby undergrowth. Thin leaf litter exists in some parts of the depression, but in the summer this is very dry.

The two workers apparently represent a rather dense population, for Wilson's notes mention, in addition to an abundance of *R. metallica* nesting in the ground, a smaller, "more slender" species, also nesting in the earth and foraging on trees and shrubs, especially at night, at the Thomas River locality. The specimens resemble the Queensland *anceps* very closely in all respects, except that the petiolar node is not quite so long. In dorsal view, the node is distinctly wider than long, but it is still much longer and lower than the nodes of *inornata* and *metallica*. In general habitus without magnification, the Thomas River *anceps* looks much like *inornata*, and probably acts like that species in the way it accompanies *metallica* in a restricted, relatively favorable habitat. If this Thomas River population is actually conspecific with *anceps* from Queensland, or even if the two populations represent very closely related but distinct siblings, as their external morphology suggests, their present distribution is a remarkable example of a relict peripheral persistence.

[13] *R. convexa* and *R. violacea* are very closely related, the best difference so far seen being the metallic green-violet surface reflections of *violacea,* lacking in its eastern twin. The ranges of the two forms appear to be separated by a broad gap in central Australia; neither has been found in the Northern Territory, despite intensive collection by G. F. Hill and others, including myself. *R. violacea,* widespread in Western Australia, has been taken along the Transcontinental Railway in that state as far east as Kalgoorlie (Wilson leg.) and even 1072 Mile Siding (Brown leg.), but it apparently does not cross the Nullarbor Plain. *R. convexa* ranges widely in eastern Queensland, and has isolated populations in the moister parts of the Flinders Ranges of South Australia **[19]**, but its western limits are yet to be determined. The species separation is maintained here arbitrarily in the absence of decisive information concerning their status relative to each other.

The form described as *opacior* by Crawley is only a variant of *violacea* in which the metallescence is more obscure than usual, the green component especially being suppressed. Such individuals have been taken from the same nest series as some with the more usual violet-green coloration, e.g., in a nest series from Pioneer Siding, north of Norseman, W. A. (Brown leg.).

R. rufescens, heretofore placed as a variety or race of *convexa,* is really a good species, distinct in its more widely-spaced punctation, as well as in the shape of its node, which averages wider at the base. The color is yellowish-ferruginous in *rufescens* specimens from Townsville (type locality by present selection), but a sample from Bowen, Queensland (F. H. Taylor leg.) is reddish-brown, approaching the hue of lighter *convexa* workers. I have true *convexa* workers also labelled as from Townsville (W. M. Wheeler leg.), but there is no sign of intergradation between the two forms in this region.

[14] *R. inornata,* described by Crawley as a variety of *metallica,* is clearly a species apart, restricted to the extreme southwestern strip of Western Australia and certain of the islands off Fremantle. On the eastern side, it reaches the Darling Range in back of Perth, where it overlaps *R. metallica* without producing intergrades so far as known. *R. metallica* appears to be scarce in the main part of the *inornata* distribution, so that the two species approximately replace each other. Workers of *inornata* vary in color from light tan to blackish-piceous, the alitrunk usually being a trifle lighter than head and gaster; metallescence is lacking. The striation of the postpetiole is coarser than in Western Australian *metallica*, with broader interspaces, and is usually strongly arched over a small median area of more or less longitudinal rugulosity situated near the slightly emarginate posterior border. Punctures on the gaster vary from strong and numerous to virtually completely obsolete.

The sculpture of the second postpetiolar (second gastric) segment is arched rather strongly, and the raised costulae are separated by shining interspaces, whereas the sculpture of this segment in *metallica* is very fine, dense and more or less sericeous.

A normal dealate female and winged males were taken November 3, 1931, at Margaret River, W. A. (W. M. Wheeler). This female differs from the worker in the ways usual for ponerine ants, and has well-developed ocelli, compound eyes, thoracic flight sclerites and wing stumps. Wheeler's name *carbonaria* applies to common variants well within the normal spread of *inornata*.

R. inornata combines several features of the two related species *tasmaniensis* and *victoriae*, from eastern Australia, where they replace *metallica* in damp forests. This situation is interpreted as "character displacement" by Brown and Wilson, 1956.

[15] RHYTIDOPONERA KURANDENSIS sp. nov.

Holotype worker: A small species, to the naked eye resembling *R. tenuis*, or to a lesser extent *R. victoriae*. TL 4.3, HL 1.02, HW 0.84 mm. (CI 82), WL 1.38 mm. Head broad-oval, almost subcircular in outline seen full-face; greatest width at or immediately behind compound eyes (excluding eyes themselves), slightly narrowed in front of eyes. Occipital angles gently rounded, occipital border convex, with a very slight flat or concave tendency in the very middle. Clypeus convex, rather strongly projecting and forming an obtusely rounded angle in the middle. Eyes large (ca. 0.21 mm. greatest diameter) and strongly convex, occupying roughly ¼ the sides of the head. Antennal scrobes short and shallow, not extending backward past the eyes. Antennae slender; scape 1.04 mm. long from basal collar; when laid directly back, surpassing the occipital border by ⅓ its length. Mandibles large, finely denticulate.

Alitrunk rather slender (more slender than in *tenuis*), convex in profile, with a feeble impression in the region of the metanotum. Propodeal dorsum and declivity forming one rather flat curve, sloping downward caudad. Petiole distinctly smaller than in *victoriae*, and slightly smaller than in *tenuis*, with a short but distinct pedicel in front; free part of node nearly as high as long, with steep anterior and posterior faces rounding into a convex dorsal face; ventral process forming an acute triangle. Node seen from above broader than long, semicircular in outline, with the curved surface anterior. Gaster a little more slender than in *victoriae* or *tenuis*, but the lengths of the postpetiole and succeeding segment are in about the same proportion (3:4) to each other.

Sculpture of head, alitrunk and petiolar node consisting chiefly of coarse, contiguous foveolae or punctures with shining bottoms. Ridges separating these foveolae form rugulae, longitudinal on the head, mixed in direction on pronotum, and finer, closer and transversely oriented on the posterior half of the alitruncal dorsum. In general, this sculpture is coarser and more shining than in *tenuis*, and it lacks the interspersed dense punctulation found over the alitrunk and node of *tenuis*. Postpetiole with loose, irregularly-spaced costulae arching over a median posterior area of indistinct, mostly obsolete costulae forming a concentric longitudinal fusiform pattern, with a few coarse, shallow elongate punctures; costular interpaces and much of the posteromedian area nearly smooth and shining. Second gastric segment costulate on the same pattern as the postpetiole, but much more weakly and with wider, smoother interspaces; a large posteromedian area completely smooth and shining, with scattered small punctures.

Erect hairs fairly abundant over most of body, mandibles, scapes and legs; similar in abundance and distribution to those of *victoriae*, but averaging a little shorter. Appressed hairs of gastric dorsum few and very small, inconspicuous, more scattered than in *victoriae*, and about the same as or fewer than in *tenuis*. Color deep, more or less reddish brown; mandibles, antennae and legs lighter, more yellowish.

Holotype worker [MCZ] collected at Kuranda, near Cairns, northern Queensland (W. L. Brown leg.). Paratypes: 14 workers representing six or more nest series from Kuranda and immediate vicinity (W. M. Wheeler leg., October 19, 1915; Brown leg. October 29-30, November 1, 1950). Also, four workers labeled "Cairns dist." (F. P. Dodd leg.) which probably came originally from Kuranda, near Dodd's home. My collections were made in rotting logs in rain forest, and consist of strays rather than colonies, probably because I did not at the time distinguish between *kurandensis* and *victoriae*, one or both of which were common at the same site. The only full colony of *victoriae* I took here, however, was in a large, rotting polypore fungus growing from the earth of the forest floor. The *kurandensis* workers may have belonged to diffuse colonies living in the rotten wood, but my notes do not mention the discovery of any brood with them.

Variation within the paratype series is slight. All workers are close to the holotype in size and proportions; in some of them, the head is a little more nearly quadrate, owing to less convex sides and occiput. There is slight variation in the height and thickness, as well as the angularity, of the petiolar node as seen from the side, and different specimens differ slightly in the density and distinctness of the gastric sculpture. Color varies from light brown (tenerals?) to piceous. The appressed pubescence of the second gastric segment is at best very sparse and inconspicuous, and in some specimens can scarcely be made out even in the best lights and magnifications. Paratypes to be deposited in USNM, MCZ and one or more Australian collections.

[16] RHYTIDOPONERA CHNOOPYX sp. nov.

Holotype worker and two paratype workers: Like *kurandensis*, but with the entire exposed tergital surface of the second gastric segment densely and uniformly covered with fine, short appressed pubescence, directed posteriorly and mesad. This pubescence forms a distinct brownish-yellow cast over the segment, but does not quite conceal the sculpture beneath. The individual setae of the pubescence arise from myriad fine, separated punctulae, but otherwise the sculpture is like that of *kurandensis*. *R. pulchella* Emery, of New Caledonia, is very different in other ways, but has somewhat similar dense pubescence on the gastric dorsum; however, in *pulchella* the pubescence is less fine and is more whitish in color.

Holotype and two paratype workers taken (apparently together) at Millaa Millaa, Atherton Tableland, northern Queensland, at an altitude of about 2500 feet, undoubtedly in rain forest (P. J. Darlington leg., April, 1932). Deposited in MCZ.

Except for the gastric pubescence, *kurandensis* and *chnoopyx* are so similar that they could represent the same species. I prefer to separate them specifically for the time being, since I feel that sibling species may be rather common in this limited Atherton Tableland-Cairns region. The similar, but longer-headed species *tenuis* and *peninsularis* **[27]** form a more or less parallel *Artenkreis*, and it is worth noting that no two of the four forms mentioned in this paragraph have ever been taken at exactly the same locality. *Rhytidoponera* of this general group are well worth further investigation in northern Queensland.

[17] The group of species related to *R. punctata* includes robust, medium-sized entities of black or brown color, very finely and evenly reticulo-punctulate over most of the body, so that the integumental surface is largely opaque. In addition, the head and alitrunk (especially) bear larger, conspicuous punctures or foveolae. These forms are distributed widely in the drier parts of South, central and southwestern Australia, but up to now, they have been only very sporadically collected, which is unfortunate for the taxonomy, seeing that there is a great deal of variation in sculptural and minor structural details from nest to nest and especially from place to place. As might be expected, there seem to be more names than there are species, in large part due to splitting by Clark and Crawley. I have not seen the types, or even topotypical material, of *R. punctata*, so I shall suggest no formal synonymy here. However, it does seem to me that *R. flindersi* is very likely to prove a synonym of *punctata*. And material referable to *punctata* from Forrest, Western Australia [C. Barrett leg., MCZ] and near Balladonia, W. A.

[E. O. Wilson and A. Douglas leg., MCZ] shows that *punctata* may be distributed widely, if sporadically, across the wastes at the head of the Great Australian Bight, or at least that the distance separating eastern and western populations of the complex is not so great as has generally been assumed. In Western Australia, the two forms *douglasi* (= *levior* Crawley) and *rufonigra* are very like *punctata;* in *douglasi* the conspicuous punctures are much smaller and farther apart; however, some specimens (e.g., from Dongara, W. A.) are difficult to assign, and may be intergradient. A close study should be made of these forms in the Perth area; if they are found to intergrade there, synonymy with each other and with *punctata* would seem fairly certain. However, it is also possible that character displacement is operating here.

The *punctata*-group representative in central Australia is *R. incisa*, of the MacDonnell Ranges, where it is fairly common in my experience. This form is the most distinct of the group, and seems to be well isolated from the other species; however, we must expect further members of this complex to turn up from ranges to the south of the MacDonnells, in South Australia, and these may well link *incisa* to *punctata* if they do occur.

[18] Wilson (MS. notes) has compared an MCZ specimen from Broken Hill, N. S. W. (F. W. Shepherd leg.) with types of *maniae* and *spatiata* in the Forel Collection. He finds that, "*maniae* is the same as *spatiata* — the types are nearly identical; *spatiata* is somewhat larger and with a proportionately broader head, but the Broken Hill specimen is intermediate in both characters." I have also found that the Broken Hill specimens (determined as *spatiata* by Clark) are very similar to some collected by Zietz, Tepper and myself in the Lofty Ranges east of Adelaide. The types of both species probably came also from this neighborhood, more precisely the dry eastern scarp of the Lofties, such as the locality, at Barren Falls, near Mannum, South Australia, where I found *maniae* avoiding the heat of the day in December, and foraging at the same time as *mayri* after late afternoon shadows fell on the canyon floor. *R. maniae* is essentially a species of the Murray-Darling drainage area. To the north and west, in the Flinders Ranges, it is apparently replaced by another, similar species that I have not yet satisfactorily determined **[19]**.

Wilson has called attention to the close similarity between *maniae* and *R. hilli* Crawley, from the north of the Northern Territory. The two are indeed similar, but *hilli* averages lighter in color. The *hilli* types (Stapleton, N. T.) are brown with reddish gaster, while a series I took at the Mataranka Hot Spring, on the Roper River, is a rather uniform rich orange-brown. In these two series, the second gastric segment is usually transversely striolate, but occasional examples have the posterior part with longitudinally or obliquely arched striolation approaching the condition in *maniae*. *R. hilli* also tends to have a slightly more opaque and finer sculpture on head and alitrunk. Whether the two populations represent separate species remains to be decided.

[19] In the Flinders Ranges of South Australia, where I searched intensively for *Rhytidoponera,* I found only three of the larger species (*R. metallica* was also present). Of these, the largest and most tolerant of xeric conditions, and hence the most continuously widespread species, is *R. mayri*. The smallest clearly agrees with *R. convexa*, which is usually thought of as a tropical Queensland species. The middle-sized species of the three is similar to *maniae* **[18]**, but it is a little larger and is more heavily and rugosely sculptured over head and alitrunk. With *convexa*, this middle-sized species occupies the more moderate localities within these largely very arid ranges, especially such moister localities, often with some woodland cover, as Mt. Remarkable, Wonoka Creek and Wilpena Pound. I have not been able to match this species satisfactorily with any of Clark's (1936) descriptions. The name *nigra* could possibly apply to it, but it seems more likely that *nigra* is Clark's designation for the Flinders Ranges populations of *convexa;* his description and figures are not good enough to make the identification certain. (A belated look at specimens of *R. nigra,* determined by Clark and belonging to the original series from which he described *nigra* [Owieandana, South Australia, Hale and Tindale leg.], establishes, as far as I am concerned, the synonymy of *nigra* with *convexa.* I have not changed the list to indicate this synonymy.)

[20] R. mayri was described from material erroneously labeled as having come from New Zealand, but which probably came instead from the hinterland of Adelaide, South Australia. Dr. Wilson has been able to compare material from various localities with the *mayri* type, and he has been able to make a very close match with specimens from Mildura, Victoria (F. H. Taylor leg.), these latter matching in turn Clark's concept of the "mallee species," *R. dixoni*. The samples of the *mayri* complex come from many arid inland localities in the southeastern quarter of Australia, ranging from southwestern Queensland through western New South Wales and Victoria into South Australia. The complex is not known from south-central Australia, and it is not yet known to extend continuously, or even as a chain of isolated populations, across the arid inland of South and Western Australia. *R. mayri* complex is absent from, or at least very uncommon in, the extreme south of Western Australia, but is met again in the dry country to the north and northeast of Perth. Specimens from Geraldton and the Mullewa area, more or less near to the coast of Western Australia, are very like eastern *R. mayri*, and show a large part of the same variation in size, head shape, color, sculpture, pilosity and especially node shape, that marks the eastern series. Going farther inland, at Meekatharra, Wiluna, Lake Violet and Yandil, W. A., (leg. W. M. Wheeler, P. J. Darlington), one encounters populations with a larger proportion of reddish individuals, and in which the rugosity of the body, especially the pronotum, tends to be reduced and looser, with wider, very finely reticulate sculpture in the interspaces. Both *occidentalis* and *glabrior* (as represented by specimens in the MCZ determined by Clark) appear to represent the more southerly, more coastal type with heavier sculpture, which I do not feel from present evidence should be nomenclatorially separated from *mayri*.

Clark relied heavily on the shape of the petiolar node in separating what he thought were different species, but it seems that he failed to realize the amount of variation in this segment. In both the eastern and western populations, and also in single nest series, one can find nodal variation completely exceeding the narrow limits Clark apparently allowed. Variation is strong in other characters, also, particularly those already mentioned.

Some series have numerous short, erect hairs over the body and appendages, others are bare or nearly so. The striolation of the gaster, particularly of the second segment, varies from transverse, through strongly arched, to longitudinal. In the population called *quadriceps* by Clark, from Tennant Creek and the MacDonnell Ranges (Mt. Frances, leg. G. F. Hill) of Central Australia, the short erect hairs are abundant everywhere on the body, limbs and scapes, and the second gastric tergite is longitudinally striolate. The sample described as *stridulator,* from inland New South Wales, is intermediate between *quadriceps* and South Australian populations in having the average second gastric segment with longitudinally arched striolation; the short hairs are mostly erect, with a sparse growth of appressed, pubescence-like hairs also, especially on the gastric dorsum. The extreme *quadriceps* variant may represent a case of character displacement in the *mayri* population of the MacDonnell Ranges, because a very similar species is known from there in *R. mirabilis,* a form notable for its virtual lack of erect hairs and for the substitution of a rather dense pubescence-like pilosity of short, appressed to decumbent, fine hairs; it is also worth noting that the dorsigastric striolation of *mirabilis* is weakly arched-transverse in contrast to the longitudinal orientation of the *quadriceps* sculpture. At present, this interpretation must be considered a very tentative one, awaiting more material from the MacDonnell Ranges and from areas between these mountains and South Australian districts in the known range of *mayri.* In my own collecting at Tennant Creek, and around Alice Springs in the heart of the MacDonnells, I found no *mayri*-group species (beginning of cold season), but took numerous samples of *taurus, incisa* and one or two other large species. Apparently, the *mayri* group is near the limit of its range here, in an area largely dominated by *taurus* (a large species that is similar in many ways).

R. petiolata refers to specimens from northeastern South Australia with "dome-shaped" nodes (type loc.: L. Killalpaninna, S. A.). Specimens in the MCZ from this general area (Cooper R., leg. Reuther; L. Callabonna, leg. Zietz) have rounded nodes much as indicated by Clark for *petiolata,* but nodes similar to these can also be found in series from the Flinders Ranges in South Australia (Brown leg.). The *petiolata* kind of petiolar node seems, therefore, to be only a part of the normal variation of *mayri* in South Australia. The variation already cited for *mayri* is of the kind that would undoubtedly be described by ornithological colleagues in terms of the "polytypic" species, with the various species of Clark mostly ranking as races. It seems preferable, however, that future students of this very interesting group be encouraged to examine it from the viewpoint of independent character variation studies. Another point worth study in the future is the relationship of *mayri* to *aciculata* **[9]**.

[21] The *metallica* complex deserves a full-scale study which, when it comes, will undoubtedly furnish wonderful data on geographical variation. The species *metallica* is one of the most abundant, easily collected and variable of Australian insects. I have examined the specimen in the British Museum labeled "type" and here designate it as lectotype; the specimen with others, is from Adelaide. These specimens are, of course, old ones, and their color may have changed, or they may have come from some distance away from Adelaide proper. However this may be, they can be matched rather closely by certain specimens taken by myself in the Adelaide district in 1950 and 1951. Here the color varies from metallic green to purple with green overtones.

As one travels northward in the dry Flinders Ranges of South Australia, the color of *metallica* series gradually and rather irregularly shifts more and more toward a uniform dark purple, and dark purple clearly predominates in the series I took around Alice Springs, in central Australia. It is to this northern desert variant that Wheeler gave the name *purpurascens*. Clark's *pulchra*, from farther west, does not seem to differ from this dark form in any significant way, at least judging from his description. *R. caeciliae* doubtless belongs here also; I have had a hurried look at a cotype in USNM.

In country with somewhat better rainfall, such as the south Victorian savannahs and the New South Wales tablelands, *metallica* workers are more often predominantly green, though with purplish tones usually present on the sides of the alitrunk. Northward in New South Wales and Queensland, one meets a form in which the alitrunk is predominantly reddish-violet, shading into golden on the lower pleura, and with the green restricted to a mid-dorsal strip, or even absent. The gaster of most such specimens, unlike that of the central desert populations, is solid, bright green. In some places, especially at the University of Queensland Farm at Moggill, near Brisbane, I found what seemed two slight color forms living side by side under stones in sparsely-treed savannah; one of these was the form just mentioned, while the other was noticeably more completely green. The difference is still visible in the cabinet series obtained, but it was more obvious as seen in the many living colonies opened in the field. Besides color, I can find no constant differences between these series. Whether this variation marks two sibling species cannot be determined from such casual and incomplete evidence, but the possibility cannot be overlooked. These same two color forms are connected by all degrees of intermediate coloration in other localities, especially farther south, but it is possible that this is only another case of "character displacement" **[14]**. However, there was no obvious sign of ecological segregation between the two forms at Moggill.

In the far north of Queensland, in the Mareeba-Koah district, the open monsoonal sclerophyll woodland and savannah woodland supports an abundant population of a smallish, rather uniformly dull green *metallica*-like form, quite distinct from the more southern types. However, we do not know how these populations hook up west and south of the Atherton Tableland, so it is impossible to say whether the Mareeba district form is an independent species (*maledicta?*) or not **[31]**.

In addition to the extensive and striking variation in color, *metallica* shows a range of minor differences in size, shape of head and of petiole, length of appendages, sculptural details, and so on.

Crawley's var. *varians* is a form in which the superficial punctures of the gastric dorsum are coarser and more numerous than usual. But such variants are found not only in the Darling Range, Western Australia, the *varians* type source, but also in various parts of southeastern Australia. Intergrades to forms with weak or obsolescent punctures are found both east and west, so that *varians* cannot be considered as a separate population. It is interesting to note that sculptural variation shows no geographical concordance with color variation over broad areas, at least in the fairly abundant material present in the MCZ. Part of the *varians* type material was teneral, it should be noted.

The *metallica* complex is represented in the extreme southwest by *inornata* **[14]**, in the far north by *borealis* and *trachypyx* **[11, 28]**, and in moister parts of the southeast, by *tasmaniensis*. All of these species are very nearly or completely non-metallescent, and in their more brownish or reddish color phases, they resemble one another, to the naked eye. *R. tasmaniensis* meets and intermingles with *metallica* at various points in the savannah country of western Victoria, in the environs of Melbourne, and on the New South Wales tablelands, but the two remain distinct and easily separable at a glance at the living colony, even when their galleries are only a few feet apart. However, teneral specimens of *metallica* isolated in the cabinet may be mistaken for *tasmaniensis*, since apart from color, the two species are closely similar. The var. *cristulata* Forel is the same as *tasmaniensis* (Emery, 1912:79): types have been compared by Wilson. *Tasmaniensis* is brown or reddish brown in color, the gaster darker brown and sometimes faintly bronzy in tone.

[22] I took a few workers of *R. reflexa* from a small nest on the Koolpinyah Track, near the western entrance of Koolpinyah Station, Darwin district, Northern Territory, Australia. Koolpinyah, one of the original localities, is here selected as type locality. My nest was taken in the middle of a typical, broad floodplain savannah, floored by heavy soil covered with hard, lumpy earthen hillocks up to 15 or 20 cm. high and about the same in diameter, formed by an unknown agency. This savannah, shallowly flooded in the wet season (my visit was made in the early dry season), is characterized by widely scattered, spindly, low *Melaleuca* and *Banksia* trees, and by a poor ground cover consisting of sedges and certain special flowering herbs. The ants taken here, while not abundant, are special forms not seen elsewhere during my stay in the Darwin area; they include *R. reflexa*, a species of *Polyrhachis*, and a small, bright yellow *Monomorium*, the first two nesting in the hillocks, and the last in rotten sticks on the ground. It is possible that the ants escape part or all of the monsoon floods by means of the hillock nest sites, although

I have never seen this area myself when it was in flood, so cannot verify the surmise. Clark's description and figure of this species are rather crude and sketchy, but it is so aberrant a form that there can be little question of identifying it. Clark records it also from Bathurst Island, and it is probably widespread in suitable localities in the Darwin area. It will be interesting to see what happens to *R. reflexa* when and if the projected rice-culture areas are begun there.

[23] I took *R. reticulata* in open savannah woodland at Katherine, Northern Territory, on July 4-5, 1951. Workers were foraging from a single small craterless nest entrance in the hard soil. Males were present; like the lighter-colored workers, they are yellowish-brown. Foraging is nocturnal.

[24] *R. rufiventris* was originally described as a variety of *R. convexa,* but the two are quite distinct in size, shape of head and petiole and in their distribution, although they are sympatric over very large parts of Queensland. *R. rufiventris* is common and conspicuous in the open forest country of north Queensland; in Western Australia, it appears to be widespread but erratic and local in occurrence. The MCZ has specimens from this state labeled as from the Fortescue River (L. Glauert leg.), from Subiaco (Hamburg S. W. Australia Expedition, ex Forel Coll., det. Forel as *R. convexa* var. *violacea*), and from Derby (J. G. Campbell leg.); the last are probably part of the type series of Crawley's synonym *R. castanea.* Many of the specimens from the region west of Kuranda, north Queensland, are rather uniformly dark brown, instead of having the gaster red. I did not find this species in the neighborhood of Darwin or elsewhere along the Darwin-Alice Springs highway in the Northern Territory.

R. rufiventris needs to be considered carefully in relation to the very close forms *maniae* and *hilli* **[18]** and also *rufescens* **[13]**. From evidence present in publications and collections I have seen, it is not impossible that some or all of these forms are geographic variants of the same species. A dark brown form with red gaster, appearing superficially very like *rufiventris* to the naked eye (when alive) occurs at Alice Springs, in the central Australian MacDonnell Ranges. However, this form is smaller and has the head shape of small *convexa;* it may represent an independent species.

[25] I have examined a specimen labeled "Typus" of *R. spoliata* from the Genova Museum, courtesy of Dott. Delfa Guiglia. This worker is further labeled as from "Kamerunga" in Queensland, probably wrongly, since the type locality cited with the description is Mt. Bellenden Ker, northern Queensland. Podenzana collected at both localities, but Bellenden Ker is the more likely locality for *spoliata;* I have other specimens taken in the Cairns-Kuranda area by T. Greaves, C. P. Haskins and others, nesting in epiphytic *Platycerium* in rain forest. Emery's brief description fits this specimen well enough, but does not mention the somewhat sunken eyes, surrounded by circular rugules. In his collection, Wheeler confused this species with *laticeps,* but *laticeps* has the gaster almost completely smooth and shining, and the rugules near the eyes do not pass circle-like around them; instead, those rugules anterior to the eye pass out radially from it (Wilson notes from type).

The species described and figured by Clark in 1936 as *R. spoliata*, from Mutchilba, northern Queensland (A. D. Selby leg.), according to a specimen sent by Clark to the MCZ, and evidently from this same series, is really *R. scabra* Mayr.

[26] I have a worker taken on the south shore of Lake Eyre North (G. F. Gross leg.) that agrees fairly well with Clark's description of *viridis*, except that in my worker, the posterior border of the head is feebly convex, not concave. The head is narrower behind than in *metallica*, the scapes are longer, the striation of the second gastric segment is finer, and the size is a little larger.

[27] There is a worker type of *R. tenuis* in the MCZ which, although it is headless, otherwise matches very closely three specimens from Cairns, Queensland (W. M. Wheeler leg., 1914). Cairns and Mackay (the type locality) are about 400 miles apart, so it is possible that *tenuis* ranges along most of the northern Queensland coastal strip. This small brown species is easily recognized by its moderately elongate head (HL 1.10-1.18 mm.; CI 72-75) with transverse, slightly convex occipital border (a slightly concave median portion is seen in some views), long scapes, and large, strongly convex eyes. Spaces between foveolae of alitrunk, sides of alitrunk, node and a broad posterior strip on the postpetiole, densely and finely reticulo-punctulate and opaque.

RHYTIDOPONERA PENINSULARIS sp. nov.

Holotype worker: Very similar to *R. tenuis*, but differing in sculpture. TL 4.9, HL 1.18, HW 0.87 mm. (CI 74), WL 1.61 mm. The foveolae or coarse punctures are larger and more closely contiguous, with strongly shining bottoms, and such interspaces as exist are mostly more or less smooth and notably shining, not densely punctulate as in *tenuis*. On the sides of the posterior alitrunk, the sculpture tends to form indefinite oblique costulae that run over the top of the propodeum and become very distinct where a few of them cross the propodeal declivity, where the interspaces are very smooth and shining. As in *tenuis*, the postpetiole is finely and regularly arched-striate, but the striation continues back to the posterior tergital border (replacing the punctulate band of *tenuis* there) and surrounds concentrically a posteromedian area where the striae form a longitudinal fusiform pattern. The posterior reticulo-punctulate band of *tenuis* is not present in *peninsularis*. Second gastric segment shining, superficially arched-striate in front, becoming smooth behind, with scattered inconspicuous punctures; no fine reticulo-striate pattern as in *tenuis*.

In addition to the sculptural differences, *peninsularis* has a slightly thicker and more squarely-cut petiolar node, as seen from the side. The anterior and dorsal slopes are separated by a more abrupt angle, and the posterodorsal angle slightly overhangs the posterior face. Color medium brown.

Holotype a single worker [MCZ] from the Rocky Scrub (rain forest) in the McIlwraith Range, northeast of Coen, Cape York Peninsula, Queensland (P. J. Darlington leg., June 19, 1932).

R. tenuis and *R. peninsularis* are distinguishable from all species of similar size and color found in northern Queensland by means of their elongate head (CI distinctly less than 80, and perhaps normally under 76) and generally convex occiput. The related species *R. kurandensis* and *R. chnoopyx* have shorter heads (CI normally 80 or more). The common *R. victoriae* is distinct from all of these species in having a short, broad head with broadly concave occipital border and salient occipital angles; also, *victoriae* has very short scapes that reach or barely surpass the occipital border, in contrast to very much longer scapes for the other four species. There are, of course, other differences as well, but the features mentioned should serve to distinguish the small brown species at present known from northern Queensland. **[15, 16, 31]**

[28] RHYTIDOPONERA TRACHYPYX sp. nov.

Holotype worker: With the general form of *R. metallica* and relatives, especially *R. borealis*. Size a little larger than that of *borealis*, but smaller than the average for *metallica*. TL 5.1, HL (including clypeus and occipital lobes) 1.22, HW 1.06, WL 1.66, petiole L 0.45 mm. Head narrower than in the average *metallica* worker; CI 87; occipital angles very prominent; posterior border seen in full-face view rather deeply concave. Antennal scape slender; when laid straight back from insertion, overreaching the occipital border (at the point of intersection) by a distance greater than the length of the first funicular segment. Petiolar node as in *borealis*, i.e., similar to that of *metallica*, but more rounded above.

The best characters are in the gastric sculpture. Large punctures of petiole and postpetiole coarse, deep and close together, with shining bottoms. Between these deep punctures the surface is finely and densely reticulo-punctulate and obscurely rugulose, the orientation predominantly longitudinal. The succeeding segment is longitudinally costulate, the costulae being numerous and distinct, although becoming more irregular and tending slightly to anastomose anteriorly. Intercostal spaces finely reticulate, and with scattered large punctures. By comparison, *R. borealis* has each of the two segments finely and densely reticulate-striate in a pattern arching over median posterior areas of fine reticulopunctulation; scattered over both segments are large punctures which, however, are shallow and sculptured like the surrounding surface.

Color brownish-red, legs more yellowish; petiole and gaster piceous, appearing nearly black to the naked eye. This color is much as in *borealis* and some samples of *tasmaniensis,* although *borealis* frequently is darker over head and alitrunk. Other characters much as in *borealis.*

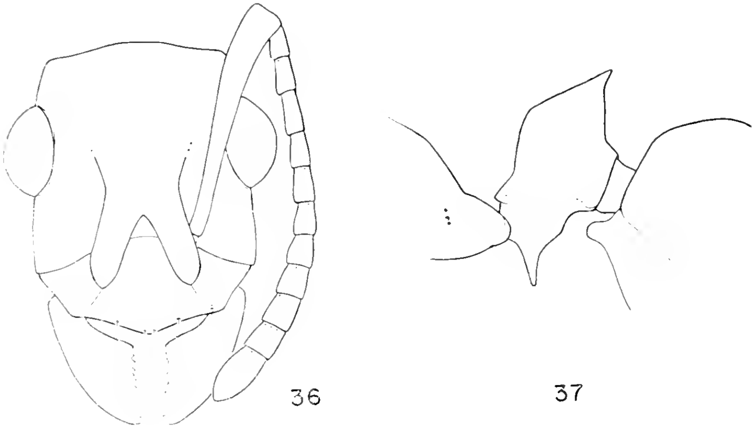
Holotype a single worker taken foraging in the late afternoon on the sandy river bank at Katherine, Northern Territory, Australia (W. L. Brown leg.); deposited in the Museum of Comparative Zoology.

Paratype a single worker in the MCZ, labeled, "Darwin, N. T." in W. M. Wheeler's hand. I consider it likely that this is not the precise locality, but represents instead a shipping point or base locality for the collector (possibly Wesselmann). Other ants, such as *R. taurus*, in the MCZ collections bear similar labels, but it is virtually certain these were collected much farther south, near the center of the Northern Territory. The upper parts of the Northern Territory, nearest Darwin, are occupied by the closely related common species *R. borealis* **[11]**, and present indications are that *R. trachypyx* may replace the latter in the drier savannah woodland zone of the central Territory.

[29] RHYTIDOPONERA TYLOXYS sp. nov., Brown and Douglas (Figures 36, 37)

Holotype worker: TL, adjusting downward for expansion of gaster 7.8, HL 1.57, HW 1.19 (CI 75), L head with closed mandibles 0.93, scape L 1.32, greatest diameter of eye 0.50, WL 2.37, petiole L 0.62, gaster L, greatly extended, 3.46 mm.

Details of form of head, mandibles, antennae and petiolar node with adjacent segments as shown in Figures 36 and 37. Alitrunk convex in profile, highest in mesonotal area, with a very shallowly concave portion along the propodeal dorsum. Promesonotal suture fine but distinct; other sutures obliterated on dorsum of alitrunk. Pronotum evenly rounded, its lower left-hand border not forming the acute tooth (this tooth is an important generic character), but instead produced only as a subrectangular (actually slightly obtuse) angle. The border on the right side forms a more conventional toothlike projection, but even this is not so conspicuous or acute as is usual for the genus.



Figures 36 and 37. *Rhytidoponera tyloxys* Brown and Douglas, sp. nov. Fig. 36, full-face view of head. Fig. 37, side view of petiole and adjoining structures.

Sculpture characteristic. The body, with mandibles and appendages, is very finely and densely punctulate and opaque, except that the posterior half of the gaster has the sculpture shallower and weakly shining. In addition, there are abundant coarse, shallow umbilicate punctures or small foveolae (not interrupting the punctulation), contiguous to subcontiguous on head and pronotum, becoming smaller, spaced and indistinct on mesonotum, sides of alitrunk and petiolar node; nearly or quite obsolete on propodeum and postpetiole. Between the foveolae on the clypeus and dorsal surface of the head are longitudinal rugulae that fan outward over the vertex and become lost in a reticulum behind the eyes. The punctulation of the mandibles passes into fine striation apicad.

Body largely devoid of conspicuous erect pilosity, those hairs remaining being mostly short and stiff: about 10 on anterior clypeus; a few on masticatory and ventrolateral mandibular borders; a few on oral border of gula and on smaller mouthparts; about 4 along the extensor surface of each scape, and a group at each tip of scapes; a circlet on each funicular segment; a widely spaced pair on the pronotal dorsum; a few on the legs, including the coxae; a row across the posterior part of the postpetiolar sternum; a spaced short pair on the middle of the second gastric segment; a circlet around the posterior borders of the second and succeeding gastric segments, the hairs becoming longer toward the apex. In addition to the erect hairs, there is a sparse growth of fine, small, inconspicuous, appressed or decumbent hairs, one each in most cephalic foveolae and in a few of the foveolae elsewhere, also forming a very dilute pubescence on scape, mandibles, gula and on legs and gaster. Color deep orange-brown, the head, alitrunk and petiole a trifle darker than the appendages and gaster.

Holotype [Western Australian Museum, Perth] one of a series of seven workers taken by Mr. K. C. Buller at Woodstock Station, about 900 miles north of Perth, Western Australia, in June, 1952. Paratypes: the remaining six workers in the type nest series differ from the holotype only very slightly in dimensions and proportions; the holotype is about average for the series. Some workers have the convex median portion of the occipital outline slightly emarginate at its summit; there is some variation in the distinctness of the inferior pronotal teeth and in the length, thickness and acuteness of the posterodorsal process or tooth of the petiolar node, some specimens having this point slightly less sharp and salient than as shown in Figure 37. There is also some difference in number and position of erect hairs, but this is at least partly due to abrasion of the integument. From the few other *Rhytidoponera* with petiolar node produced to an apical point, *R. tyloxys* can be distinguished immediately by means of the structure of its head, particularly the large eyes, and by the peculiar sculpture.

[30] Wilson manuscript notes on comparison of types in the Forel Collection: "*R. haeckeli* and *R. turneri* are closely related but distinct species. In *haeckeli*, sculpture of posterior half of head consists of fairly regular rugae which originate in the space between the frontal lobes and radiate outward toward the occipital corners. In *turneri*, sculpture in the same area consists of a solid rugo-reticulum with no orientation." *R. lamellinodis* Santschi also belongs to this group of species, which have high, angulate propodeum and thin, scale-like, dorsally emarginate petiolar node. Differences, if any, separating *haeckeli* and *lamellinodis* remain to be clarified.

[31] *R. victoriae* is a common and widespread eastern Australian species, ranging from Mt. Spurgeon, northern Queensland (P. J. Darlington leg.) around the moister eastern and southeastern fringes of the continent to the grasslands of Western District in Victoria. It is the smallest of the common Australian members of its genus, and is a familiar inhabitant of home gardens in the suburbs, and even in the large central parks of a city like Melbourne.

The variants called *modesta*, *scrobiculata* and *cedarensis* were never satisfactorily distinguished from *victoriae*, and it seems that they were described only because Emery and Forel lacked sufficient material of *victoriae* to appreciate the extent of its variation. Wilson has now been able to compare the types of all these forms in the Emery, Forel and André collections, either directly or with samples furnished from MCZ. *R. modesta* is a variant showing very feeble bluish metallescence over a blackish or piceous ground pigmentation; this form is most prevalent in moist forests and upland grassy clearings in southeastern Queensland. In northern Queensland, the ground color varies from dark to very light brown in fully adult workers; and metallescence is not present. In northern Queensland also, especially near Kuranda, the gastric sculpture shows extremes of variation in the fineness and coarseness of the postpetiolar and gastrodorsal striation. It is not possible from the present material to rule out entirely the occurrence of more than one sibling species in northern Queensland, but now it seems better to take the conservative course in recognizing only the single species *victoriae* as representing the complex in northern Queensland.

R. maledicta, described as a race of *victoriae*, seems distinct in lacking a well-defined posterior scrobal area; the corresponding area is coarsely rugo-reticulate instead of longitudinally rugo-striate. The relationship of *maledicta* to the dull-green North Queensland *metallica*-like population needs study **[21]**.

[32] The *Chalcoponera hilli* described by Clark in 1941 becomes a homonym of *R. hilli* Crawley through the merger of the two genera, a fact duly noted by Donisthorpe when he proposed the new name *clarki* to replace Clark's *hilli*. The MCZ has cotypes or nidotypes of this large, robust, *metallica*-like brown species; these specimens lack metallescence entirely. It seems likely that Forel's *obscurum*, an earlier but also preoccupied name, applied in part to the same form. Forel mentioned that some specimens had greenish heads, but it seems possible that he may have had mixed samples, including some large examples of *metallica* with faded or otherwise obscured metallescence on head and especially on alitrunk, petiole and gaster. The available name is *clarki* Donisthorpe. This species apparently is not common, and is found only along the central Queensland Coast and on certain Barrier Reef islands.

[33] THE RHYTIDOPONERA OF NEW CALEDONIA

So far as our present information goes, there are seven species of *Rhytidoponera* on New Caledonia and the islands on its coasts. This figure includes two species described here as new, and leaves out two now placed as synonyms. Undoubtedly there yet remain species to be described, particularly from the poorly-known highlands of the north and from the coastal islands, but a key should help to make further study easier.

Up to now, most of the work on the *Rhytidoponera* has been done by Emery (1883, 1914), although André and Viehmeyer each described a single species. Unfortunately, in his 1914 paper, Emery momentarily confused the two common species *R. fulgens* and *R. numeensis*, so that most of his remarks on *numeensis*, at least on the workers, actually apply to *fulgens*. In this work he described the real *numeensis* over again as *acupuncta*. The suspicion that some such mixup applied here has been fully confirmed, and the confusion itself finally cleared, by Wilson's examination of the types and other specimens in the collections of Emery (Genoa) and André (Paris), with fresh specimens of the species concerned at hand for comparison. Wilson has also noted that the type of var. *socrula* differs from "typical" *fulgens* chiefly in the more definitely oriented rugation of the head (longitudinal) and alitrunk (transverse, especially on pronotum); in Wilson's extensive series from the southern half of New Caledonia, one can find all degrees of intergradation linking extremes of the two kinds of sculpture, without particular territorial attachment of the variation.

Along with the two new species he collected in the country, Wilson's most helpful contribution is the detailed information contained in his notes on the distribution, ecology and behavior of the New Caledonia species. This information can be summarized as follows. Collections were made in several localities, both disturbed and relatively undisturbed, in the southern half of New Caledonia. In all of these localities, at altitudes below about 800 m., there occurred the large metallic green species, *R. fulgens*, and usually also the smaller, black or brown species, *R. numeensis* and *R. pulchella*. At three of the forested upland localities, there was found a new small species close to *numeensis*, but with a thinner node. All of these species were taken foraging during broad daylight on low foliage in the forest understory or at the forest border, and all of them were taken in Berlese funnel samples from the forest floor leaf litter. Mostly, their nests were found under rocks in the soil, but occasionally one or more of these forms nests in rotting wood.

A second new species of the small-sized group was taken twice at a single locality (*R. versicolor*, Montagne des Sources), at altitudes of about 800 and 1000 m.; significantly, no other members of the genus were seen at these altitudes at this locality, nor, except for *R. acanthoponeroides*, were any other species of *Rhytidoponera* taken above 800 m. anywhere by Wilson.

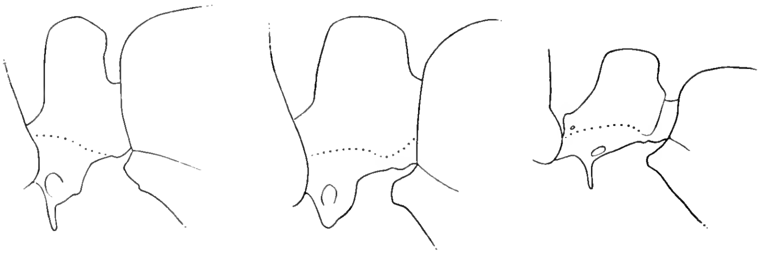
The food of these species, so far as observed, consisted of small arthropods, some of which were certainly taken alive. To what extent the New Caledonia *Rhytidoponera* feed on plant sugars and other foods is not yet known.

The brief review of the species offered below is based on Wilson's ample collections from New Caledonia, made during December, 1954, and January, 1955; smaller samples, all from the vicinity of Noumea, were sent me by N. L. H. Krauss.

Key to the Rhytidoponera species of New Caledonia — workers

1. Larger forms, full length of alitrunk (WL) exceeding 2.0 mm.; body color of mature specimens with rich metallic green or purple tones . . 2.
Smaller forms, full length of alitrunk (WL) less than 2.0 mm.; body color black, brown or combinations of these with red or yellowish; no metallic colors . . . . 4.

2. Petiole produced backwards as an acute apical tooth; gastric dorsum smooth, with only shallow traces of coarse punctures, the surface cloudy with a bluish opalescence . . . . *acanthoponeroides* Vieh.
Petiole bluntly subtruncate or rounded above, not produced as a tooth from the apex; gastric dorsum largely or wholly striate or reticulate . . 3.


38 39 40

Figures 38-40. *Rhytidoponera* spp. from southern New Caledonia. Workers, side view of petiole and adjoining structures. Fig. 38, *R. wilsoni* sp. nov., paratype. Fig. 39, *R. numeensis* André. Fig. 40, *R. versicolor* sp. nov., paratype.

3. Coarse sculpture of body overlain by finer sculpture, rendering the surface largely opaque; postpetiole and succeeding segment very finely reticulate *atropurpurea* Emery
Coarse punctures of body shining, without overlying fine sculpture of much account; postpetiole and succeeding segment transversely- to arched-striate . . . . *fulgens* Emery

4. Ventral process of petiole forming a long, straight, very slender spine; the small oval fenestra is situated behind the spine near its base (Fig. 40) .... 5.
Ventral process of petiole not wholly slender spiniform, but more subtriangular, irregularly tapered, and much broader, wholly containing the oval fenestra (Figs. 38, 39) .... 6.

5. Gastric dorsum, especially of the second segment, covered densely with fine whitish pubescence which nearly obscures the finely reticulate-striolate sculpture of much of its surface; color black, with brown legs, mandibles and antennae, becoming yellowish toward the apices .... *pulchella* Emery
Gastric dorsum very smooth and shining, except for some feeble striation across the postpetiole anteriorly; pubescence very sparse and inconspicuous; color mahogany or piceous, the gaster orange, brown or piceous; legs, antennae and mandibles yellow throughout (Fig. 40) .... *versicolor* sp. nov.

6. Petiolar node strongly compressed anteroventrally, its ventral process narrowed to a digitiform apical portion; spaces between pronotal punctures not densely and finely striate (Fig. 38) .... *wilsoni* sp. nov.
Petiolar node not strongly compressed anteroventrally, its ventral process without a digitiform apical portion; spaces between pronotal punctures densely and finely striate (Fig. 39) .... *numeensis* E. André

RHYTIDOPONERA ACANTHOPONEROIDES Viehmeyer

This species was described from a single worker from New Caledonia, locality unspecified. It has not been reported since the description, but now Wilson has taken a colony on Mt. Mou, north of Païta, under a stone in an opening in cloud forest dominated by *Araucaria* and *Podocarpus* on the summit ridge below the summit, altitude probably somewhere near 1000 m. This sample fits the original description well except for the color, stated to be "dark brown, with more yellowish brown appendages and mandibles; body steely blue." Viehmeyer describes the smooth gastric dorsum well, with its cloudy blue-gray opalescence; Wilson notes that his samples were predominantly metallic green while alive, and these were the colors seen in the specimens as they came out of alcohol two months after capture. After two years in the dry state, they have changed to a predominantly bluish-purple over head and alitrunk; the legs are a contrasting light reddish, as are also the mandibles and antennae. The worker of this species is unmistakable because of the posterodorsally mucronate petiolar node, found in no other New Caledonian species, but occurring in similar form in several Australian *Rhytidoponera,* as well as in other ectatommine genera in both hemispheres.

The male (previously undescribed) measures TL 7.1, HW 1.30 (across and including compound eyes), WL 2.41, scape L (excluding basal neck) 0.27 mm. Scape only about twice as long as broad, twice as long as the first flagellar segment, and half as long as the second flagellar segment. Mesothorax robust; notauli distinct, impressed, forming a complete "Y." Wing venation of the complete type; fine traces are present of first radial crossvein in one of two male specimens examined. Hindwing (of measured specimen and one additional specimen) with 6-8 subapical and 0-3 submedian hamuli.

Petiole nearly twice as long as high, feebly arched, profile rising slowly from front to gently rounded summit near posterior end; ventral process lacking (ventral process of worker is of the *versicolor* and *pulchella* type, Fig. 40). Genital capsule a little more elongate than in some other species of the genus; parameres and hypopygium (IX sternite) rather more slender than average, the latter rounded apically. Penis valves obliquely truncate at apex, the corners rounded off.

Integument predominantly smooth, moderately to strongly shining, on the body overlain by weak bluish opalescence; certain areas slightly roughened or vaguely punctulate, such as the dorsum of head mesad of compound eyes. Propodeum and petiole more definitely roughened, the latter opaque, and with a few superimposed, separated rugae.

Pilosity of abundant fine light brown hairs, more tapered and mostly more curved than in the *numeensis* male. Pubescence dense, appressed to decumbent, yellowish-gray and conspicuous over most of body and appendages. General body color dark brown (with faint opalescence), head darkest; mandibles, legs, and antennae lighter; genital capsule yellowish.

RHYTIDOPONERA PULCHELLA Emery

Emery (1914) noted the variation in size and gastric sculpture shown by this species, evident in the extensive series before me. The largest of these are as large as large *numeensis*, while the smallest are slightly smaller than the smallest *versicolor*, so that *pulchella* just about matches the total size variation of the other three small New Caledonian species taken together.

This species is readily distinguished by the shape of its ventral petiolar process, which is like that of *versicolor* (Fig. 40), by the conspicuous whitish pubescence of the second gastric segment, by the fine, centrally obsolescent sculpture of this same segment, which is consequently rather strongly shining under its vestiture, and by the more or less yellowish apices of the antennae and tarsi, and edges of the mandibles, which contrast with the black of the body. Both Wilson and Krauss found this form rather common in relatively moist forested localities all over southern New Caledonia. It nests commonly under stones in the earth.

RHYTIDOPONERA NUMEENSIS E. André

An average worker of this species measures 5.5 mm. TL; the HL is 1.28, HW 1.15, WL 1.82 mm.; CI 90, ex Mt. Mou, No. 147. This dark brown species is the commonest and ecologically most tolerant of the smaller *Rhytidoponera* of the island. It is easily recognized by its light reddish legs and antennae, contrasting with the darker body, by the robust build, by the striation mixed with the coarse punctures of the alitrunk, and by the shape of the ventral process of the petiolar node (Fig. 39).

Wilson found *numeensis* foraging on the ground and on foliage, together with *pulchella*, and, in forested areas in the hills, with *wilsoni*. It was not taken in southern New Caledonia above 800 m., and the majority of collections came from below 500 m. This species nests in rotten wood where it is available; Wilson's nests were taken in rotten branches lying on the forest floor, as well as in larger, moss-covered logs. In shaded pastures and other disturbed areas, more nests of this species seem to occur under rocks in the ground. Colonies were usually small, with 100 workers or so, but one or two larger nests were seen. In one nest, the larvae were seen feeding upon a small talitrid amphipod.

RHYTIDOPONERA ATROPURPUREA Emery

I have not seen this species, and Wilson's notes do not mention the type material. Emery's description compares it with "*Rh. numeensis*" chiefly; as mentioned already, he was really referring to *fulgens*, but curiously enough he also mentions *fulgens* by name in the description. At any rate, the picture emerges of a large form similar to *fulgens*, but with a superficial, finely reticulate sculpture overlying the coarser sculpture, and replacing the striation of the gastric dorsum so characteristic of *fulgens*. The color is cited as "violaceous black; mandibles, funiculi, legs and apex of gaster deep brown." The male is stated to be like that of *fulgens*, except that the gaster is subopaque, finely and superficially reticulate. Known only from Ouedjo I., near Hienghiène, in the northern part of the main island.

RHYTIDOPONERA VERSICOLOR sp. nov.

(Figure 40)

Holotype worker: TL 4.5, HL 1.04, HW (excluding eyes) 0.92 (CI 89), WL 1.38, scape L 0.90, max. diameter eye 0.22 mm. Similar to *numeensis*, but smaller and less robust. Occipital border of head feebly and broadly concave in full-face view, but occipital angles gently rounded; as seen from the side, the posteroventral corners a bit better developed and more nearly rectangular. Clypeal apron distinct, translucent, forming a bluntly rounded angle in the middle. Alitrunk lower and more slender, in profile forming a single convexity, with only the propodeal declivity breaking the outline slightly as it falls off steeply from the dorsum. Petiolar node (Fig. 40) much lower than in *numeensis* (Fig. 39), and with the ventral process very long and slender, like that of *pulchella*. Seen from above, the node is only slightly broader than long (much broader than long in *numeensis*).

Head, alitrunk and petiole coarsely reticulopunctate throughout; a few of the dorsomedian rugules on the head forming longitudinal costulae (including a median carinula), but the sculpture otherwise without definite orientation, and without the interspersed striation so widespread in *numeensis*. Gaster smooth and shining, with scattered small piligerous punctures;

postpetiole with a few indistinct striae arching from the sides across the anterior face. Ereet pilosity much as in *numeensis*, the hairs fine, whitish, abundant on all parts, uneven in length. Appressed pubescence extremely sparse except on extremities of antennae and legs.

Head, alitrunk and petiole deep mahogany (nearly black to naked eye). Gaster bright orange-yellow. Legs, antennae and mandibles clear yellow.

Holotype [MCZ] from near the Dumbéa Road, just below Montagne des Sources, New Caledonia. This locality is mixed forest, mainly angiosperm evergreens, but with large *Araucaria* and *Agathis* prominent in the upper story, surrounding the headwaters of the Dumbéa River; altitude ca. 800 m. (E. O. Wilson leg., XII-17-1954, No. 185). The holotype and several paratype workers were collected from the vegetation at the forest border during daylight hours. Another collection from Montagne des Sources (Wilson, No. 169) was made on the same day higher up (ca. 1000 m.) in second-growth *Araucaria* forest, where the workers were taken foraging on a small angiosperm shrub in the understory during midafternoon.

Variation: The workers from the upper site (No. 169) are much darker in color; the head and alitrunk are dead black or very nearly so, while the petiole and gaster are dark brown above (blackish to naked eye), medium brown below. This darker coloration is approached by certain specimens from the lower site (No. 185) with brownish-orange or brown gaster. All specimens maintain the clear yellow mandibles, antennae and legs. In several specimens, particularly in the upper-site series, the petiolar node is a little more rounded above, and the sculpture of its anterior face varies more or less toward a smooth, shining surface crossed by weak transverse rugae or costulae, becoming concentric or longitudinal on the summit. These same specimens often tend to have the obsolescent striation of the postpetiole a little better developed and extending back over as much as 2/3 of the surface, which is consequently often not so strongly shining as in the holotype. A few individuals have the declivity of the propodeum meeting the dorsum through a distinct but obtuse angle, and in these, the declivity may be weakly concave as seen in side view. One specimen has a feeble impression or step in the region of the metanotum. Variation in size and in the chief proportions is very slight; the darker specimens from the upper site average a trifle smaller. The paratypes are to be deposited in MCZ, USNM, and one or more Australian and New Caledonian collections.

RHYTIDOPONERA WILSONI sp. nov.

(Figure 38)

Holotype worker: TL 5.2, HL 1.25, HW (excluding eyes) 1.06 (CI 87) WL 1.73, scape L 1.12, max. diameter eye 0.26 mm. Very similar to *numeensis*, from which it differs principally in having a notably more strongly anteroposteriorly compressed node, with a different ventral petiolar process (Fig. 38); the posterior face of the node is concave as seen from the side. The head of *wilsoni* has a more broadly concave occipital margin (straighter in some views) and slightly more sharply rounded occipital corners than in *numeensis*. The sculpture differs in several details; generally speaking, the punctures are coarser and more closely contiguous over head, alitrunk and gaster, and the ridges between tend to form coarse, rather indefinite rugules (longitudinal on head, diagonal on sides of alitrunk, transverse on propodeum and anterior face of petiolar node) in place of the fine, dense striation of these same areas in *numeensis*. Postpetiole rather finely arched-striate, passing into a posteromedian area of finer, concentric striae that are interrupted by and interspersed with fine, indistinct punctulation. Coarse piligerous punctures of this segment very shallow, indistinct, and not so clearly elongate as the corresponding ones in *numeensis*. Second gastric segment very finely and densely striate, the pattern arched over a posteromedian weakly shining area of very superficial elliptical-concentric striation (longitudinal axis) that is very finely interrupted or coriaceous (clearcut, uniform, and predominantly longitudinal striation in *numeensis*). Coarse piligerous punctures of this segment small and inconspicuous, much smaller than the corresponding ones of *numeensis*.

Erect pilosity and appressed pubescence fairly abundant but not dense, uneven in length, the pubescence conspicuous at all only on the gaster and appendages. Color piceous, the head, petiole and gaster lighter and a bit more reddish than the alitrunk. To the naked eye, the body appears very dark, nearly or quite black. Legs, mandibles and antennae orange-brown. Coloration in general much like that of *numeensis*.

Holotype [MCZ] a stray diurnal forager taken on foliage at 180-400 m. on Mt. Mou, north of Païta, New Caledonia (E. O. Wilson leg., XII-10-1954, No. 110). Paratype workers were taken with the holotype and at Le Chapeau Gendarme, east of Yahoué, and at Ciu, near Mt. Canala (Wilson Nos. 73, 74, 80, 84, 96 and without numbers). These were taken foraging during the daylight hours on foliage and over rocks on the forest floor. One nest was found beneath a stone; other workers came from leaf litter berlesates. The Ciu sample was very dark, and had the legs dark brown. The occipital border varied in degree of concavity. Paratypes in MCZ, USNM and elsewhere.

[34] Among *Ectatomma* species, the closest to *aztecum* (judging from the holotype, kindly sent by Dott. Delfa Guiglia) is *ruidum*. The color is dark, as in *ruidum*, but the node of *aztecum* is slightly thicker as seen from the side. The sculpture of gastric segment I (postpetiole) is slightly different in *aztecum*; the costulae are arched transversely across the anterior descending face of the segment, but otherwise are longitudinal, close and at most feebly undulant in a few places. The outstanding distinction, however, is the extreme development of the erect pilosity; this is rather short, but present in great abundance on most body and appendage surfaces. The species has never been taken a second time; its type locality is "Michoacan." Since this form is very close to the highly variable *ruidum*, it would be desirable to have additional material from southwestern Mexico in order to see exactly what the relationship is between these two species.

[35] The type locality of *E. confine* apparently lies somewhere in the present Colombia or Panama. Mayr's description is very sketchy, and the only specimen I have seen that fits it fairly well is a unique worker (Fig. 2) from Tela, Honduras (D. M. Bates leg.). This worker was found mixed with *ruidum* and *morgani* in the Wheeler Collection, and at first glance it appears to be intermediate between these two species. However, it differs from both in the disproportionately strong development of the median pronotal eminence; this is high, somewhat compressed laterally, and forms a blunt angle as seen from the side. The lateral pronotal eminences are rather small, but their size is probably somewhat variable in this as in other species. The greatest eye diameter and the apical antennal segment are very nearly precisely the same in length, and the petiolar node is thicker than that of *ruidum* as seen from the side. The sculpture of the second gastric segment is composed of fine, sericeous striolation, as in *ruidum*.

Whether this identification is correct can only be determined after the review of more material in comparison with the type in the Mayr Collection in the Vienna Museum. It is not impossible that *confine* will finally prove to be a geographical variant of the species represented in the Amazon Basin by *morgani* **[38]**.

[36] *E. edentatum* has been confused with *muticum* several times (Forel, 1912b:31), but the two are easily separated by eye size (see key) and sculpture of gastric segment II. In *edentatum*, the tergum of the second segment is very regularly and very finely striolate in a pattern of varying direction, and in general is sericeous-opaque. In *muticum*, the same segment has a much more indefinite and looser transverse striation that is virtually effaced over a large area discad; the surface in general is definitely shining, even glassy in the center and between striae.

Forel's arrangement of 1912 depends on characters, such as antennal proportions and metallic luster of integument, that seem too variable (and often allometric in expression) to have more than local or individual significance; neither Forel nor Santschi seems to have expended much effort in trying to define limits of variation for these forms. *E. macdonaghi* is poorly described as a race of *edentatum*, of which species it may be an ergatoid or pathological intercaste. *E. morgani* **[38]** may be a northern variant of *edentatum*.

[37] The names *strigosum*, *permagnum*, *confusa* and *aerea* seem to me to represent slight local variants of one species, widespread in southern Brazil and Bolivia. The name *strigosum* unfortunately must fall as a primary homonym of *Rhytidoponera strigosa* (Emery), originally described in *Ectatomma*, and Forel's name *permagna* (emended to the proper form *permagnum*), being next available, is raised from varietal to species rank to take its place. Since *permagnum* and *lugens* are separated only by minor and variable characters and are allopatric as at present known, it is possible that these two names represent extreme geographical populations of the same species. Collections from the region just south of the Amazon are needed to decide whether intergradation is completed in this area. In addition to the sculptural differences (see key, couplet 1), which may only reflect character displacement against the closely related species *opaciventre* in the south, the samples of *lugens* I have seen have narrower heads and are generally more slender overall than are the *permagnum* examined from Bolivia and southeastern Brazil.

[38] *E. morgani* is uncommon in collections, and has remained enigmatic due to its almost universal confusion with the similar *ruidum*. MCZ has stray workers taken near Port-of-Spain, Trinidad (R. Thaxter leg., beating foliage) and in British Guiana: source of R. Essequibo (Ogilvie leg.); Kartabo vic. (W. M. Wheeler, H. O. Lang leg.). Constant characters distinguishing this species from *ruidum* (see key) are the proportionately longer and narrower head, somewhat more convex behind as seen in full-face view; eyes smaller and placed a little farther from the posterior border; scapes and legs a trifle longer; petiole thicker from front to rear, and not biconcave in side view, as in *ruidum;* fine striolation of second gastric segment less distinct basad, where it merges with some fine, dense, irregular reticulo-punctulation or broken striation (but this last character is very variable).

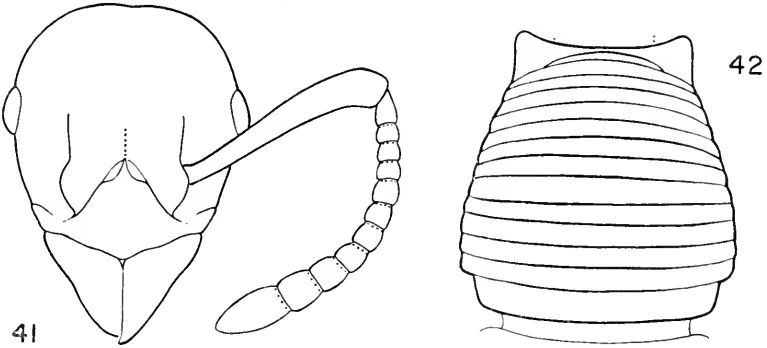
There is no doubt that *morgani* is really very closely related to *edentatum*, and the two forms may well be geographical segments of the same species. A worker sent by Father Borgmeier from the Mato Grosso is intermediate in some respects between my Guiana-Trinidad *morgani* samples and the few specimens of *edentatum* available from the State of São Paulo (W. W. Kempf leg.). The material available to me is not sufficient as a basis for formal action on this probable synonymy at the present time.

[39] *E. opaciventre* is a large species of the La Plata-Paraná drainage. It apparently does best in districts that are arid, or at least that have prolonged annual dry spells. The color is very variable, ranging from reddish through a series of bicolored forms to piceous; the variety *concolor* is a part of this variation. Shape of head and complete lack of transverse rugules on the postpetiolar dorsum distinguish this species from *permagnum*.

[40] *E. planidens* is a puzzling species very close to *quadridens* (see key, couplet 4), but both of these are present at some localities in Brazil, without known intergradation (Agudos, S. Paulo State, leg. W. W. Kempf). A small, light female from central Brazil owned by Father Borgmeier, however, appears transitional to *quadridens*, and it is not beyond possibility that *planidens* is merely a morph of the more familiar species. Wilson (MS notes) has located the probable type of *E. quadridens* in the Museum d'Histoire Naturelle in Paris; it is a specimen from the Bosc Collection, now in the general collection.

[41] *E. muticum* has been confused with *E. edentatum;* the characters are discussed under the latter species **[36]**. The records and specimens of *muticum* I have seen indicate that this species is restricted to the dry eastern bulge of Brazil, in Ceará and neighboring states. There is only one exception to this pattern, and this exception is so far off that it is difficult to credit it. I refer to a single worker in the MCZ bearing the label "Acapulco, Mex./Fredk. Knab." and which is identical, so far as I can tell, to specimens from northeastern Brazil collected by W. M. Mann, now in the same museum. Acapulco is close to Michoacan, the type locality of *aztecum*, but this circumstance is probably only a coincidence. Until such time as the Mexican record for *muticum* is confirmed by further collections, the occurrence of the species in that country should be regarded as doubtful.

[42] *E. tuberculatum* varies widely in color and sculpture, as pointed out by Weber (1946). The greatest variation seems to focus in northern South America and the Amazon Basin, where hardly two nest series can be found that are alike. Especially striking is the brown variant, contrasting with the more familiar yellowish types from farther north and south, as well as from this same area in the middle of the range. *E. acrista* differs modestly from *tuberculatum* in having the occipital margin of the head more rounded as seen in full-face view; I have specimens of this kind from the Paraná River, Paraguay (Fiebrig leg.). Other samples from central South America may represent transitions to *acrista* from *tuberculatum*, but at present the evidence is not as complete as it should be to dismiss *acrista* as a southern peripheral variant of *tuberculatum*.



Figures 41 and 42. *Gnamptogenys* spp., workers. Fig. 41, *G. grammodes* sp. nov., paratype, full-face view of head. Fig. 42, *G. mecotyle* sp. nov., paratype, dorsal view of petiolar node.

[43] *G. acuminata* samples in the MCZ: Campinas, Goias, Brazil (Schatzmaier leg.); Santa Helena, Bolivia (W. M. Mann leg.); Bartica District, British Guiana (A. E. Emerson leg.). Varies from ferruginous to black in color; very similar to *G. sulcata*, but differing in the more striking posterodorsal production of the node.

[44] *G. annulata.* Samples in the MCZ indicate a very wide range for this species in the Amazon-Orinoco drainage, west as far as Ecuador, Peru and Bolivia, and north to Costa Rica and Honduras. I have seen specimens from Rio de Janeiro State, and the species is reported from Santa Caterina.

The male is a little shorter than workers from the same nest, piceous with brown legs and antennae, smooth and shining except for rugose propodeum; petiole finely rugulose, shining; front of head finely punctulate, shining. Notauli complete, well-marked. Forewing with "complete" venation, i.e., Rsf2 and 3 and Mf2 and all present.

[45] Samples of *G. aculeaticoxae* were examined from Kamakusa, British Guiana (H. O. Lang leg.), Barro Colorado Island, Panama Canal Zone (J. Zetek leg.), and from Bolivia: lower Rio Madidi and Blancaflor and Huachi on the Rio Beni (W. M. Mann leg.).

[46] In a recent paper (Brown 1957), several forms were dealt with under *Holcoponera*. Var. *antillana* Santschi was placed as a synonym of *striatula* Mayr **[79]**, and the nominal species or subspecies *satzgeri* Forel, *spurium* Forel and *foreli* Santschi were synonymized under *simplex* Emery. The new species *mina* and *acuta* were described, and *Rhopalopone relicta* Mann was transferred to *Holcoponera*. There are some new records of *acuta* from Peru: Tingo Maria, Monson Valley; and Colonia Perene, 18 miles northeast of La Merced, Junin (E. S. Ross and E. I. Schlinger leg.).

[47] In a review of the *Stictoponera coxalis* group (Brown, 1954c) all of the species here indicated were discussed, and synonymy proposed for some of them. *S. biroi* Emery (Fig. 17) has been taken by E. O. Wilson at Bisianumu, near Sogeri, Papua, at about 500 m. A single dealate female (No. 654) and a small colony with callow winged males and females (No. 675) were taken in moist rotting logs in rain forest.

[48] *G. panda* is very close to *G. taivanensis*, but the adult color is reddish-brown (blackish in *taivanensis*), and the postpetiole of *panda* is much more closely, finely and opaquely sculptured, with the interfoveolar spaces forming distinct oblique costulae, so that the surface appears in some lights to be punctate-striate. In *panda*, the sculpture of the second segment is nearly closed in across the middle, whereas in *taivanensis* nearly the whole dorsal-discal area is smooth and shining, with only the coarse piligerous punctures. I have seen additional specimens of *panda* from Muping (2000 m.), on the Ya An to Mou Kung track, Sikang Province, about 90-100 miles west of Chengtu, western China (D. C. Graham leg.); this locality is not far airline from the type locality near Kuanhsien, Szechuan. The petiole of *panda* is shown in side view in Figure 18.

[49] I have examined specimens of *G. bispinosa* taken by G. C. Wheeler at Changuinola district, Bocas del Toro, Panama, and by W. M. Mann in Costa Rica at Zent, Colombiana Farm and Hamburg Farm, Santa Clara Province. The Hamburg Farm series includes a male: TL 8.2, HL without cervical rim of occiput 1.28, L head with closed mandibles 1.73, HW with compound eyes 1.33, greatest diameter of compound eye 0.52, WL 2.61, petiole L 0.80 mm. Antenna: scape L 0.35, L funicular segment I 0.19, fun. II 0.55, fun. III 0.54 mm. L forewing ca. 5.5 mm. Mandibles triangular, distinctly dentate. Ocelli large and clear, set close together on a darkened callus; distance between anterior and posterolaterals less than an ocellar diameter, distance between posterolaterals slightly greater than an ocellar diameter. Notauli and parapsidal furrows very distinct, complete. Maxillary palpi with 5, labials with 3 segments. Petiolar node long and low, nearly twice as long as high, with a subrectangular ventral process in front below. Wings as in other larger *Gnamptogenys*, Mf2 short or completely contracted, Rsf2·3 present. Body and appendages shining, completely smooth except for mandibles and clypeus, which are feebly and obscurely longitudinally striate, and propodeum, which bears a bold pattern of sharp rugae. Color ferruginous yellow; gaster yellowish-tan.

The worker of this species has a palpal formula of 3, 2.

The Wheelers have described and figured the larvae (1952a, pp. 132-133, pl. 5, figs. 1-5).

[50] *G. alfaroi*. I have examined a short series (USNM, MCZ) from Turrialba, Costa Rica (O. L. Cartwright leg.) of this very rare, local and interesting species. It is a rather aberrant member of the *mordax* group, large in size, black in color, long-headed, with short, thick mandibles. In many respects, it resembles species of the genus *Cylindromyrmex* (Subfamily Cerapachyinae?), and the relationships between *Cylindromyrmex* and *Gnamptogenys* are worth investigation on this account.

[51] I was able to compare the female type of *G. haenschi* with workers from the lower Rio Madidi, Bolivia (W. M. Mann leg.); the workers are very similar in their robust build and very fine costulation, but they are decidedly smaller than the female. Like the type, their color is brownish red. In the worker, the petiolar node is compressed anteroposteriorly, but is not quite twice as broad as long. A female from Tingo Maria, Peru (E. S. Ross and E. I. Schlinger leg.) is similar to the type, but is much darker, nearly black in color.

[52] *G. hartmani* remains known only from the unique type worker, from Huntsville, Texas, far outside the known range of other species of *Gnamptogenys*. Creighton (1950, p. 36) gave it as his opinion that the tarsal claws of *hartmani* were simple, a condition he "regularly encountered in . . . subgenus *Gnamptogenys*." However, careful examination of the *hartmani* holotype, as well as all available species of *Gnamptogenys* and *Parectatomma* in the old sense, reveals that all have an extra tooth on each of the six pairs of tarsal claws. Among these groups, simple tarsal claws must be exceptional, if they occur at all.

[53] The dealate female type of *epinotalis* has been examined and compared with workers of the same species (Fig. 20) taken by Wilson at Ebabaang, ca. 1400 m. altitude, on the Mongi Watershed, Huon Peninsula, New Guinea, in irregular galleries in the earth under a stone. The Ebabaang locality is in mountain rain forest. The ants resembled *Ponera* in life. *G. epinotalis* is very close to *G. luzonensis* Wheeler, differing mainly in details of sculpture. The extra teeth on the posterior tarsal claws of *epinotalis* and *luzonensis* are very minute and reclinate, and are situated close to the base of each claw. They can be seen only at magnifications over 120×, and then only under the most favorable conditions. Dr. Chapman has turned over to me some workers of *luzonensis* taken by D. Empeso in the vicinity of

Dumaguete, Negros Oriental, Philippine Islands. These two species are among the smallest *Gnamptogenys;* and the eyes are much reduced in the workers.

Among the other small species of the Indo-Melanesian area, formerly placed in *Rhopalopone,* I have seen types of *malaensis* (Mann) and reliable specimens of *dammermani* (Wheeler) determined by Wheeler himself from Buitenzorg, now Bogor, Java (Dammerman leg.), as well as a series from the Cuernos Mts., near Dumaguete, Negros Oriental, Philippines, at about 1800 feet altitude (J. W. Chapman leg.). Wilson has compared these with the types of *cribrata* (Emery) and *diehli* (Forel), as well as with the very different *major* (Emery), on deposit at Genoa and Geneva. Wilson took *cribrata* twice at the lower Busu River, near Lae, New Guinea, in lowland rain forest leaf litter. The worker does have vestiges of compound eyes, but these are minute.

[54] Dr. Wilson has compared worker specimens from the MCZ Collection, taken at Kartabo, British Guiana (A. E. Emerson leg.), with the female type of *exarata,* and he feels that they are conspecific. He notes that the type female has a head length of about 0.93 mm., or less than females associated with the Kartabo workers, but a little larger than these workers themselves. A Kartabo female has HL 1.12 mm., compound eye L 0.27 mm. The compound eye L of the type female was about 0.23 mm. Wilson's measurements were, however, not made under ideal conditions.

The type has about 30 costulae between the compound eyes, with a possible error of about ±1. In the females of the Kartabo series, the costulation of the petiolar dorsum varies from concentric to longitudinal; in the type, it is longitudinal. *G. exarata* is a member of the *mordax* group, related to both *continua* and *interrupta*, but it does not compare with the types of these two species **[55, 56]**. In *exarata,* the anterior clypeal border is concave in the middle.

[55] The worker type of *G. interrupta* borrowed from the Vienna Museum has HL 1.12, HW 0.95 mm. The eyes are very small, with about 12 pigmented facets, surrounded by a ring of unpigmented facets, colored like the surrounding integument. The pigmented part of the eye is slightly smaller than the greatest scape thickness, but if the unpigmented part is included, the eye diameter would more or less equal the scape thickness. The sculpture is fine, 50 ±3 costulae between the compound eyes. Second gastric segment smooth and shining, with a few coarse punctures. Color rich ferruginous red; legs and antennae more yellowish. "Patr.? M. Dresd./Sudamerika." Like *continua*, but larger and with finer sculpture. (Lectotype.)

Specimens from Lombardia, Honduras (W. M. Mann leg.) agree well with the type, but have coarser costulation. The size variation in this series is marked.

[56] *G. continua* is the smallest known species of the *mordax* group; lectotype HL 0.74, HW 0.58 mm.; about 35 costulae between the compound eyes; eyes themselves small, only about 5-6 facets, their diameter less than the greatest scape thickness. Sides of head subparallel; greatest width at about the anterior third. Clypeus as in *mordax*. Metanotal groove shallow, but distinct. Propodeal angles blunt, sublaminate, feebly overhanging the concave borders of the declivity. Petiole approximately as broad as long, broadest behind, longitudinally costulate; anterior face of node distinct, its sculpture effaced. Second gastric segment rather finely longitudinally costulate above, but smooth and shining on the sides behind.

I have seen samples referred to *continua* from the following localities: Las Hamacas, near Santiago Tuxtla, Veracruz, Mexico (E. O. Wilson leg.); nest in a piece of rotten wood in leaf litter, tropical evergreen forest. Boquete, Chiriqui Mts., Panama (F. M. Gaige). Barro Colorado Island in the Panama Canal Zone, April, (A. E. Emerson, No. 110). Mandeville, Jamaica (A. Wight). Tingo Maria, Monson Valley, Peru (E. S. Ross and E. I. Schlinger leg.). Variation among samples extends to density of costulation, size, extent of shining area on second gastric segment, and depth of pigmentation; some series are deep reddish, others are almost black. The Las Hamacas series was most like the lectotype ("Brasilien") among my samples, even though it was on the opposite extreme of the range.

The Barro Colorado series includes a male, which is a little shorter than the accompanying workers, is dark piceous in color with yellowish antennae, legs and genitalia, and which has deep and complete notauli. The integument is smooth and shining except for the cephalic dorsum, propodeum and petiole, which are finely and densely punctulate and more or less opaque. The second and third abscissae of Rs are lacking.

Some of the Panamanian specimens have additional suturation on the alitruncal dorsum and otherwise betray themselves as ergatoid females or other worker-female intermediates. Santschi's Panama variety appears to be about the same as the Barro Colorado sample from the brief characterization; there seems no need to maintain his name *panamensis*. The Jamaican record of *continua* indicates an introduction, very probably made within historical times. This island has received many introduced ants from South and Central America.

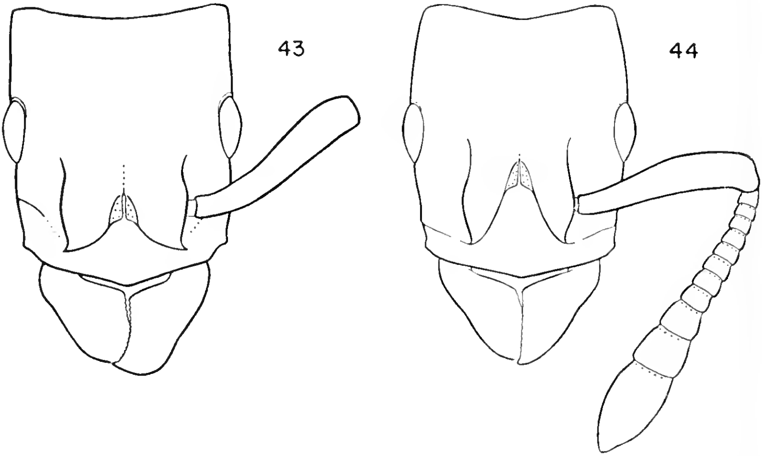
[57] The three varieties of *concinna* were described chiefly on sculptural differences now recognized as individual variations that can be expected even in single nest series. This is confirmed for the type of *semicircularis*, matched with a worker from one variable nest series in the MCZ. The var. *romani* had as an additional character the color of the gaster, "entirely black." Whether this blackness is caused by decomposed gastric contents or some secondary influence, I do not know, but it does not seem likely that it is a character of specific value.

[58] GNAMPTOGENYS CHAPMANI sp. nov.

(Figures 19, 44)

Holotype worker: TL 3.4, HL 0.71, HW 0.56 (CI 79), L head with closed mandibles 0.93, scape L 0.47, greatest diameter of eye 0.17, WL 1.04, petiole L 0.38 mm.

Head as shown in Figure 44. Extremities of occipital angles rather sharply rounded and laterally compressed, but in side view not forming distinct "ears" as in *costata* and *menadensis*. Masticatory borders of mandibles feebly crenulate, almost straight. Alitrunk subcylindrical, only slightly narrower than head, tapering only slightly from front to rear. Humeri bluntly subangulate seen from above; dorsal sutures of alitrunk obliterated. In lateral view, dorsal profile gently convex, almost straight in central portion, falling off through a sharper curve to the almost vertical upper part of the propodeal declivity (Fig. 19), which is marginate above and on the sides, but there are no propodeal teeth. The node is also shown in the figure; seen from above, it is widest behind, and slightly wider than long. Gaster slender, the first segment (postpetiole) truncate in front, slightly wider than long. Second segment longer than the first, but slightly narrower, strongly downcurved. Apical segments retractile.



Figures 43 and 44. *Gnamptogenys* spp., workers, full-face view of head. Fig. 43, *G. kalabit* sp. nov., paratype. Fig. 44, *G. chapmani* sp. nov., holotype.

Integument smooth and shining, with abundant round foveolae spaced on dorsum of head, becoming more crowded and finally contiguous on sides and gula; numerous but separated on alitrunk dorsum, very few on sides; few on sides of petiolar node and succeeding segment, becoming fewer and obsolescent on dorsal surfaces of these segments. Second and apical gastric segments, undersurface of first, propodeal declivity, sides of alitrunk, scapes, legs and mandibles predominantly smooth and shining, with occasional coarse punctures, especially on mandibles.

Fairly abundant erect fine hairs of uneven length over most surfaces of body, becoming more frequently reclinate on appendages and mandibles. Color brownish red; mandibles, legs and antennae yellowish.

Holotype [MCZ] taken by Dr. J. W. Chapman near his vacation home, Camp Lookout (altitude about 600 m.), in the Cuernos Mts., near Dumaguete, Negros Oriental, Philippine Islands, on March 19, 1924.

Paratype workers: two workers taken with the holotype; one worker taken with the female paratype (see below) at or near the type locality, on April 27, 1924 (J. W. Chapman leg.); two workers from Romblon Island, Philippines, April 5, 1924 (L. Morato leg.). Dr. Chapman thinks that the Cuernos Mts. collections came from nests in rotting wood in rain forest ravines. The paratype workers range downward in size from the holotype to one of the two specimens from Romblon: TL 3.0, HL 0.66, HW 0.48 (CI 74), WL 0.90, petiole L 0.35 mm. In smaller specimens, the head is disproportionately narrower, and even more noticeably so is the petiole; in the smallest specimens, the node is distinctly longer than broad; in these same specimens also, the foveolae of the sculpture tend to be smaller and farther apart. The shape of the occipital concavity varies slightly by individuals. In some workers and the female, the margins of the propodeal declivity form a distinct angle with the dorsum, in some the angle being almost like a blunt tooth or tubercle.

Female paratype, dealate: Size and proportions much as in larger workers, but alitrunk a little more robust and with flight sclerites differentiated in normal (but minimal) queen fashion; wing stumps present. Compound eyes only very slightly larger than in worker of same size; ocelli modest in size, but distinct.

G. chapmani is close to *G. laevior* Forel, but is much smaller and much lighter in (full adult) color than any of the *laevior* specimens I have seen; also, *laevior* has the node slightly longer than broad, a circumstance that is reached only in the smaller workers of *chapmani*.

[59] GNAMPTOGENYS KALABIT sp. nov.

(Figure 43)

Holotype worker: TL 5.0, HL 1.06, HW 0.84 (CI 79), L head with closed mandibles 1.37, scape L 0.76, greatest diameter of eye 0.24, WL 1.47, petiole L 0.62 mm. Head as shown in Figure 43; note the almost perfectly straight and parallel sides and the rather sharp occipital angles. Seen from the side, the occipital corner is rather sharply rounded and margined by a narrow translucent border or carina, but no distinct "ear" is formed. Antennal scapes do not quite reach occipital angles, but reach the occipital border when laid straight back from their insertions. Clypeus not or very indistinctly sulcate in the middle; mandibles denticulate. Antennal funiculus stout, median segments very short, only about half as long as broad; last three segments forming an indistinct club; only the first and apical funicular segments longer than broad.

Alitrunk seen from above with obtusely angled (vertically margined) humeri; inferior border of pronotum forming a salient right angle in front of each fore coxa. Seen from the side, the alitrunk is deeper and a little more convex dorsally than in *chapmani*, but the conformation of the propodeum is similar. Coxal tooth acute but subconical, with broad base. Petiolar node paniform, of the general form of *costata*, *menadensis* and *chapmani*, slightly longer than high, with rounded dorsal surface; seen from above, node about as broad as long, narrowed anteriorly. Ventral process with posterior border sloping back gradually from an obtuse posterior angle. Base of postpetiole subtruncate (more rounded than in *chapmani*); postpetiole slightly broader than long; succeeding segment considerably longer and slightly narrower, strongly downcurved. Middle and hind tibiae each with a single slender, very minutely denticulate or subpectinate spur; all tarsal claws with a single extra strong subbasal tooth.

Head covered with deep, circular, umbilicate shining-bottomed foveolae, the ridges separating these forming a coarse reticulum; cervical surface of occiput smooth and shining, with a few fine striae in the middle; clypeus coarsely longitudinally striate, foveolate along sides of triangular median lobe; mandibles smooth, shining, coarsely punctate. Alitrunk, petiole and sides of postpetiole with conspicuous, shining, mostly separated foveolae, still more widely separated over the postpetiolar dorsum (disc). The following areas smooth and shining: a median mesonotal-propodeal strip, metathoracic portion of sides of alitrunk, propodeal declivity, a small area on the nodal summit, the broad interfoveolar spaces on the postpetiolar dorsum, tergum of the second segment (except for posterior and lateral margins), and the apical segments of the gaster. Scapes and legs smooth and shining, with scattered punctures. There is also a superficial fine sculpture, characteristic of this species, found on the alitrunk, node and sides of the first two gastric segments in those interfoveolar spaces that are not smooth and shining. This fine sculpture ranges from a fine striation to a broken striolation or even to a finely coriaceous or reticulo-punctulate condition, the extremes grading through all intermediate substriate stages. This sculpture is more arched-striate and weakly shining on the disc of the pronotum and on the petiolar node; obliquely substriate or striate on the sides of the alitrunk and on the lateral and lateroventral surfaces of the gaster, which are subopaque, especially the sides of the postpetiole; transversely striolate along the posterior marginal band of the postpetiole. Fore coxae transversely striate, middle and hind coxae densely and finely punctulate, opaque, pubescent. Sternum of postpetiole more or less smooth and shining in the middle. Pilosity, etc. much as in *chapmani*. Color medium brownish-red; antennae and legs more yellowish.

Holotype [MCZ] one of a nest series labeled, "Kalabit Country/N. Borneo/E. Mjöberg/ 3000 ft."

Paratype workers: 13 workers from type nest series: TL 4.6-5.3, HL 1.00-1.12, HW 0.79-0.90 (CI 79-80), WL 1.37-1.56 mm. Variation in form and sculpture is very slight. In some specimens, the ventral process of the petiole is a rounded lobe; in some, the occipital concavity is a little more or less broad and rounded than in the holotype.

Paratype female, dealate (from type nest series): TL 5.7, HL 1.08, HW 0.88 (CI 82), L head with mandibles 1.40, scape L 0.78, greatest diameter of compound eye 0.29, WL 1.73 mm. Alitrunk bulky, normal flight sclerites and wing sclerites present.

Mesonotum longitudinally rugose-foveolate; propodeal dorsum smooth and shining in the middle. Ocelli small but distinct, each with an adjacent blackened callus.

Males, 2 specimens from holotype nest series, of which one was measured: TL without genital capsule 4.9, forewing length ca. 3.8, HL 0.76, HW including compound eyes 0.87, WL 1.54, petiole L 0.52 mm. Antennal segment lengths: scape 0.38, funiculus I 0.15, fun. II 0.22, fun. III 0.21 mm. Occipital margin broadly and shallowly concave in the middle as seen full-face. Mandibles finely dentate, with the clypeus finely and indistinctly striolate, the mandibles and anterior clypeal apron longitudinally, remainder of clypeus transversely striolate. A strong median carina connects clypeus to anterior ocellus. Ocelli large, clear, separated by their own diameters or a little more. Compound eye large and rounded, greatest diameter 0.31 mm. Dorsum of head with distinct, circular, contiguous to subcontiguous foveolae; interfoveolar ridges forming a reticulum. Pronotum sculpture like head, but smooth and shining in the middle; scutum smooth, shining, with scattered foveolae; notauli very distinct, complete, coarsely foveolate. Scutellum rugose-foveolate. Propodeum smooth, shining along anterior margin and in center of declivity; elsewhere rugulose, weakly shining. Sides of mesothorax smooth to obscurely striolate, shining. Node smooth and shining above, foveolate laterally. Gaster and legs smooth, shining, with scattered punctures. Wings with venation as in *macretes* male **[61]**; microtrichiae yellow-tan. Color piceous to black; gaster, legs and antennae more reddish or brownish, genitalia yellowish.

Larva described and figured by G. C. and J. Wheeler (1952a: 122-123, pl. 3, figs. 1-8) as *Stictoponera* sp. This species is easily recognized by means of its rectangular head and substriate interfoveolar sculpture, especially of the sides of the postpetiole.

[60] GNAMPTOGENYS GRAMMODES sp. nov.

(Figure 41)

Holotype worker: TL 4.9, HL 1.09, HW without eyes 0.93 (CI 85), L head with closed mandibles 1.44, scape L 0.97, greatest diameter of eye 0.28, WL 1.56, petiole L 0.52 mm.

Head shape as shown in Figure 41, drawn from a paratype, except that in the holotype the occipital border is a trifle flatter and longer, and the occipital angles not quite so gently rounded to the compound eyes. Seen in side view, occipital lobe rounded, but with a small, thin, subrectangularly rounded lamina or "ear" on the curve.

Alitrunk much as in the other medium- and large-sized Old World *Gnamptogenys,* convex, but the humeral angles rounded, with scarcely a trace of the corners prominent in *menadensis* and relatives. Promesosuture marked by a faint line; mesonotum with a narrow but deep and well-defined median longitudinal sulcus; metanotal groove fairly well marked, and the alitruncal dorsum slightly impressed in this region. Propodeum convex above and rounded evenly into the declivity, the latter short, feebly concave, bounded above and laterally by indistinct margins, and guarded on each side by a very small, rectangular to subacute vestige of a tooth. Coxal tooth slender, tapered to a blunt point. All tarsal claws with well-developed subbasal teeth.

Petiolar node paniform, shaped much as in the *menadensis* group, but with the ventral process reduced to a very small anterior tooth, directed obliquely downward and forward; node seen from the side a little longer than high; seen from above just about as long as it is broad; greatest breadth at about the posterior third. Gaster much as in *menadensis;* second segment perhaps a little shorter relative to first, but still long and strongly downcurved.

Apical borders of mandibles finely denticulate; shining, striate and with scattered punctures. Clypeus shining, with large punctures behind and short longitudinal rugulae in front; bisected by a narrow, deep longitudinal sulcus with shining bottom. Head with circular, shining-bottomed foveolae numerous, smaller in the median dorsal region, where they are mixed with longitudinal striation; larger and contiguous on the sides and beneath. Alitrunk covered with large, circular, shining foveolae, mostly contiguous above, becoming smaller and separated on the sides; in the metanotal area, the foveolae are mixed with some indistinct transverse striation. Interfoveal spaces here, especially a posteromedian triangular area on the pronotum, smooth and shining, as is also the upper part of the propodeal declivity. Metapleura and lower declivity with a few coarse horizontal striae. Node of petiole smooth and shining, with a few separated, shallow foveolae scattered over its surface; a few indistinct transverse rugulae or coarse striae across the lower anterior face of node. First gastric segment rather irregularly costulate or coarsely striate, with coarse, elongate punctures interspersed, transversely, across the basal third, longitudinally over the remainder of the dorsum, becoming a little smoother along the lateral margins. Sternum of first segment smoother, shining, loosely rugulose in a transverse direction and with large shallow foveolae. Second segment mostly smooth and shining discad, with small scattered punctures, although this smooth area is bordered along both side margins and in the posterior corners by short costal remnants with large punctures; along the anterior border there is a narrow band of transverse striation, followed by a brief zone of longitudinal costulation with coarse punctures or foveolae, extending about ⅕ to ¼ the length of the segment. The sternum of the second segment is rugoso-punctate. Apical segments retracted in holotype, but these are smooth and shining in a paratype worker. Coxae of middle and hind legs finely punctulate, subopaque, as are also the antennal funiculi and the tarsi. Anterior coxae finely and closely striate horizontally, shining. Femora, tibiae and scapes smooth and shining, the scapes with one or two fine longitudinal rugae on inner and outer margins.

Body generally with abundant long, tapered, erect hairs, mostly 0.15-0.20 mm. long, becoming shorter, more nearly decumbent and denser on the extremities, including a dense brush on the gastric apex.

Color reddish piceous, almost black to the naked eye; antennae and legs light red.

Holotype [MCZ] a worker from Bisianumu, near Sogeri, Papua, at about 500 m. altitude, from a small colony or colony fragment nesting in a piece of rotten wood on the forest floor (E. O. Wilson leg., No. 671, March 15-20, 1955). Paratypes consist of 8 additional workers from collection No. 671 with the holotype, plus a stray worker, No. 655, taken from a rotten log in which lived a dealate female of *G. macretes* as well as colonies of *Pheidole* and *Cardiocondyla*, at the same locality as the holotype nest series. Size variation was relatively slight: HL 1.04-1.12, TL

4.7-5.1 mm. In some specimens, the occipital border is more evenly rounded (Fig. 41) than in the holotype, the clypeus is more sharply striate, even within the sulcus, and the propodeal teeth may be either more acute and more dorsally directed, or smaller and more obtuse, scarcely distinguishable from the sculpture. The transverse costulation of the first gastric segment may extend back over nearly half of the tergum of the segment, and in some specimens there are rather wide, shining spaces between some costulae. The distinctness and extent of the bordering remnant sculpture on the second gastric segment is also very variable, in some examples being almost completely obsolete, so that the entire tergum is smooth and shining, with only the scattered piligerous punctures to mar the surface. The color of the callows is dull yellow, and all intergradations of pigmentation occur in nest series No. 671, from yellow through brownish-red to nearly black. The legs are usually conspicuously lighter and more reddish or yellowish than the rest of the body. The female and male are unknown.

[61] GNAMPTOGENYS MACRETES sp. nov.

Holotype worker: TL 5.3, HL 1.25, HW 1.07 (CI 86), L head with closed mandibles 1.67, scape L 1.20, greatest diameter of eye 0.31, WL 1.90, petiole L 0.62 mm.

Very similar to *grammodes*, but larger overall and with a finer, more regular and more extensive striate or costulate component of the sculpture. Head shape as in *grammodes*, but the occipital border a little more broadly transverse (more truncate) and with the concave section in the middle broader and shallow. Humeri more distinctly angulate as seen from above, rectangular. Ventral process of petiole broader and longer, averaging larger than the coxal tooth of the same specimen.

Sculptural differences: Foveolae of head averaging a trifle smaller, the spaces between longitudinally striate right out to the sides, curving above and behind the eyes and then running transversely across the gula. Dorsum of pronotum coarsely striate longitudinally between foveolae on its posterior half, especially in the middle, where a narrow sulcus is all that represents the broader smooth triangular space of *grammodes*. Mesonotum with interfoveolar rugae converging posteriad, transverse along posterior margin, so as to form a U. Median sulcus here obscure, partitioned into a row of coarse foveolae. Sides of alitrunk sculptured much as in *grammodes;* propodeal declivity very short, smooth and shining. Petiolar node shining, coarsely transversely striate, with a few scattered shallow foveolae. First gastric segment (postpetiole) evenly and distinctly striate or costulate (more finely and densely than in *grammodes*), transverse across the anterior quarter of the tergum, arching over the longitudinally-oriented remainder, with coarse interspersed punctures. The sides of this segment are smooth and shining, with sparse coarse foveolae. Second segment somewhat more finely striate longitudinally, with interspersed punctures, the striae reaching nearly half the length of the segment in the middle. A small anteromedian sliver, separated from the remainder of the surface by a curved line resembling the mark left by pressing a fingernail into something soft, is delicately transversely striate. Sides and posterior half of this tergal surface smooth and shining, with scattered piligerous punctures. Sternum of first segment predominantly smooth, with a few indistinct transverse wrinkles and grooves, shining. Sternum of second segment shining, indistinctly obliquely striate over the triangular side pieces. Sculpture otherwise as in *grammodes*, except that tarsi are only sparsely punctulate and are shining, and mandibles and clypeus more distinctly and more completely striate, including median clypeal sulcus.

Color brownish-red; mandibles, antennae and legs yellowish. The darker-colored parts of the body, especially alitrunk and gaster, overlain with a feeble pinkish-violet to bluish metallescence as viewed in certain lights.

Holotype [MCZ] a worker from colony series of collection No. 649, taken at Bisianumu, Papua, the same locality from which came the types of *grammodes* (see above), by E. O. Wilson.

Paratypes: 6 workers from the holotype nest series (No. 649): TL 5.2-5.4, HL 1.21-1.28, HW 1.04-1.11 mm. (CI 86-87). These specimens vary slightly in density of sculpture (especially on the petiolar node), in size of ventral petiolar process, and in striation of second gastric segment, which in some examples reaches, and even surpasses, the midlength of the segment. Some specimens have the occipital border straight or nearly so, seen full-face.

Paratypes: 3 dealate females — 2 from the holotype nest series, and a unique (Collection No. 655) taken from a rotten log in which a *G. grammodes* worker was also taken (see under *grammodes* paratypes, above) at Bisianumu by Wilson. TL 6.7-6.8, HL 1.27-1.29, HW 1.11-1.12 (CI 87 in all 3 specimens), scape L 1.22-1.23, greatest diameter of eye ca. 0.35, WL 2.2, petiole L 0.65-0.66 mm. Alitrunk bulky; mesonotum foveolate, with longitudinal rugae between. Pronotum coarsely foveolate, the interspaces smooth and shining, especially at midline; sides of alitrunk behind pronotum predominantly coarsely longitudinally striate. Color darker than worker, mahogany, nearly black to naked eye; legs, scapes reddish-yellow.

Males, 3 specimens for holotype nest series, of which only one was measured: TL without genital capsule 6.0, forewing L ca. 4.2, HL 0.86, HW including compound eyes 0.98, WL 1.76, petiole L 0.52 mm. Antennal segment lengths: scape 0.33, funiculus I 0.14, fun. II 0.29, fun. III 0.29 mm. Mandibles triangular, finely dentate, with larger apical tooth. Mandibles and convex clypeus finely longitudinally striate. A strong median carina connects clypeus and anterior ocellus. Ocelli large, clear, separated from one another by a distance a little greater than the diameter of each. Compound eye large and strongly rounded, greatest diameter ca. 0.29 mm. Dorsum of head and alitrunk shallowly foveolate, with predominantly longitudinal rugae interspersed. Epimera convex, mostly smooth and shining, with a few foveolae. Propodeum steep, gently rounded, declivity not distinct from dorsum, unarmed, vermiculate-rugose. Petiolar node depressed-paniform, longer than broad and about half again as long as high, mainly smooth and shining, with a few scattered shallow foveolae; ventral process represented by a small oblique tooth or angle.

Gaster slender, smooth and shining, with piligerous punctures; an irregular transverse wrinkle or fold line across the tergum of the first segment in all of my specimens. Veins Mf2 and Rsf2·3 missing from forewing. Abundant long, fine, tapered erect hairs on most surfaces of body, becoming shorter and more decumbent on legs. Wings densely covered with brown microtrichiae. Color piceous to black, legs brown, trochanters and genitalia yellowish.

The holotype nest contained 30-40 workers and several males and dealate females; the colony was in a large rotting log in rainforest. Paratypes will be deposited in MCZ and elsewhere.

[62] *G. horni* is clearly a good species apart from *regularis; horni* is much smaller, and differs in other ways; besides, it is sympatric with *regularis* in the Guianas and probably elsewhere in South and Central America, but no intergrades between the two forms have yet been reported. The MCZ has numerous examples from each of several localities in British Guiana and the Panama Canal Zone, plus a sample each from Huachi, Rio Beni, Bolivia (W. M. Mann leg.) and from San Francique, Brasso, Trinidad (A. E. Emerson leg.).

[63] The status of *Spaniopone haytiana* has been discussed in the main section of the generic revision as one of the *Holcoponera* Group of genera. See p. 218.

[64] *G. menozzii* is represented in the MCZ by type workers from Rio Grande do Sul, and by a worker from Volta, Parana: color blackish-brown, HL 1.16-1.21 mm., CI 109, 21-24 costulae between eyes. The ventral process of the petiole has a salient posterior corner, either digitiform or acutely dentiform. Two types of *G. schubarti* (Monte Alegre, São Paulo, 900 m.) are also blackish-brown, HL reaches 1.40 mm., but CI is still 109; 25-26 costulae between eyes. Ventral process of petiole with posterior corner reduced, obtusely rounded, shorter than anterior corner. A specimen similar to both foregoing species is from Corcovado, Rio de Janeiro (T. Barbour leg.): color bright ferruginous (probably teneral), HL 1.28 mm., CI 106; 22 or 23 costulae between the eyes. Ventral process of petiole with posterior corner obsolete, the process consisting only of the short, digitiform remnant of the anterior angle. It looks as though *menozzii*, *schubarti* and the Corcovado specimen may belong to one geographically variable species. More collections are needed.

[65] In 1896, when Emery first set up *Alfaria,* he included two species then new: a larger, very finely striolate one (*simulans*) and a smaller, opaquely and extremely finely subgranulose one (*minuta*). Since then, other authors have added six species to *Alfaria.* In addition, Mann's *Opisthoscyphus scabrosus* is clearly a member of the same group, and thus makes seven additions since the original description of the first two species.

Bufonis is close to *simulans*, and in fact resembles in nearly every particular moderate-sized dark brown *simulans* specimens from Costa Rica; the *simulans* types I have seen are somewhat larger and are dull yellowish in color, but they may be teneral. The only clear difference shown by *bufonis* is the well-developed metanotal groove in Mann's unique type, which conceivably could be an ergatoid female or some other departure from the true worker caste. Until we know more about the normal variation in *simulans*, it seems best to recognize the Mexican *bufonis* as a species apart.

Five of the six other post-Emery species all appear to merge into a single variable species indistinguishable from *minuta*. This has been determined from careful comparison of types (except *mus*) one against another and against what little other material could be assembled. To begin with the final and most important check: Wilson has compared the types of *A. minuta* and *A. emeryi* found in the Forel Collection, and in turn matched these with a topotypic worker of *panamensis* that I had previously checked directly against a *panamensis* cotype, *carinata* cotypes, and the holotype of *O. scabrosus*, as well as additional samples from southeastern Brazil and Costa Rica sent by Father Borgmeier. Although there is some variation in size and sculpture, particularly of the gaster, these samples all appear to represent one species, *minuta*, which ranges from Central America to Bolivia and southern Brazil. The integument of this species is frequently fouled with a whitish incrustation, apparently a dried secretion like that found on many dacetines; this deposit very deceptively alters the appearance of the surface features, and can make even nest mates look very different.

Examinations of the *O. scabrosus* holotype [USNM] reveals that this genus and species was described on the basis of the artist's unrepresentative depiction of the mandibles, rather than from the specimen itself. Actually, the mandibles are in no way unusual for *minuta*. Most of the differences cited in the other species descriptions are based on small errors of observation or differences in viewing planes. The type review showed these distinctions to be non-existent or completely trivial. Though the *mus* type was not seen, the description tells enough to make this synonymy reasonably safe. The frontal groove mentioned by Santschi is undoubtedly the weak frontal carina as viewed in haste.

The most recently described species, Borgmeier's *striolata*, provides a link between the more "typical" *Alfaria* and the other *Gnamptogenys* species, and is itself a distinctive form.

[66] GNAMPTOGENYS MECOTYLE sp. nov.

(Figure 42)

Holotype worker: TL 6.0, HL without cervical flange of occiput 1.16, HW 1.10 (CI 95), L head with closed mandibles 1.70, scape L 1.16, greatest diameter of eye 0.30, WL 1.85, petiole L 0.69 mm. General habitus of the larger species in the *G. rastrata* group, particularly *aculeaticoxae*, *menozzii*, etc., but differing in the following respects.

(1) Scapes long, when laid straight back from insertions, surpassing occipital margin by more than ¼ their total exposed length; their dorsal surfaces coarsely longitudinally striate throughout.

(2) Costulation of head much less even, the costulae nearest the middle mostly much coarser than those near the eyes, mixed in gauge. Although a count is difficult and uncertain, it appears that there are about 28 costulae between the compound eyes, and about 11 between the frontal carinae. The longitudinal costulation of the clypeus is finer and regular.

(3) The longitudinal costulation of the alitrunk does not continue all the way forward to the anterior pronotal margin, but instead runs into an arched pattern across the anterior pronotum, where 5 or 6 costulae are transverse.

(4) Propodeal teeth (L. ca. 0.13 mm.) distinctly longer and broader at base than in *aculeaticoxae*, and about ⅓ as long as the distance between the centers of their bases. Propodeal declivity narrowed above, margined, smooth and shining.

(5) Node (Fig. 42) longer than deep and slightly longer than broad, gently arched, crossed by about 13 transverse costulae. Ventral process shallow, in the form of two short, blunt subequal teeth joined by a low concave lamina.

(6) Extreme base of postpetiole truncate in both dorsal and lateral views, leaving a small vertical anterior face that is nearly or completely smooth and shining. At the center of the border limiting this face above, the border is produced forward slightly as a blunt tubercle. Coarse costulae of postpetiole slightly wavy, becoming more wavy and erratic on sides of this segment near base.

(7) As minor characters, may be mentioned the cervical flange of the occiput, which is quite plainly visible in full-face view, and is convex in the middle; and the gula and postpetiolar sternum, both predominantly transversely costulate. Mandibles coarsely striate (smooth, punctate at apices) and weakly dentate along the masticatory borders. Color deep brownish-red; mandibles, antennae and legs more yellowish.

Holotype [USNM] taken by W. M. Mann on the lower Rio Madidi, Bolivia, in February, 1922. Four worker paratypes [USNM, MCZ, Coll. Borgmeier] taken with the holotype are similar, differing slightly in size, depth of color and sculptural details. The size ranges from that of the holotype up to that of a worker: TL 6.3, HL without cervical flange 1.22, HW 1.14 (CI 94), L head with closed mandibles 1.77, scape L 1.23, greatest diameter of eye 0.33, WL 1.96, petiole L 0.73 mm.

This distinct species is intermediate between *bispinosa* and *aculeaticoxae*, but is closer to the latter. It is apparently sympatric with *aculeaticoxae* at or near the *mecotyle* type locality.

[67] The variety *ericae* was based on a small Colombian specimen of *tornata* having the costulae on the propodeum, especially the declivity, longitudinal. Such specimens are commoner south of Guatemala, but Costa Rican and other series are found in which the patterns of this region are longitudinal, transverse, and intermediately U- or V-shaped, even in single nest series.

[68] The name *fiebrigi* applies to specimens from south of the Amazon (type locality is San Bernardino, Paraguay). I have seen material from Goias, Minas Gerais and São Paulo states with the shallower and more shining costulation and the less acutely bidentate ventral petiolar process described by Forel. The more northern of these series tend toward the "typical" *regularis* from Ecuador, British Guiana and Venezuela (in the MCZ). Var. *splendida* apparently applies to somewhat callow Mexican specimens. Samples in the MCZ come also from Costa Rica.

[69] *G. mordax* is a very variable species. Size and gastric sculpture are particularly unstable characters, but extremes of variation are connected by intergrades both inter- and intranidally. From its description, it seems fairly certain that Latreille's *Formica nodosa* is the same as *mordax.* However, the name *nodosa* has not been used except in catalogs, and I believe that it should not replace *mordax,* which has been used for this common ant for nearly a century.

Forel's description of var. *purensis* applies well to one common variant of *mordax,* and I have examined a type of *sebastiani,* which is close to *mordax* types received from the British Museum.

[70] Specimens in the MCZ from Mexico (Guadalajara, Guerrero, Chiapas), as well as from Guatemala and Costa Rica, show that Santschi's differentiation of *curtula* and *stolli* as races is based on individual, partly allometric variation. Larger workers have transverse sutures on the posterodorsal alitrunk indicated as impressed lines. Apparently this species can live in somewhat drier places than the habitat of *G. strigata,* the related species having much the same range.

[71] In a nest series of *porcata* from Hamburg Farm, Costa Rica (F. Nevermann leg.), some specimens have the costulation of the posterodorsal alitrunk departing from a strictly longitudinal pattern; in one specimen, the propodeal area is covered by a well-developed whorl, approaching the condition as described by Santschi for the *magnifica* types. The distinction between *porcata* and *magnifica* is thus seriously weakened, and it may be that these two names represent a single relict species now in the process of being replaced by the centrifugally spreading relative, *G. pleurodon.*

[72] *G. pleurodon* is closely allied to *porcata,* but is smaller. It is widely distributed in the Amazon drainage. After examining the nidotype series from Bolivia of var. *recta* (USNM, MCZ), assigned by Santschi to *emeryi,* as well as a series from Yurac, 67 miles east of Tingo Maria, Peru (E. S. Ross and E. I. Schlinger leg.), I believe that the characters upon which Santschi differentiated *pleurodon, emeryi* and *recta* are individual or allometric variates that may be expected in almost any nest. Emery's female *pleurodon* was separated as *vidua* by Santschi, but the differences are only those one might expect between worker and female of one species.

[73] *Gnamptogenys rastrata* group. This group is essentially the old subgenus *Parectatomma.* There exist in this group many uncertainties at the species level, due to the present scarcity of material, to the fact that several names were based on single specimens (and even these hardly adequately described), and to the circumstance that females are mostly not yet properly associated with workers. Some species must remain in doubt for the time being, but it seems wise here to review the material available and outline the problems involved.

G. rastrata. The type (NM Vienna) is a winged female from "Brasil/F. Sahlb. [erg]." HL 0.90, HL plus closed mandibles 1.40, HW including compound eyes 0.92, HW without eyes 0.83 mm. About 24 or 25 costulae between compound eyes: 9-10 between frontal carinae. Mandibles as in *menozzii* and *schubarti,* etc. (Fig. 16), masticatory border almost straight, feebly concave in basal third, faintly convex in mid third, then feebly concave again in apical third, showing a tendency toward the condition in *mediatrix;* no defined denticulation. Dorsal costulation of mandibles coarse, but not as bold as in *schubarti,* shading off to a shining, nearly smooth surface near the inner basal angle; costulation replaced by a smooth surface with shallow punctures on the apical third of the blade. Teeth of propodeum minute blunt tubercles; coxal tooth short, triangular, as in *schubarti* worker; shape of petiolar node and its ventral process also very much as in *schubarti* types, and like those of *aculeaticoxae.* Costulae of petiole longitudinal, diverging behind as seen from above; transverse across anterior face of node. Color brownish red.

The worker from Alajuela, Costa Rica, determined by Emery as "*rostratum* Mayr" can scarcely be the same as the *rastrata* type from Emery's account, and considering the remoteness of the locality. For the present, I am unable to guess what Emery had from Costa Rica (Emery, 1890a:41).

Wheeler (1925:5) determined some specimens collected by Holmgren at Llinguipata, Peru, as *rastrata,* but I have examined four of these specimens and found them to be the form described by myself as *Holcoponera mina,* now placed in *Gnamptogenys* **[46]**.

A worker in the collection of Father Thomas Borgmeier, from Nova Teutonia in southeastern Brazil, 300-500 m. altitude (F. Plaumann leg.) is close to *rastrata*, and may actually be its worker. HL 0.82, HW with compound eyes 0.86, HW without eyes 0.83 mm., 27-28 costulae between compound eyes. Eyes large. General habitus, mandibles, etc. about as expected for worker of *rastrata*, as compared with the female type. Petiolar node slightly but distinctly broader than long; costulae transverse across the anterior face; as seen from above, costulae longitudinal in the center, but around this concentrically circular, with only 2-3 transverse at the posterodorsal border. The ventral process is as in the type worker of *G. menozzii*, i.e., with concave ventral border, rounded anterior corner, and acute posterior corner. Color red-brown, head slightly darker than rest of body. The variation in nodal sculpture and form of ventral process of petiole may be normal for a single species; only further material will tell.

G. trigona. Emery described this form from a unique female from Novo Friburgo, Santa Caterina, Brazil. The description is in the form of a very brief comparison with *triangularis* Mayr; the size is "a little smaller . . . L. 4.5 mm." Sculpture much coarser than in *triangularis;* antennae thicker and shorter, the scape scarcely surpassing the occipital border. On the petiole, the costulation is disposed in concentric, but transverse, arches.

Except for the transversely concentric petiolar costulation, this characterization would match fairly well the type of *rastrata;* however, the petiolar sculpture may possibly be variable enough to include the *rastrata* and *trigona* patterns within one species. Other specimens I have seen, determined as *trigona* in various collections, are as large as or larger than *triangularis,* and have coarse costulation, but this is concentric on the petiole without being in the least transverse in orientation. I believe that these large specimens, such as the worker from Corcovado, discussed above **[64]**, are probably not the true *trigona.*

I conclude for the present that *trigona* may be the female of the small species next described below, or else it is a synonym of *rastrata.*

Borgmeier Coll., Nr. 5756. Angra dos Reis, Rio de Janeiro State, Brazil (Lopes et Lent leg.). Four workers: HL 0.74-0.76, HW without compound eyes 0.69-0.73 mm., CI 93-96. Eyes large, but only feebly convex. 24-28 costulae between eyes. Mandibles as in *rastrata* type and the possible *rastrata* worker (Nova Teutonia, see above), but costulation coarse and extending more completely into basal corners. Propodeal teeth reduced to small tubercles, inconspicuous alongside the larger, protruding, obliquely-facing spiracles, just as in *menozzii*. Petiolar node about as broad as long; costulae concentric, forming a transversely elliptical pattern, variable in its center from specimen to specimen. Ventral process of petiole of the *menozzii* type. Teeth of posterior coxae shorter than in *menozzii*, but still digitiform or spiniform. Color red-brown. The total length of these specimens varies from about 3.1 mm. to 3.5 mm., outstretched with mandibles. This size is considerably less than the 4.5 mm. measurement Emery gave for the *trigona* female, and Emery's measurements usually fall under the ones I make on the same specimens of other ant species. Nevertheless, the correspondence of other characters, particularly the sculpture, with Emery's description, leaves the possibility open that Sample 5756 represents the worker caste of *trigona*.

G. triangularis. Four workers from: Ipiranga, S. Paulo State, Brazil (Luederwaldt leg.); Tafi Viejo (F. Silvestri leg.) and Tafecillo (N. Kusnezov leg.) in Tucumán, Argentina, measure HL 1.14-1.21, HW 1.12-1.16, eyes excluded. The head is variable in proportions, some specimens having the length slightly greater, others the width (CI 94-102). Only slight variation in gauge and density of costulation, from about 31 to about 35 costulae between the compound eyes. Propodeal teeth small but distinct and acute. Petiolar node varying from about as broad as long to distinctly broader than long, as seen from above more or less transversely costulate; sometimes only one or two transverse costulae in the middle, surrounded by concentric, ellipsoidal pattern on a transverse axis; sometimes the costulae transverse, meeting far down the sides of the node in a V or U pattern. Ventral process of petiole concave beneath, anterior corner rounded, posterior corner subrectangular. Color red-brown to blackish. Forel's race *richteri* reads like a common variant of *triangularis*, and it seems likely that Forel misidentified typical *triangularis*.

[74] Santschi's *reichenspergeri* is not a *Heteroponera,* to judge from a type worker, several males and a dealate female received from the Basel Museum and from Father Borgmeier. The frontal carina is lacking, and habitus and sculpture clearly place the species in *Gnamptogenys,* among the species of which *reichenspergeri* seems nearest to *relicta.* However, *reichenspergeri* has a well developed air of propodeal angles, and the striate sculpture of the alitruncal dorsum is effaced medially in the worker; the gastric sculpture is also largely effaced, broken up into short, bilaterally oblique sections of striation or fine rugulation, with large areas virtually smooth and definitely shining. The males are blackish in color, and generally resemble the species formerly placed in *Holcoponera,* but vein Rsf2·3 is present and situated as in *G. mordax* (Brown and Nutting, 1950, Pl. 8, fig. 5). The eyes of the worker are minute but distinct, and the promesonotal suture is cut through on the dorsum; the position of the metanotal groove is indicated by a faint impressed line. The petiolar node is anteroposteriorly compressed, and resembles those of *relicta* and the former *Spaniopone* and *Rhopalopone* species. Everything considered, this aberrant *Gnamptogenys* appears to be close to a perfect intermediate species linking the old genera *Gnamptogenys, Spaniopone, Holcoponera* and *Rhopalopone.*

[75] *G. rimulosa* is known only from the vicinity of Rio de Janeiro, where it is infrequently collected. Specimens sent by Father Borgmeier under this name agree well enough with the description.

[76] From the brief original characterization, *quitensis* is apparently only a minor variant of *tortuolosa,* which is widespread in Ecuador.

[77] GNAMPTOGENYS SEMIFEROX sp. nov.

(Figure 14)

Holotype worker: TL 7.0, HL 1.43, HW (across eyes) 1.44, HW (at anterior corners) 1.39, closed mandibles extend about 0.81 mm., WL 1.99, petiole L 0.74, greatest eye diameter 0.29, scape L 1.11, absolute exposed length of left mandible 1.32; CI

97. Differs from *Gnamptogenys* (=*Emeryella*) *schmitti* workers of about the same size in its narrower head; shorter, broader, differently formed mandibles (Fig. 14); and in the longer petiolar node, which is a trifle longer than broad seen from above. The median clypeal lobe is more prominent, and its anterior border is entire and evenly convex in outline. The sculpture differs in a number of ways.

The costulation throughout, but particularly on the head and pronotum, is finer, less uniform and even, less shining, and a little less distinct. The interspersed punctation, very sparse and insignificant in *schmitti*, is more abundant, coarser and considerably more distinct in *semiferox*, especially on the head, but it still does not interfere seriously with the regularity of the costulation except in the areas just mesad of the compound eyes and on the dorsolateral surfaces of the propodeum. The punctures are mostly indistinctly bounded, but contain piligerous tubercles. The dorsal face of the propodeum is longitudinally and subvermiculately costulate (evenly and transversely in *schmitti*). Color deep piceous, as in fully pigmented *schmitti*, appearing black to the naked eye. The appendages are more reddish.

The holotype [MCZ] and two very similar paratypes [Coll. Borgmeier, MCZ] all bear the same data: Mt. Diego de Ocampo, 3000-4000 feet altitude, Dominican Republic, July, 1938 (P. J. Darlington leg.). Dr. Darlington tells me that the type locality was chiefly rain forest in which small palms were prominent, but that the land was being cleared for agriculture even at the time of his visit.

In the development of the mandibles, *semiferox* is intermediate between *schmitti* and *banksi* on the one hand and *mediatrix* sp. nov. on the other. In sculpture, *semiferox* is closest to *schmitti*, but shows tendencies toward the irregular, coarse, partly reticulate or punctate sculpture even better developed in *banksi*. In the lack of a dorsal tooth on the posterior coxa, and in the smooth postpetiolar sternum, *schmitti* and *semiferox* are alike and distinctive, but other *Gnamptogenys* lack the coxal armament, and *banksi* has a partly smooth postpetiolar sternum.

[78]

GNAMPTOGENYS MEDIATRIX sp. nov.
(Figure 15)

Holotypye worker: TL 5.4, HL 1.04, HW (across eyes) 1.13, HW (near anterior corners) 1.08, closed mandibles extend about 0.53 mm., WL 1.64, petiole L 0.59, scape L 1.02, absolute exposed L of left mandible 0.88; CI 104. Very similar except in size and subfalcate form of mandible (Fig. 15) to *G. aculeaticoxae* and to *menozzii* and *schubarti*. Propodeal teeth short but subacute; coxal teeth very slender, with feebly clavate apices. Petiolar node broader than long and very nearly as long as high, its dorsal profile only feebly convex and only slightly higher posteriorly than in front (similar in shape to that of *aculeaticoxae*); anterior face steep, posterior face distinct and abruptly vertical (not distinct from dorsal convexity in *aculeaticoxae*). Subpetiolar process with both anterior and posterior free corners rounded, the latter obtuse, oblique ventral margin very feebly concave in outline, nearly straight (form of process as in *schubarti* types). Petiolar costulation predominantly transverse, as in *aculeaticoxae*.

Eyes large, convex, their anterior margins about at midlength of head. Costulation almost precisely as in *aculeaticoxae* samples from British Guiana so far as density and direction are concerned; 26-28 costulae between the eyes. Mandibles costulate on basal ⅔, except near basal angles, where costulation becomes finer and then obsolescent; apical third of blade smooth, with coarse piligerous punctures. Color piceous, with reddish tinge; appendages lighter, more yellowish.

Holotype and one very similar paratype [MCZ and Coll. Borgmeier respectively] collected together at the present Belém do Pará, Brazil (Dr. Fred Baker leg.), presumably in the outskirts of the suburb of Souza (Mann, 1916:399).

Other paratypes are all from the environs of Rio de Janeiro [Coll. Borgmeier, MCZ]: 3 workers from "Rio de Janeiro" and one from the Jardim Botanico (H. Souza Lopes leg.); one alate female from Engenho Novo (C. R. Gonçalves). The workers vary somewhat in size, the largest being about the same size as the female in dimensions and proportions of the head. There is slight variation in the density of costulation and in the shape of the subpetiolar process. The female is scarcely larger than the largest worker, and the eyes are only a little greater in diameter. HL 1.14, HW (near anterior corners) 1.21 mm. Forewing L 4.5 mm. Venation of typical *Gnamptogenys* pattern; Mf2 present but very short. Petiolar node a trifle shorter and broader than in the worker. CI 106.

[79] The material available to me, in conjunction with the discussions and figures of Santschi's 1929 revision, leads me to consider the names provisionally synonymized as representing parts of the continuous variation of one species. I have already discussed in general terms (Brown, 1957, pp. 489-490) the difficulties in Santschi's treatment of the variation of characters like gauge and density of costulation, body color, development of mesepisternal lobe or flange, and shape of ventral petiolar process; these very difficulties are most exaggerated in his handling of *striatula, brasiliensis* and relatives. From Santschi's own data, it seems unlikely that the types he saw of *striatula* and *brasiliensis* can be different species. But it seems possible that not all the infraspecific forms he described under *brasiliensis* also belong to the same species. Just what constitute species separations between *striatula*, the form with nominal priority, and other forms in or near this complex, we cannot yet say because of the lack of sufficient material and the inadequacy of detail in our knowledge of distributions of the various populations. In general, one might guess that most *striatula*-like specimens with more than 30 costulae between the compound eyes are *striatula* itself, while most with less than 30 are other, closely related species. An indication that this is so may be furnished on sympatric series from Agudos, S. Paulo State, Brazil (W. W. Kempf leg.), one of which is finely costulate (ca. 40 costulae between eyes) and has large eyes, while the other has smaller eyes and about 26-28 costulae between them. This latter type with coarser sculpture perhaps corresponds to the forms named by Santschi as *regularis, arcuata* and *rustica*, from southern Brazil and Paraguay, and may also be the same as the variant *simplicoides* of *brasiliensis*. At first view, there seems to be intergradation between the coarse and fine sculpture types, but this may be due in part to Santschi's inaccuracy in counting the costulae (his counts are sometimes grossly contradictory as between key and text). Other intergradation in costular density may indicate that a character displacement situation exists between coarse and fine sculpture types when they occur sympatrically. The value of the eye diameter as a character has not been determined.

G. striatula is widespread in tropical South America, where the subpetiolar process usually or always has two rather distinct, subequal corners or lobes in its free portion. Specimens from Venezuela and Colombia look like *striatula*, but have the posterior corner or lobe much reduced, so that the process is more or less triangular or forms a single lobe, the condition characteristic of *G. curtula* **[70]**. The possibility should be entertained for the time being that *curtula* is the geographical variant of *striatula* in Central America and Mexico. In Costa Rica, there is a counterpart of the *rustica* group of South America in *wheeleri*, which maintains itself distinct from the *curtula* of Costa Rica in the form of the ventral process.

The relationship of *striatula* to *wasmanni* cannot be decided without more material; its node is rather thick and its ventral process subtriangular, so *wasmanni* seems to me to be closer to *pleurodon.*

The synonymy suggested and the opinions offered here concerning species-level relationships are strictly to be considered as "shooting from the hip," although it is felt that such treatment is justified at this time as a small beginning at making the necessary revision of the *striatula* group. It will perhaps be worthwhile reemphasizing for the benefit of future revisers the unreliability of one particular character given much weight by previous authors dealing with "*Holcoponera*" species. I refer to the mesepisternal lobe or flange. Not only is this structure highly variable in single nest series, but it has been very loosely dealt with by Santschi. Reviewing a substantial part of the same material, including unique types, that Santschi used in writing his revision of 1929, I have found that in several cases his drawings or descriptions are unrepresentative. For instance, his figure 19 shows the mesepisternal lobe of *wheeleri* with a small posterior portion that does not exist in the types; actually, it seems that Santschi was drawing a small ridge that traverses the sternum at this level, and which can be seen by focusing down only slightly from the plane of the lobe. In other cases, the "tooth" at the posterior end of the lobe proved to be a stray bit of glue or dirt. In some series, the lobe was visible on only one side of one specimen; in the other specimens it was covered by glue or otherwise hidden. This means that Santschi's idea of the form and constancy of the lobe was usually drawn from a small fraction of the actual specimens he saw.

[80] *G. strigata* is a small, coarsely sculptured forest species. Wilson took it in rotten wood at Las Hamacas, near Santiago Tuxtla, Veracruz (tropical evergreen forest), and at Las Perlas, near Orizaba, at about 2000 m. in *Liquidambar*-hornbeam forest. C. and M. Goodnight took a specimen at about 1600 m. altitude in a pine grove at Union Juarez, Chiapas.

[81] *G. teffensis* is a large species for which we now have quite a few localities in the Amazon-Orinoco drainage, from the Guianas to Bolivia. The color is variable, but is most often some shade of ferruginous brown. The holotype of *teffensis* has been compared directly with the type of var. *concinna,* and in my opinion the two specimens fall within the normal variation of a single species; the posterior tooth of the *teffensis* type's mesepisternal lobe proved to be only a piece of dirt adhering to the lobe, and once cleaned, the lobe looks like that of *concinna.*

The very closely related *moelleri,* with its color variant *splendens,* has been recorded by specific locality only from the southeastern extremity of Brazil, particularly from Santa Caterina. Mann's Madeira-Mamore record applies to *teffensis.* Actually, *teffensis* and *moelleri* may be geographic strains of one species, although the more slender funicular segments of *moelleri* still seem to separate this form satisfactorily from *teffensis,* even considering that the funicular segments of *teffensis* are variable in thickness to some extent.

[82] *G. sulcata* is highly variable in color, and less so in density and gauge of its costulate sculpture. The principal color of worker and female ranges from uniform ferruginous (perhaps usually in callows) to black. The head is always dark in adults near or past full coloration, and is piceous or black; the mandibles are always pale yellowish. The MCZ now has a number of series representing the stages of intergradation in both color and sculpture, and I have matched the types of *ypirangensis, bufonum* and var. *nitens* directly with these. Var. *lineata* has long been considered only a color variant of *sulcata,* and this follows the description well. Var. *cearensis* is described as a fine-sculpture form, and the details fit MCZ specimens well enough.

A male from Barro Colorado in the Panama Canal Zone (N. Banks leg.) is blackish in color, but has the pronotum a bright contrasting ferruginous yellow in hue. It is about the right size to fit workers of *sulcata* from the same locality, so I believe that it may well be the corresponding sex of this species.

[83] Just as Wheeler puts it, the only important difference (size) between the *minor* syntype series and the *schmitti* workers taken by Mann at Diquini, Haiti, is an "average" one. Differences between Forel's type and later collections are not apparent from Forel's description. Normal size variation is clearly great even within single limited series. Internidal size and sculpture variation is stronger in this than in some other *Gnamptogenys* species, but not as strong as, for instance, in *mordax*.

[84] Kennedy and Talbot (1939) claimed for the worker-female of *P. silaceum* one-segmented maxillary palpi, but their figures 9, 10 and 12 show that these palpi have two segments — a flattened apical one and a short basal one. The labial palpi were depicted with two elongate segments. This pattern has been found also in dissections of *croceum* and *relictum;* the maxillary palp of the former is shown in Figure 26. The arrangement of the first and second segments, with the second segment attached to the first by a slender lateral neck, holds through all of the species for which palpi have been examined, and is apparently characteristic of the genus.

Kratochvíl (1944) shows the palpi of worker *melinum* (under the name *fialai*) in his figures 2a, 2b, and these are like the sample of *pergandei* I dissected, with a formula of 4, 3, the apical segments being fairly elongate in form. The holotype of *stictum*, viewed without dissection, shows three exposed segments for the maxillary palpus, the basal one evidently corresponding well to the second segment of the foregoing species; from this, I assume that *stictum* has four-segmented maxillary palpi, although the labial palpi of this species cannot be made out.

A single female of *micrommatum* dissected had two segments in the labial palps, while the maxillary palps appeared to have three segments on the right side, and two on the left. The two-segmented palpus has resulted from what seems to be a fusion of the basal segment with the slender basal neck of segment II. This condition may be an anomaly for the species; only further material will settle this.

According to Kennedy and Talbot (*loc. cit.*), the male of *silaceum* has a formula of 4,2, but here again their figures show that they did not count the small basal segment of the maxillary palpus. The formula is actually 5,2 as interpreted from their figures, and the second segment of the maxillary palpus is formed in much the same way as in the worker and female. We should expect that the formula for other species of *Proceratium* males is ordinarily 5,3 or 5,2.

[85] The distinctions drawn between the southern European *mayri* and the North African *algiricum* do not appear to be very striking. I have not seen any North African specimens referable to either species, but judging from the characters cited in the literature, it would seem that *algiricum* merely represents geographical variation of the European species. Final decision in this case must wait for critical comparison of the available material.

[86] Dr. George Arnold has kindly sketched for me the type worker of *arnoldi*, and I have presented these drawings here (Figs. 1, 34, 35) with the realization that they are perhaps not strictly comparable with the remainder of the figures of the genus given here. Undoubtedly Dr. Arnold and I have emphasized different points in a slightly different fashion, and, of course, the scale is not the same.

[87] *P. californicum* was described by Cook on the basis of a male stated to have been taken by himself at Glenwood in the Santa Cruz Mountains of coastal California. The description and figure fit well enough a *Proceratium,* but of course so few males are known in the genus that this stray specimen cannot easily be compared with any other species. This is the only record of a *Proceratium* from west of the Great Plains in North America north of Mexico. The type locality is not an impossible one by any means; undoubtedly the mountains of California still hold some surprises for ant collectors. Nevertheless, it would be well to confirm the presence of *Proceratium* in California through further collections before this record is unreservedly accepted, especially since other data in Cook's book is open to some question (see reviews: Brown and Wilson, 1953; G. C. Wheeler, 1954; E. S. Ross, 1954).

[88] A series from the Cuernos Mts., near Dumaguete, Negros Oriental, Philippines (J. W. Chapman leg.) fits the diagnosis of *carinifrons* well enough. The relationship of this species to *longigaster* needs investigation.

[89] This species, closely related to *micrommatum,* lacks the median clypeal projection supposed to be characteristic of *Sysphincta.*

[90] I have examined a specimen of *P. itoi* through the courtesy of Dr. K. Yasumatsu; this example is from Setagaya, Tokyo (A. Haga leg.).

[91] Wilson has compared the type of *lombokense* with Philippine specimens of *carinifrons;* the latter are much smaller than *lombokense* — according to Wilson's rough guess, only about ¼ the bulk of the *lombokense* type.

[92] In the MCZ there is a dealate female of *mancum* from Quirigua, Guatemala (W. M. Wheeler leg.) and a worker labeled simply, "Guatemala."

[93] Roger's description of *micrommatum* was good for its time, and from certain aberrant features mentioned, especially the contiguous frontal carinae, its identity seems assured with specimens from the following localities: Barro Colorado I., Canal Zone (N. A. Weber leg.); the *cavernicola* type, from Chilibrillo Caves, Panama; from Soledad, Las Villas Prov., Cuba (H. B. Mills leg.); Chichicastle, Tabasco (F. Bonet leg.); and Pueblo Nuevo, near Tetzonapa, Veracruz, Mexico (E. O. Wilson leg.). *S. micrommatum* is apparently widespread but rare in circum-Caribbean lands. With the exception of the *cavernicola* type, the above specimens were all taken in soil-cover berlesates. Borgmeier (1957:118) has recently dealt fully with *P. micrommatum;* he concurs in synonymizing *cavernicola.*

[94] When Roger first described *melinum* from specimens in the Berlin Museum, he recorded them as having come from "Carolina," mentioning that they were "with" the specimens he made the types of *P. croceum.* In view of other evidence, it seems possible that the association of *melinum* and *croceum* specimens in the Berlin Museum may have been the reason why both of these species have been considered to be North American since Roger's time. The record might have come under serious doubt had not Wheeler (1905) reported *P. melinum* (as *Sysphincta melina*) from the collections of P. J. Schmitt, made in southwestern Pennsylvania; this Pennsylvania record has been repeated since (e.g., Creighton, 1950:42), but without anyone's having reviewed the specimens upon which the report was based. I have tried to locate the relevant specimens in all the major collections in the United States and Europe, as well as in Schmitt's collection, now at St. Vincent Archabbey, near Latrobe, Pennsylvania, but the only species I could find collected by Schmitt were *silaceum* and *pergandei* (among Pennsylvania-collected material). In view of the fact that Wheeler did not mention directly any specimens that he had examined and determined as *melinum*, and since no specimens can be found corresponding to this record, the record is open to question. To my knowledge, no one has taken *melinum* in North America for about a century. Of course, such negative evidence must not be over-emphasized; after all, *Discothyrea testacea* Roger, described from the same general area, has now been rediscovered in the southeastern U. S. **[103]**.

However, there is other evidence to be considered. *Melinum* belongs to a group not otherwise known from North America, but which is widespread in temperate Eurasia. In 1895, Emery published reasonably good figures of all castes of *melinum* from the types, and careful examination of these figures reveals no significant difference between the types and the species described by Forel in 1886, and later by Emery himself, as *europaea*. In my opinion, *melinum* and *europaea* represent one and the same species, regardless of where their types came from. Of course, I consider it most likely that the *melinum* types really were collected in Europe, and I do not believe the species occurs naturally in the United States. In view of the greater familiarity of the name *europaea*, it might seem best to attempt to conserve it despite the priority of *melinum*. However, the best characterization of the species up to recent times was that of Emery under the name *melinum* (1895a), and the name *melinum* has been used in numerous publications since. In this case, I favor the prior name.

The other *melinum* group members are *itoi* of Japan, *fialai* of central Europe, and *rossica* of southern Russia. The last two seem to me to be slight geographical variants of *melinum* that are not worth formal names. The characterizations are based on scanty material, and little allowance is made for normal variation within series of "typical" *melinum*, which includes specimens with more convex alitruncal profiles approaching the condition as described and figured for *fialai* and *rossica*. Kratochvíl shows clearly that in *fialai* the palpal formula is 4,3, probably the same for all *melinum*. I have examined a *fialai* eutopotype or paratype through the kindness of Dr. K. Samšinak.

[95] From Santschi's characterizations of *numidicum* and *normandi*, it is not clear that the differences between them are worth species separation. I have not seen any North African material myself, but Wilson has kindly compared for me a specimen in the MCZ Collections (ex Finzi Coll.) from Tirana, Albania (Ravasini and Lona leg.), with a *numidicum* type in the Emery Collection at Genoa. Wilson states that the type has more abundant erect hairs on head and alitrunk than does the

Albanian specimen, a point which apparently also is supposed to distinguish *numidicum* from *normandi*. Probably future study will show that *normandi* represents only slight individual or internidal variation within one species, *numidicum*. The Albanian record is, I believe, the first from Europe for this species, and represents a very considerable range extension; older records are all North African.

[96] A specimen taken by Wilson in a mixture of rotten wood chips and soil between the buttresses of a rain forest tree at Tumnang, Mongi Watershed, 1500 m., Huon Peninsula, New Guinea, agrees well with Emery's description and with a type of Donisthorpe's *Ponera caeca* (nec *Ponera coeca* Santschi) that was compared directly, courtesy of Dr. E. S. Ross of the California Academy of Sciences. The type of Donisthorpe's species came from Maffin Bay, New Guinea.

A single specimen taken in rotten wood in rain forest at Malanda, 800 m., northern Queensland (W. L. Brown leg.), is similar to the Tumnang specimen in size and in its weak, more or less shining sculpture, but has the propodeum gently rounded into the declivity as seen from the side, with only the most obtuse trace of angulation; the color is also lighter, but color means little in this genus.

Another *Proceratium* worker was taken by myself in a small rotten log on the floor of second-growth, *Eucalyptus gigas*-dominated rain forest on the summit of Tamborine Mt., southeastern Queensland, at about 600 m. altitude. The Tamborine worker may well belong to a species apart from *papuanum,* for it is slightly larger than the Tumnang and Malanda specimens, and a little more robust in body build; the petiolar node is slightly lower and thicker, and the sculpture is definitely rougher and opaque over the head and alitrunk, subopaque over the postpetiole. I do not find it expedient to describe a new species from a unique worker in such a tightly-related and little-known group of the genus at this time. However, with the description of *P. stictum* sp. n. below **[99]** added to the above records, it is clear for the first time that *Proceratium* is represented rather well in eastern Australia, nearly or quite south to New South Wales, and that at least two, and possibly even three, species are included in the fauna.

[97] Several workers of *pergandei* were found by myself under a rock in rich mesophytic forest on Great Blue Hill, Milton, Massachusetts, the most northeasterly record for the species yet known. These workers were confined in a plaster nest for two weeks, but could not be induced to feed on various dissected fresh insects offered them; they finally died one at a time. Dr. Wilson tells me that Mr. D. W. Pfitzer of the University of Tennessee once told him that he had observed workers of *pergandei* clustered around a spider egg-case, into which they appeared to be trying to bite their way.

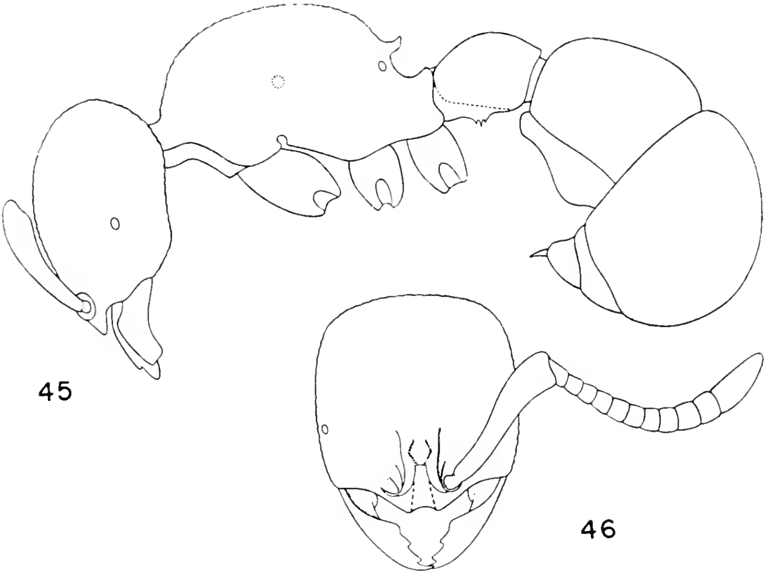
[98] *P. silaceum* is the common species of the genus in North America. Wilson and I have found it feeding on spider and other arthropod eggs in nature, and have maintained it on spider eggs almost exclusively for weeks in the artificial nest. When well supplied with spider eggs, it will have nothing to do with other insect remains, including eggs, larvae or pupae of other ant species, upon which the related species *croceum* was fed by Haskins (1930). In both natural and artificial nests so far examined, the *silaceum* workers tend to store more eggs than they will immediately need. *P. silaceum* ranges northward as far as Lexington and Woburn, Massachusetts, where I have found it extremely rare, nesting under stones. It nests under stones also in moist, wooded hilly sections of eastern Pennsylvania, but in the adjacent lowlands and pine barrens along the Delaware River and in New Jersey, the nests are almost invariably in rotten logs or stumps.

The synonymy of *silaceum*, long a source of confusion, was settled by Creighton in his penetrating study of 1950 (pp. 36-40); his conclusions are followed here.

[99] PROCERATIUM STICTUM sp. nov.

(Figures 45, 46)

Holotype worker: TL (to posterior curve of second gastric segment) 4.7, HL 1.08, HW 0.97, WL (with cervix) 1.48 mm.; CI 90. The general form of the head and body is shown in Figures 45 and 46. Notable is the broad clypeus, separated from the remainder of the cranium by a reasonably distinct suture, and not markedly tilted from the horizontal position. The broad median lobe is bicarinate, the space between the carinae concave and emarginate at the anterior border; this broad lobe corresponds to the much more strongly reduced median process in the *pergandei* and *melinum* group workers and females, and it may well be the homologue of the various modifications of the bicarinate or bidentate clypeus as found in *Monomorium* and many other myrmicine genera. Maxillary palpi with at least three segments (probably four); labial palpi not seen. Antennae 12-segmented, gently incrassate toward apex, not forming a distinct club, but the apical segment much longer and thicker than the rest.



Figures 45 and 46. *Proceratium stictum* sp. nov., holotype worker. Fig. 45, lateral view of head and body. Fig. 46, full-face view of head. Drawings by Dr. F. Y. Cheng.

Mandibles triangular, with oblique apical (masticatory) margins set with four coarse teeth counting the blunt basal angle. Eyes distinct but small, each with a single clear, convex facet, placed a little anterior to the cephalic midlength.

Alitrunk stout, compact, convex above, without traces of dorsal transverse sutures, seen from above broadest across the humeri. Propodeal teeth short but prominently projecting, dorsoventrally flattened and with upturned apices. Propodeal declivity short and broad, not margined above or on sides between upper and lower (metapleural) teeth; the latter teeth broad, laterally compressed, subtriangular. Petiolar node low and paniform; seen from above slightly but distinctly longer than broad and very slightly narrowed in the anterior half, suggesting incipient formation of a peduncle; node anteriorly squarely truncate, with prominent anterodorsal angles opposing the mesial surfaces of the lower propodeal teeth; upper nodal surface evenly convex in both directions; ventral appendage divided into three small, acute teeth.

Basic sculpture of head, alitrunk, petiole and postpetiole densely and irregularly rugulose and with numerous well-spaced, narrow, but deepset punctures with central tubercles at their bottoms, this sculpture boldest on the petiole. Cephalic dorsum inside the eye with punctures indistinct, but the rugules more linear and running obliquely posterolaterad from the region of the antennal insertions; vertex with transverse rugulation. Cervical dorsum and lower propodeal declivity smooth and shining; first gastric segment also smooth and shining, but abundantly sown with small, distinct punctulae. Clypeus very finely rugulose. Mandibles very strongly striate up to apices, which are smooth, their bases with elongate punctures between striae. Legs and antennae very finely and densely punctulate, subopaque. (Legs stout, middle and posterior tibiae each with a single broadly pectinate spur; tarsal claws moderately well developed, simple, as in other *Proceratium* species.)

Pilosity fine and erect, moderately long and abundant, distributed evenly over the entire body, including mandibles, antennae, legs and gula. Pubescence fine, dense, suberect to subreclinate, but not hiding sculpture. Color rich ferruginous red; appendages, mandibles and apical segments of gaster yellowish-ferruginous.

Holotype [MCZ] a unique worker taken at Kuranda, northern Queensland, Australia, in a rotten log in heavy rain forest at an altitude of about 370 m., November 1, 1950 (W. L. Brown).

This species is abundantly distinct from the members of the *pergandei* and *micrommatum* groups, to which it is most similar. The broad median clypeal lobe, the form of the propodeum and its teeth, and the low, elongate petiolar node are key characters, all of which seem to be near the generalized type of the genus. The single-facetted eyes and solidly fused alitrunk are, however, as specialized as these structures ever become within the genus, except that the single facet of the eye, while hyaline, is somewhat larger than the eyes in some other species. It would be most interesting to see the winged sexes and the larva of this apparently very primitive *Proceratium.*

[100] The holotype of *P. toschii* has been examined through the kindness of Prof. Athos Goidanich. I have drawn the middle front section of the head (Fig. 25) and the petiolar node and adjacent segments (Fig. 30) from the holotype; the difference between my figure of the node and Consani's figure 1, no. 2, may be explained by the fact that Consani included in his drawing a large piece of dirt that adhered to the apex of the node and was matted in the hair, appearing to be a part of the node itself.

[101] The four species described from southern Australia are *bidens, crassicornis, leae* and *turtoni.* I have collected workers that compare well with the types of *turtoni* in the National Museum at Melbourne; these specimens come from the Dandenong and Warburton Ranges to the east of Melbourne, where the species is fairly common in the fern gullies as well as under stones in grassy-floored sclerophyll forest at 600-700 m. on the Dandenong summits. I am unable to separate this species, which varies somewhat in color of integument in the queens, from the type of *leae,* and I think that further study may prove them synonymous. The type of *bidens* in the MCZ is a large, dark-colored worker with fairly prominent propodeal angles or teeth that are directed obliquely upward, in this differing from the workers of *turtoni* I have seen. The *bidens* type, however, has a very faint trace left of the promesonotal suture across the alitruncal dorsum, and therefore it could be an ergatoid female. Thus, its specific identity with *turtoni* or *leae,* or with both, is not ruled out. The species *crassicornis,* retaken by W. M. Wheeler at Margaret

River in southwestern Australia, is smaller than *turtoni*, and, at least in the series before me, has eight-segmented antennae. Clark states that the antennae of his types had nine segments, but his figure 4 shows ten segments, indicating that he really did not have a clear count of the segments. The propodeal angles of *crassicornis* workers are also more prominent than are those of *turtoni.*

Clark told me personally in 1950 that he thought *turtoni* and *leae* were probably synonyms. The original collector of *bidens*, Mr. F. E. Wilson, informed me in a conversation that the real type locality of this species was Cement Creek, at about 700 m. altitude, and some miles up into the Warburton Range, away from the town of Warburton.

In addition to the species already discussed, I have found what appears to be another distinct species at One Tree Hill in the Dandenong Range, east of Melbourne. This species is smaller than *turtoni*, has less noticeable pubescence and more distinct propodeal angles, and has seven-segmented antennae (two worker specimens, antennae on both sides counted). I have considered that these differences might be due to allometry within a single species, and continuing to take allometry into account, it seems best to wait until all of the available Australian *Discothyrea* material can be examined in one place before attempting to decide the status of the seven-segmented variant. Most of this material, including some belonging to the MCZ, is still with the Clark Collection at Canberra.

[102] The African species of *Discothyrea* fall into two groups: those with the clypeo-frontal fusion process flat-topped and broad (Fig. 48) — *oculata, sculptior* and *mixta;* and those in which the process forms a simple convex or angular vertical plate — *traegaordhi, hewitti, poweri* and *patrizii.* In the first group, *mixta* is distinct by the characters mentioned in the description **[105]**. Santschi's *sculptior*, described as a variety of *oculata,* may in fact be no more than a variant of that species. I have not seen the types of either *oculata* or *sculptior,* although I have seen a single worker collected by N. A. Weber in Kenya that in most respects answers to the *oculata* description, except that the eyes have less than 30 facets.

In the second group, the species are apparently all very close, and they may, in fact, represent only a single species. *D. poweri*, with its twelve-segmented antennae, seems the most distinctive form, and possibly it is really distinct. Antennal segmentation is particularly dangerous to use as a species character in this group, since Santschi, in his original description of *traegaordhi*, mentioned that segmentation varied between eight and nine in this species, and he later admitted that he had seen balsam preparations of the same species with only six segments, "the others more or less fused and indefinable," according to Bruch (1919: 400). The statement of Weber (1949:3) in differentiating *patrizii* is accordingly of little value; he states, "The eight-segmented antennae separate this species from nine-segmented *hewitti* Arnold, *oculata* Emery, and *traegaordhi* Emery [*sic*], as does also the smaller size. The lobate fused frontal carinae of *hewitti* are produced as a triangular plate." Santschi gave as the original measurement for *traegaordhi* worker, "Long. 1,5 mill.," while Weber gives 1.6 mm. as the length of his *patrizii* worker, so Weber's "smaller size" does not hold, from this information. *D. hewitti* differs from *traegaordhi* only in characters that usually differ between female and worker castes of the same species, so far as their respective descriptions go, so we cannot tell whether they are really distinct or not. The fronto-clypeal plate of these species is probably not so different as the characterizations indicate; the posterodorsal margin is probably always nearly straight and steep, while the anterior margin is broadly rounded. The plate could therefore be variously described as convex, rounded, or even "triangular," according to what feature of the outline is stressed. I have two workers that belong to this complex, which I shall call *D. traegaordhi* at least provisionally, from Ebolowe, Cameroons (A. I. Good).

[103] The New World species so far described number eight, seven of which are keyed by Borgmeier (1949:205); the eighth species was added by Borgmeier (1954:191); see also Borgmeier 1957:122. Smith and Wing (1954) have redescribed and discussed the type of the genus, *D. testacea*, from southeastern North America. Some of the species are described only from females, others only from workers, and the total material so far placed under study is so small that the present arrangement cannot be considered close to final. In separating the species, too much reliance has been placed on antennal segmentation counts, which may be unstable in single species here as elsewhere; the comparative statements on total length are also suspect, because measurements of ants this small have been notoriously inaccurate, due to lack of standardization as well as to poor optical aids. Perhaps four to six good species are represented. A definitive study must await more material and re-examination of the types. One additional word of warning should be heeded in studying *Discothyrea* species, particularly the New World forms: it is entirely possible that some forms now established in the Americas are tramps originating in Africa or Asia. This possibility makes it imperative that the Old World forms all be duly considered in any New World study of the genus.

[104] *D. remingtoni* was described from a single worker from near La Foa, New Caledonia. Wilson has since collected two unique workers of this species or near it; one of these is larger than the type, the other is smaller; the larger specimen has the head as well as the alitrunk dark brown, while in the smaller one, the head is yellow and the alitrunk ferruginous. These specimens also show variation in the convexity of the alitruncal profile, and in the thickness and height of the petiolar node. They may or may not belong to the same species as *remingtoni;* with such limited material, it is impossible to decide. The larger specimen comes from Ciu, near Mt. Canala, 300 m., rain forest soil cover berlesate; the smaller worker is from Mt. Mou, at about 180 m., both localities in New Caledonia.

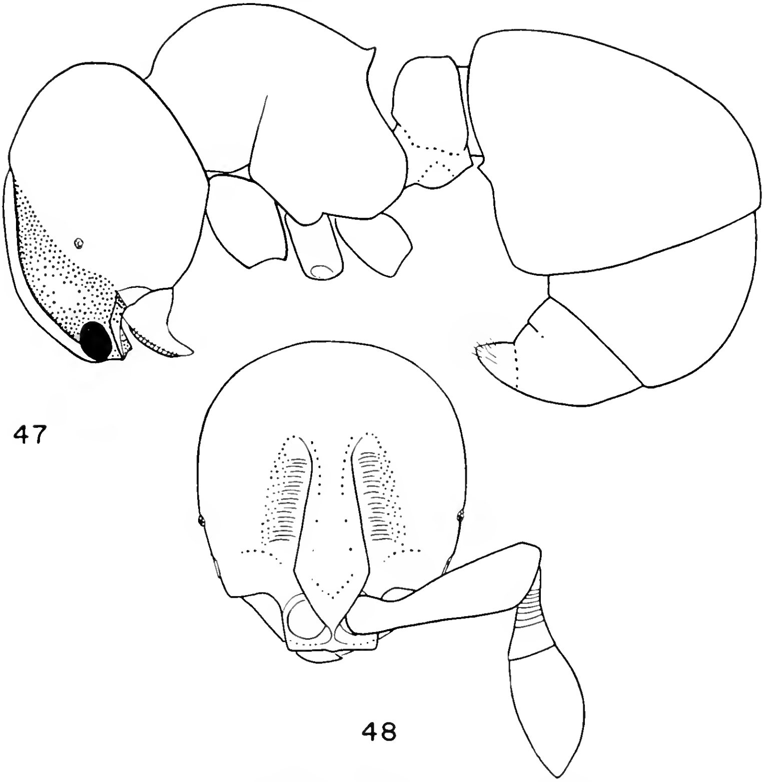
Another, much larger *Discothyrea* was taken by N. L. H. Krauss at an unspecified locality in southeastern New Caledonia (southeast of Noumea); this individual is 2-3 times the bulk of the workers, and has a faint sutural line behind the pronotum, indicating that it may be an ergatoid female. The eyes are larger, and the sculpture of the head is coarsely but shallowly punctate, with coriaceous intervals, the whole surface virtually opaque. This may be the ergatogyne of *remingtoni*, but if so, the caste differences are unusually strong in this species.

[105]

DISCOTHYREA MIXTA sp. nov.

(Figures 47, 48)

Holotype worker: TL 2.4, HL (without mandibles) 0.66, HW 0.59, WL 0.61, scape L 0.43, funiculus L 0.52 mm. Form of head and body shown in Figures 47 and 48. Similar to the species *D. velutina*, *D. bryanti* and *D. oculata*, particularly the last, but smaller in size and with smaller compound eyes. Funiculus 10-segmented, as determined from examination of two funiculi under compound microscope; median segments extremely short, not distinct on the intact specimen as viewed with reflected light.



Figures 47 and 48. *Discothyrea mixta* sp. nov., paratype worker. Fig. 47, lateral view of head and body. Fig. 48, full-face view of head.

Frontoclypeal platform narrower than in *oculata,* with slightly raised borders. Depressed scrobal areas distinct. Palpal segmentation undetermined. Propodeum concave, with a sharp concave margin above joining the propodeal angles, which are subrectangular as seen from above, though acute and dorsally inclined as seen from the side. Petiole thick disciform, as seen from above, truncate anteriorly and posterodorsal border without a distinct tooth or process. Postpetiole longer than broad, ovoid as seen from above, much larger than the succeeding segment.

Head and body densely and rather coarsely punctulate, the punctulae nearly or quite contiguous, but becoming a bit more spaced on the gaster. Scrobal depressions indistinctly and finely transversely striolate, becoming smooth and shining mesad. Mandibles and appendages very finely and superficially punctulate. Integument generally opaque, except for shining bottoms of scrobes and parts of the gastric dorsum, which are feebly shining in some lights.

Body, including mandibles and appendages, covered with dense, fine, very short, whitish decumbent pubescence, becoming more nearly erect on alitrunk, and obliterated from the shining parts of the scrobes.

Color medium ferruginous, appendages more yellowish.

Holotype [MCZ] one of five workers taken together at Bolahun, Liberia (J. C. Bequaert leg.). Paratypes [MCZ, USNM] are the four workers taken with the holotype, one of which has now been destroyed during the course of dissection. Varying only slightly in size, and scarcely at all in form, from the holotype. In the smallest workers (HL 0.63 mm.) the head tends to be a little narrower in proportion to its length, and the sides of the head may be a trifle more nearly straight. In some specimens, the occipital margin is a little straighter than as shown in the figure. Color varies from yellowish ferruginous to medium ferruginous. The lighter specimens show a more or less distinct pair of brownish-tinged longitudinal bands on the gastric dorsum; these may be internal structures showing through the integument.

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INDEX

Included here are names of ant species, genera and higher categories mentioned in the body of the paper. Names mentioned in the Appendix and captions to figures are excluded where direct reference is made to them through bracketed numbers at the primary reference. The pages of the primary references are given in bold face below. Abbreviations for generic names are as follows: Ac. = Acanthoponera, D. = Discothyrea, E. = Ectatomma, G. = Gnamptogenys, H. = Heteroponera, Pr. = Proceratium, R. = Rhytidoponera.

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
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THE SPIDER SUBFAMILY CLUBIONINAE OF THE UNITED STATES, CANADA AND ALASKA (ARANEAE: CLUBIONIDAE)

By Robert J. Edwards

With Twenty-Three Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
June, 1958

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No. 6 — *The Spider Subfamily Clubioninae of the United States, Canada and Alaska (Araneae: Clubionidae)*[1]

By Robert J. Edwards

Introduction. The subfamily Clubioninae has been in a state of confusion for some time, and little has been done to rectify this condition except for the fine paper by Gertsch (1941, Amer. Mus. Novitates, no. 1148) on the *abbotii* group of the genus *Clubiona*. Many of the original descriptions and figures are of no diagnostic value.

During this study it became evident that common and widely distributed species have subspecies. Lack of sufficient material prevented a careful study of these.

Acknowledgments. This study was conducted in the zoological laboratories of the University of Rochester under the supervision of the late Dr. S. C. Bishop, to whom I am greatly indebted for his constant interest, helpful advice and criticism. I am especially grateful to Dr. W. J. Gertsch of the American Museum of Natural History, and to the late Miss E. B. Bryant of the Museum of Comparative Zoology, for the use of the very extensive collections at those institutions and for very valuable suggestions and information. Large collections were also made available for study through the courtesy of Dr. H. K. Wallace, University of Florida; Mr. T. Kurata, Royal Ontario Museum of Zoology; and Dr. H. Dietrich, Cornell University. All figures were drawn by Miss Carolyn Fallon, former staff artist for the Department of Zoology at the University of Rochester.

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[1] This thesis was submitted, in partial fulfillment for the degree of Doctor of Philosophy, to the faculty of the University of Rochester in May 1951. Since it remained unpublished, I received permission from the author to prepare it for publication. It was rewritten, shortened, and keys to the females of the genus *Clubiona*, and plates of the cleared epigyna were added. I want to express my thanks for the help of Prof. K. Cooper; to the editors of the American Midland Naturalist for providing engravings they had made before they knew the paper could not be published there; to Dr. W. J. Gertsch for his valuable suggestions and help in bringing the paper up to date, and reading the revised version; to the J. H. Emerton Legacy for providing funds for publishing the manuscript; to Mrs. Lorna R. Levi for help in making a key to the females; to Mr. R. X. Schick for providing some California specimens. Complete descriptions, additional measurements and collecting data can be found in the original thesis deposited in the University of Rochester library. The extensive bibliography was omitted and references to the two recent catalogs on spiders have been added. Some misprints have been corrected and a few records were added.
— Herbert W. Levi

Methods. Where large numbers of specimens were available, at least twenty mature individuals of each sex were measured for length; with fewer, all specimens were measured. The average length for each species was determined, as well as the extremes for the specimens at hand. For the rest of the measurements, individuals were selected which were as close as possible to the average length. In determining the length of a specimen, the distance between the anterior edge of the clypeus and the tip of the anal tubercle was measured.

An asterisk placed before a record indicates that it was taken from literature. Illustrations were made with a camera lucida, and are not to scale.

Clubionidae

Characteristics. As in the Thomisidae and Heteropodidae, clubionid species have eight eyes in two rows, and tarsi with two terminal claws. These spiders differ from those of the two aforementioned families in body form and in that the legs are not laterigrade. They differ further from the Thomisidae in the possession of a distinct, toothed lower margin of the furrow of the chelicerae. The truncate end of the endite is furnished with a scopula, and the tarsi are usually furnished with bundles of complex terminal tenent hairs. The clubionids have contiguous fore spinnerets, while those of the related family Gnaphosidae are widely separated.

Subfamilies. The four subfamilies are difficult to separate with a key. In the Clubioninae, the labium is usually much longer than wide and extends beyond the middle of the endites whereas in the closely related Liocraninae, the labium is not at all or just barely longer than wide and does not extend beyond the middle of the endites. The Clubioninae have the endites narrower at the middle than at the apex, a characteristic which aids in separating them from the Liocraninae. The Micarinae and Corinninae are readily separated from the Clubioninae in that the apical segment of the posterior spinnerets is always very short, flattened or rounded and usually very indistinct, whereas in the Clubioninae, this structure is conical and always distinct.

Clubioninae

Characteristics. In addition to the characters mentioned above, the margins of the chelicerae are oblique, and all tarsal claws are pectinate in a single row. The female palpus is armed with a single claw. The tarsi are all furnished with bundles of terminal tenent hairs, forming conspicuous cushions beneath the tarsi in the common light-colored species.

There is little difference between the sexes. The males are usually slightly smaller, often with longer and more attenuated chelicerae, somewhat longer and more noticeably spinose legs, and somewhat narrower pars cephalica.

Natural History. All Clubioninae build flat tubular silken retreats on plants, in rolled leaves, on the ground, under stones or rubbish or in moss. Most species are nocturnal, hiding in their nests during the day, hunting and foraging at night. Mating occurs in the retreat where the egg cocoons are kept, the female usually guarding them. In mating, these spiders usually assume the following position: male right side up with the ventral surface of the cephalothorax resting on the dorsum of the cephalothorax of the female, the male facing the posterior end of the female. The male uses the first three pairs of legs to grasp the female around the abdomen and legs, the last pair of legs resting on the ground. The male transfers the sperm by extending the palps around the sides of the female's abdomen at the anterior end. In *Chiracanthium* the mating position is as follows: the female hangs head down from the nest, the male takes up a position under her, facing so that their ventral surfaces are opposed. The male grasps the female with the first two pairs of legs and transfers sperm to the sperm duct openings of the female by means of the palpi.

Key to Genera

1.	Median groove present on thorax	2
1.	No median groove present on thorax	*Chiracanthium*
2.	Posterior row of eyes straight or slightly procurved	3
2.	Posterior row of eyes obviously recurved	*Lauricius*
3.	Anterior median eyes much larger than anterior laterals	*Strotarchus*
3.	Anterior median eyes at most slightly larger than anterior laterals	4

4. First femur with one distal prolateral spine; dorsum of abdomen pale yellow-brown to red-brown .... *Clubiona*
4. First femur with two distal prolateral spines; dorsum of abdomen pale gray to yellow-gray, usually with dark gray stripes and spots .... *Clubionoides*

CHIRACANTHIUM C. Koch

Cheiracanthium C. Koch, 1839, Die Arachniden, vol. 6, p. 9. Type species: *C. punctorium* (Villers).

Description. Carapace without median thoracic groove. Eyes subequal in size. Posterior median eyes farther from laterals than from each other. Chelicerae long and powerful, armed with three contiguous teeth on lower furrow. Leg length 1,4,2,3. Cymbium of male with a slender process directed backward; this process varying in length even in the same species. Coloration pale without conspicuous markings.

Natural History. Nocturnal in habit; during the day they are found in their silken tube retreats on brush and low vegetation.

Misplaced species. Chiracanthium falculum Chamberlin, 1925, is *Aysha velox* (Becker).

Key to Males

1. Tibia of palpus with two rather short apophyses, one dorsal, the other retrolateral in position. (Fig. 7) .... *C. mildei*
1. Tibia of palpus with a single long, retrolateral apophysis. (Fig. 10) .... *C. inclusum*

Key to Females

1. Epigynum a simple oval depression (Fig. 13) .... *C. inclusum*
1. Epigynum with a dark, sclerotized transverse bar, laterad of which are kidney-shaped dark areas (Fig. 14) .... *C. mildei*

CHIRACANTHIUM INCLUSUM (Hentz)

Figures 10-13, 17, 202

Clubiona inclusa Hentz, 1847, Jour. Boston Soc. Nat. Hist., vol. 5, p. 451, pl. 23, fig. 18. (Types from "South Carolina, North Carolina, etc." lost.)

Chiracanthium viride Emerton, 1890, Trans. Connecticut Acad. Sci., vol. 8, p. 184, pl. 5, fig. 12 (♂ type from Saugus, Massachusetts, in the Museum of Comparative Zoology.)

Cheiracanthium inclusum, Roewer, 1955, Katalog der Araneae, vol. 2a, p. 488.

Chiracanthium inclusum, Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1057.

Measurements. Female: Length: 4.80-9.24 mm.; average 7.20 mm. Carapace 3.12 mm. long, 2.28 mm. wide. First femur, 3.48 mm.; patella, 1.20 mm.; tibia 3.00 mm.; metatarsus, 2.94 mm.; tarsus, 1.32 mm. Fourth femur, 3.12 mm.; patella, 1.20 mm.; tibia, 2.10 mm.; metatarsus, 2.70 mm.; tarsus, 0.86 mm.

Male: Length, 4.08-7.56 mm.; average 5.76 mm. Carapace 2.52 mm. long, 1.86 mm. wide. First femur, 4.08 mm.; patella, 1.20 mm.; tibia 4.08 mm.; metatarsus, 4.20 mm.; tarsus, 1.68 mm. Fourth femur, 3.24 mm.; patella, 1.02 mm.; tibia, 2.64 mm.; metatarsus, 3.72 mm.; tarsus, 1.10 mm.

Structure. Median eyes separated by one diameter, the same distance or less from the equal-sized laterals. The second row straight to weakly procurved, medians separated by twice their diameter, same distance from subequal laterals in the female, three-fourths as far in the male.

Natural History. This is the most common member of the Clubioninae in the region. This species has been collected on shrubs and low vegetation in woods which fringe streams and in moist woods. *Chiracanthium inclusum* overwinters mainly in the penultimate instar, maturing in May and June. Adults have been found hibernating under leaves and debris on the ground. The non-agglutinate eggs are laid in a loose mass and are covered only with a thin coat of loosely spun silk as in *Strotarchus*. A female encased in a cocoon with her egg sac was collected in New Jersey on August 18. The egg sac was spherical, measuring 6.70 mm. in diameter, and contained 112 pale yellow, spherical eggs, each measuring about 1.08 mm. in diameter. Another female was collected in a nursery composed of a folded blade of a broad-leafed grass, on August 17, in Florida. With the female were found 34 spiderlings.

Distribution. All but the most northern parts of the United States; Mexico and West Indies, South America.

Records. Alabama: Grove Hill; Moundsville; Birmingham; Auburn; Clearcreek; Pea Riv. Project; Silver Hill. *Arizona:* Mount Lemmon; Elgin; Flagstaff; Sabino Canyon; Tucson; *Grand Canyon; *Bright Angel; Prescott. *Arkansas:* Hope; Washington Co. *California:* Santa Barbara; *Berkeley; Fresno; Los Angeles Co.; *Paint Seer, *Live Oak Park; *Mill Valley; *Claremont; Los Angeles; Yosemite Natl. Pk.; Felton; Fort Seward; Tracey; Castro Valley; Riverside; Needles. *Colorado:* Cameron. *Connecticut:* *Bethany; *Cheshire; *Colchester; *Killingworth; *New Haven; Northford; *South Meriden; *Voluntown. **District of Columbia. Florida:* *Runnymede; *Punta Gorda; *Altoona; *Enterprise; *Miami; *Winter Park; nr. Oldtown; Big Tree, nr. Longwood; Gainesville; Ocala; Dade Co.; Olney; Lake Placid; Arcadia; Indian Town; nr. Sarasota; Lido Key, Sarasota; Okeechobee, Titusville; Orlando; Sanford; Lake City; Naples; Tamiami Trail, Pinecrest; Clearwater; MacDill Field, Archbold Biol. Sta.; Sebastian; Tallahassee; Wakulla Springs. *Georgia:* Waycross; Thomasville; *Sardes to Waynesboro; *Burke County; *E. and W. of Sylvania; Okefenokee Swamp; *Gainesville; *W. of Athens; *S. of Lake Park. *Illinois:* *Waukegan; Kankakee Co.; Pulaski Co. *Indiana:* *Vincennes. *Louisiana:* Shreveport; Kisatchie Natl. For.; Sorrento; East Baton Rouge Par.; Lake Charles; Tallulah; *Baton Rouge. *Maryland:* Wicomico Co. *Prince Georges Co. *Massachusetts:* *Nantucket; *Blue Hill; *Sharon; *Charlestown; *Hyde Park; *Dedham; *Saugus. *Michigan:* Sanford. *Mississippi:* E. of Morton; Centerville; Agricultural College; Holly Springs; Lucedale; Hattiesburg; Kessler Field. *Nebraska:* Valentine. *New Jersey:* Orange Mountains; Lakehurst. *New Mexico:* *Mesilla Park. *New York:* Flushing, L. I.; Coram; Cranberry Lake; Amagansett; Greenport. *Nevada:* Las Vegas. *North Carolina:* Raleigh; Woodsville; *Southern Pines. *Ohio:* Columbus; Ceder Point. *Oklahoma:* Carter Co.; Norman. *Oregon:* The Dalles. *South Carolina:* 10 mi. S. of Columbia; Bethune. *Tennessee:* Irving; Knoxville. *Texas:* 32 mi. SW. of Laredo; Harlingen; Jourdanton; Texas City; Houston; Pharr; Monte Cristo; swamp 9 mi. W. of Athens; Victoria; SE. of Oak Cliff, Dallas; Livingston; Raymondville; 4 mi. SE. of Edinburg; 5 mi. E. of Edinburg; Edinburg; Brownsville; Bon Wier. *Utah:* Bluff; Salt Lake City; Zion Natl. Pk.; Brigham; Big Cottonwood Canyon. *Washington:* Mountain Lake.

CHIRACANTHIUM MILDEI L. Koch

Figures 7-9, 14, 16, 203

Cheiracanthium mildei L. Koch, 1864, Abhandl. Naturhist. Gesell. Nürnberg, vol. 3, p. 144. (Types from Meran, Southern Tyrol.) Bryant, 1951, Psyche, vol. 58, p. 120. Roewer, 1955, Katalog der Araneae, vol. 2a, p. 480.

Chiracanthium mildei, Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1061.

Measurements. Female: Length, 9.84 mm. Carapace 3.66 mm. long, 2.64 mm. wide. First femur, 4.32 mm.; patella, 1.44 mm.; tibia, 3.84 mm.; metatarsus, 3.96 mm.; tarsus, 1.38 mm. Fourth femur, 3.84 mm.; patella, 1.32 mm.; tibia, 2.58 mm.; metatarsus, 3.72 mm.; tarsus, 0.96 mm.

Male: Length, 7.20 mm. Carapace, 3.48 mm. long; 2.40 mm. wide. First femur, 5.28 mm.; patella, 1.56 mm.; tibia, 5.58 mm.; metatarsus, 6.06 mm.; tarsus, 2.04 mm. Fourth femur, 4.25 mm.; patella, 1.44 mm.; tibia, 3.60 mm.; metatarsus, 5.16 mm.; tarsus, 1.14 mm.

Description. The carapace and eye arrangement as in *C. inclusum.*

Distribution. Mediterranean countries, probably introduced in this country.

Records. Alabama: Colbert Co., ♀. *Connecticut:* *New Britain, ♂, ♀. *Massachusetts:* *Cambridge, ♀. *New Jersey:* Newark. *New York:* New Rochelle, ♀. *Utah:* Black Pavilion, Salina, ♀ (W. J. Gertsch).

LAURICIUS Simon

Lauricius Simon, 1888, Ann. Soc. Ent. France, vol. 8, p. 208. Type species: *L. hemicloeinus* Simon.

Description. Carapace relatively flat and broad, with median groove well developed. Eyes subequal in size. Anterior medians closer to laterals than to each other; posterior row distinctly recurved and eyes equidistantly placed. Chelicerae short and robust, swollen at base.

LAURICIUS HOOKI Gertsch

Figures 4-6, 18, 204

Lauricius hemicloeinus, Gertsch, 1935, Amer. Mus. Novitates, no. 792, p. 29. Gertsch, 1935, *ibid.*, no. 805, p. 111, figs. 16-19. (both err. det.).

Lauricius hooki Gertsch, 1941, *ibid.*, no. 1147, p. 20. (♀ type from 17 mi. NE. of Whiteriver, White Mtns., Arizona, in the American Museum of Natural History.)

Measurements. Female: Length, 10.68-18.00 mm.; average, 13.86 mm. Carapace 5.52 mm. long, 4.80 mm. wide. First femur, 4.80 mm.; patella, 2.04 mm.; tibia, 3.84 mm.; metatarsus, 3.48 mm.; tarsus, 1.80 mm. Fourth femur, 5.40 mm.; patella 2.16 mm.; tibia, 3.96 mm.; metatarsus, 4.44 mm.; tarsus, 1.86 mm.

Male: Length, 10.08-10.80 mm.; average 10.49 mm. Carapace 4.92 mm. long, 3.84 mm. wide. First femur, 4.68 mm.; patella, 2.26 mm.; tibia, 4.68 mm.; metatarsus, 4.35 mm.; tarsus, 2.30 mm. Fourth femur, 5.06 mm.; patella, 2.00 mm.; tibia, 4.80 mm.; metatarsus, 5.20 mm.; tarsus, 2.38 mm.

Description. Chelicerae armed with two teeth on lower margin. First pair of legs spined: femur 1-1-0 dorsal, 0-1-1 retrolateral, 1-1-1 prolateral; tibia 2-2-0 ventral; metatarsus 2-2-0 ventral. Carapace dark red-brown with darker margins and sutures. Chelicerae, labium dark red-brown. Sternum yellow-brown. Abdomen brownish gray. The male has longer chelicerae and legs than the female.

Comments. Although this species differs from the Mexican *L. hemicloeinus* by its smaller size and by having a shorter scape in the epigynum, it is quite possible that *L. hooki* is a subspecies of *L. hemicloeinus.*

Distribution. Arizona, New Mexico.

Records. Arizona: Santa Catalina Mtns., ♀, ♂; 17 mi. NE. of Whiteriver, ♀; Beaver Creek, ♂; Santa Rita Mtns., ♀; *Mount Lemmon, ♀; *Water Camp, ♂, ♀. *New Mexico:* Camp Mary White, Otero County, ♂, ♀.

STROTARCHUS Simon

Strotarchus Simon, 1888, Ann. Soc. Ent. France, vol. 8, p. 210. Type species: *S. nebulosus* Simon.

Bedriacum O. P. Cambridge, 1898, Biologia Centrali Americana, Araneidea, vol. 1, p. 250. Type species: *B. praedator* O. P. Cambridge.

Marcellina Bryant, 1931, Psyche, vol. 38, p. 103. Type species: *Clubiona piscatoria* Hentz.

Description. Carapace with a long thoracic groove. Clypeus high. Anterior median eyes much larger than others. Ocular quadrangle slightly wider in front. Posterior eyes subequal in size and equidistant, slightly procurved. Chelicerae robust. Anterior legs longer than posterior.

STROTARCHUS PISCATORIUS (Hentz), new combination

Figures 1-3, 15, 205

Clubiona piscatoria Hentz, 1847, Jour. Boston Soc. Nat. Hist., vol. 5, p. 450, pl. 23, fig. 15 (Types from Alabama lost).

Marcellina piscatoria, Roewer, 1955, Katalog der Araneae, vol. 2a, p. 542.

Measurements. Female: Length 7.60-9.20 mm.; average 8.32 mm. Carapace 4.00 mm. long, 2.96 mm. wide. First femur, 4.16 mm.; patella, 1.68 mm.; tibia, 3.44 mm.; metatarsus, 3.60 mm.; tarsus, 1.60 mm. Fourth femur, 4.00 mm.; patella, 1.44 mm.; tibia, 2.88 mm.; metatarsus, 3.28 mm.; tarsus, 1.28 mm.

Male: Length. 7.20-8.72 mm.; average 8.08 mm. Carapace, 3.60 mm. long, 2.68 mm. wide. First femur, 4.24 mm.; patella, 1.44 mm.; tibia, 4.00 mm.; metatarsus, 4.00 m.; tarsus, 1.68 mm. Fourth femur, 3.76 mm.; patella, 1.28 mm.; tibia, 2.96 mm.; metatarsus, 3.68 mm.; tarsus, 1.32 mm.

Description. Anterior median eyes separated by slightly less than their diameter, closer to laterals. Second row slightly procurved. Posterior medians separated by one and three-fourths diameters, slightly closer to laterals. Median ocular quadrangle slightly wider than long, narrower behind. Two widely separated teeth on lower margin of chelicerae.

First femur with 1-1-0 dorsal spines and two distal prolaterals: tibia with 0-2-0 ventral spines and a single distal prolateral in female; 0-1-1 in male; metatarsus with 2-2-1 ventral spines and 0-1-0 prolaterals. Spines short and dark brown in color. Carapace light brown. Chelicerae dark red-brown. Sternum yellow-brown with dark brown margins. Abdomen pale yellow-gray.

Comments. The cymbium of the male palpus is greatly elongated (Figs. 1, 2). The posterior spinnerets are considerably longer in this species than in most others of this subfamily.

Natural History. This species has been collected from very thin silken sacs under stones, and from trees with the use of a flashlight at night. Specimens of both sexes in the penultimate instar were collected by Kaston May 8th, these individuals maturing between the 12th and the 18th of May. Kaston also observed the copulation of this species in the laboratory (1938, Canad. Ent., vol. 70, p. 12). The copulatory act took place by one pair on two successive days, the female tolerating the male in an adjacent silk bag between mating acts. No males were in evidence by the 4th of July and several females were guarding the egg sacs. The eggs are pale yellow in color, semiagglutinate, and loosely grouped together in a thin transparent silken cocoon. The egg sacs are usually found on the under-side of stones. One such egg sac was found to contain 46 spherical eggs and another 47 eggs, each of which had a diameter of about 1.08 mm. Hentz claimed that this spider made an even web like the Agelenidae. When disturbed, these spiders feign death, making no attempt to escape.

Records. Alabama: Alberta City; *Auburn; *Opelika. *Connecticut:* *Portland; *Redding; *Southbury; Stamford; *North Stamford. *Florida:* Jackson County; Giles County; N. of Winter Park. *Georgia:* *Millen; NE. of Sylvania. *Louisiana:* Kisatchie Natl. For. *Maryland:* *College Park. *Massachusetts:* *Newton. *New Jersey:* Oakland.

STROTARCHUS PLANETICUS, new species

Figs. 159, 179, 206

Type. Female holotype from Laguna Madre, 25 miles southeast of Harlingen, Texas, June 13, 1945 (D. E. Hardy and V. L. Wooley), in the American Museum of Natural History. This specimen was taken from the nest of *Neotoma micropus* Baird.

Measurements. Female: length 8.08 mm. Carapace 3.60 mm. long, 2.64 mm. wide. Abdomen, 4.72 mm. long, 2.80 mm. wide. First femur, 3.90 mm.; patella, 1.44 mm.; tibia, 3.44 mm.; metatarsus, 3.28 mm.; tarsus, 1.60 mm. Fourth femur, 3.84 mm.; patella, 1.20 mm.; tibia, 2.80 mm.; metatarsus, 2.48 mm.; tarsus, 1.20 mm.

Description. Clypeus equal in height to diameter of an anterior median eye. First row of eyes weakly recurved as seen from the front. The median eyes separated by slightly more than the diameter of one of them, less than half as far from the subequal lateral eyes. The second row of eyes gently procurved, the median eyes separated by one and a half diameters, nearer to slightly smaller lateral eyes. Chelicerae armed with two rather widely spaced teeth on lower margin. First femur with 1-1-0 dorsal spines and two distal prolateral spines; tibia with 2-2-0 ventral spines and 0-1-1 prolateral spines; metatarsus with 2-2-1 ventral spines and 1-1-2 prolateral spines. All spines are short and dark brown in color.

Carapace light yellow-brown posteriorly and on sides, light brown anteriorly shading to a light red-brown in pars cephalica. Chelicerae dark brown. Labium and endites brown except for small pale yellow area on distal margin of endites. Sternum light yellow-brown except for brown margins. First pair of coxae longest; concolorous with sternum; other coxae pale yellow-brown with thin, dark brown proximal margins. First two pairs of legs light amber, the posterior pairs somewhat lighter in color. Coxae and legs clothed with rather long sub-erect hairs and scattered erect dark setae. Abdomen pale gray-white and unmarked, clothed with recumbent dark hairs and scattered suberect bristles which are most numerous and longest at base of abdomen.

Diagnosis. This species is closely related to *Strotarchus piscatorius* (Hentz), but is readily distinguished, in that the anterior median eyes are considerably smaller in *S. planeticus.* The median ocular quadrangle of *S. planeticus* is broader behind, whereas it is narrowed behind in *S. piscatorius.* The shape of the opening of the epigynum differs in the new species, as do other details (Fig. 159).

CLUBIONOIDES new genus

Type. Clubionoides (fem.) has the type species *Clubiona excepta* L. Koch.

Description. Carapace with a median groove. Posterior eyes equidistant, or medians closer to laterals. Fourth legs longer than first. The first femur with 1-1-1 dorsal spines and 2 distal prolateral; tibia with 2-2-0 ventral spines; metatarsus with a single pair of ventral spines at base. Second femur with 1-1-1 dorsal spines and one distal, prolateral; tibia usually with 1-2-0 ventral spines; sometimes 2-2-0 (as in *Clubiona*); metatarsus with 2-0-0 ventral spines. Third tibiae with 1-1-1 ventral spines (instead of 1-1-0 as in *Clubiona*); metatarsi 2-2-2 ventral spines (instead of 2-0-2 of *Clubiona*). Hind spinnerets longer than fore spinnerets. North American species all pale with dorsum of abdomen usually distinctly marked by gray to gray-brown chevrons and stripes.

Diagnosis. Male palpi with a single, simple flat retrolateral apophysis, variable in shape (Figs. 24, 29, 33, 34). Bulb also distinctive and different from that of *Clubiona;* the embolus and conductor being relatively short and often hidden. The epigynum has a free anterior median scape. Receptacles near posterior edge of epigynum rather than anterior as in *Clubiona.*

Distribution. Most species of this genus occur in Central and South America: there are only five known species north of Mexico.

Key to Males

1. Tibial apophysis of palpus crescent-shaped; bulb spherical as seen from the side . . . . *C. texana*
1. Tibial apophysis of palpus not crescent-shaped; bulb as viewed from side rather flattened 2
2. Tibial apophysis of palpus quite broad, with a gently rounded ventral division and a sharply pointed dorsal division . . . . *C. excepta*
2. Tibial apophysis of palpus not as above 3
3. Tibial apophysis of palpus forming a single point directed distally; cymbium with a heavy spine on ventral surface at distal end . . *C. mulaiki*
3. Tibial apophysis of palpus very small and forming a single point directed somewhat dorsally; cymbium without heavy spine . . *C. dorothea*

Key to Females

1. Epigynum with a very short anterior median scape 2
1. Epigynum with a distinct longer anterior median scape 3
2. Epigynum with openings of sperm ducts near anterior end; oval-shaped receptacles near posterior edge of epigynum . . . . *C. dorothea*
2. Epigynum with hidden sperm duct openings; main portion of epigynum a truncated triangular depression . . . . *C. mulaiki*

3. Epigynum with sperm duct openings near posterior edge; median scape not finger-like 4
3. Epigynum with sperm duct openings near center; median scape long and comparatively narrow, finger-like . . . . *C. excepta*
4. Median scape of epigynum bi-lobed behind; sperm duct openings flattened ovals . . . . *C. texana*
4. Median scape of epigynum bluntly rounded behind and with a sclerotized, dark posterior edge . . . . *C. kohlsi*

CLUBIONOIDES EXCEPTA (L. Koch)

Figures 19, 31-33, 211

Clubiona pallens Hentz, 1847, Jour. Boston Soc. Nat. Hist., vol. 5, p. 449, pl. 23, fig. 13. (Syntypes from North Carolina and Alabama, lost.) Name preoccupied by *Clubiona pallens* Hahn, 1834.

Clubiona excepta L. Koch, 1886, Die Arachniden-Familie der Drassiden, p. 300, pl. 22, fig. 191. (Types from Baltimore, Maryland.) Roewer, 1955, Katalog der Araneae, vol. 2a, p. 514. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1123.

Measurements. Female: Length 5.28-8.56 mm.; average 6.96 mm. Carapace 3.20 mm. long, 2.19 mm. wide. First femur, 2.16 mm.; patella, 1.08 mm.; tibia, 1.56 mm.; metatarsus, 1.26 mm.; tarsus, 0.72 mm. Fourth femur, 2.64 mm.; patella, 1.04 mm.; tibia, 1.80 mm.; metatarsus, 2.46 mm.; tarsus, 0.72 mm.

Male: Length 5.04-6.96 mm.; average 5.92 mm. Carapace 2.75 mm. long, 1.92 mm. wide. First femur, 2.10 mm.; patella, 0.90 mm.; tibia, 1.74 mm.; metatarsus, 1.38 mm.; tarsus, 0.66 mm. Fourth femur, 2.58 mm.; patella, 0.96 mm.; tibia, 1.83 mm.; metatarsus, 2.46 mm.; tarsus, 0.75 mm.

Description. Anterior median eyes separated by one-half to two-thirds diameter, closer to laterals. Posterior median eyes separated by two to two and one-fourth diameters, closer to laterals. Chelicerae with three teeth on lower furrow.

Natural History. This species is usually found under stones, loose bark, dead leaves and other ground debris. These spiders overwinter in the penultimate instar or in the mature state. Eggs which were laid in June and July had young emerging in late July and August. Eggs are ivory in color, non-agglutinate and spherical in shape, measuring approximately 0.92 mm. in diameter. The egg sacs are nearly spherical in shape and are made of loosely woven silk which is usually covered with small pieces of debris. Kaston reports one such egg sac as having measured 7.5 by 8.5 by 7.0 mm., and containing 95 spiderlings. One egg sac was found to contain 56 eggs, and two others contained 85 and 36 spiderlings respectively.

Distribution. Ontario, eastern United States, West Indies.

Records. Alabama: Tuscaloosa; Dauphin Island, Mobile; Clear Creek; Cheata State Park; E. of Opelika; *Gallant Co. *Arkansas:* Washington Co. *Connecticut:* Orange; New Haven; Westville; Shelton; Windsor Locks; Branford; North Stamford; South Meriden; Cheshire. *Delaware:* Wilmington. *District of Columbia:* Washington. *Florida:* Liberty Co.; Alachua Co.; Lake Hall, Royal Palm Park; Green Cover Springs; Winter Park. *Georgia:* Okefinokee Swamp; *Burke Co.; *N. of Sylvania; *3 mi. SE. of Savannah; *Lavonia to Toyston; *Demorest; *Clayton to Tallulah Falls. *Illinois:* Gillespie; Bell Smith Springs; West Port; Troy; Collinsville; Saint Anne; *Waukegan Flats. *Indiana:* Valparaiso; *Richmond; *8 mi. S. of Momence; *Smith. *Louisiana:* Grant Par. *Maryland:* Baltimore; Beltsville; Suitland; *Prince Georges Co. *Massachusetts:* Concord; Holliston; *Salem; *Dedham; *Nantucket; *Swampscott; *Brookline; *Clarendon Hills; *Sharon. *Michigan:* Porcupine Mts. *Minnesota:* Minneapolis. *Mississippi:* Lucedale; Leaksville; Hattiesburg. *Nebraska:* *Valentine; *Plattsmouth. *New Hampshire:* Three Mile Isl., Lake Winnepesaukee. *New Jersey:* Ramsey; Lakehurst; Morganville. *New York:* Sloatsburg; Lake Sebago; Interstate Park; Saugerties; Coram, L. I.; *Ithaca; Flushing, L. I.; Mastic, L. I.; Enfield Glen; Lake George; Sterlington; Lake Charlotte; Rockville Center; Oak Ridge; *Canandaigua Lake; Voorheesville; Juanita Island, Lake George; Elizabeth Island; *Shelving Rock; Wappingers Falls; Baiting Hollow, L. I.; *Long Island. *North Carolina:* Raleigh; Bridgewater; Blowing Rock; *Swannanoa Valley; *Oteen. *Ohio:* *Rockbridge; *Columbus. *Rhode Island:* *Providence. *Tennessee:* Montvale; 30 mi. W. of Knoxville; 30 mi. N. of Nashville. *Texas:* Houston; Denton Co.; 12 mi. N. of Temple. *Virginia:* Mountain Lake, Siles Co. *Wisconsin:* Adams Co.; Door Co.; Jackson Co.; Vernon Co.; Washburn Co.; Trempeleau Co.

Ontario: Pointe au Bavil; Point Pelee; Franks Bay, Lake Nipigon; Minaki; Tioncky Point; 3 mi. N. of Wellington; Jones Beach; Mindemoya, Manitoulin Lake.

CLUBIONOIDES KOHLSI (Gertsch and Jellison)
Figures 21, 37, 209

Clubiona kohlsi Gertsch and Jellison, 1939, Amer. Mus. Novitates, no. 1032, p. 10, fig. 3. (♀ type from Hamilton, Ravalli Co., Montana, in the American Museum of Natural History.)

Measurements. Female: Total length, 12.80 mm. Carapace 6.00 mm. long, 4.00 mm. wide. First femur, 3.68 mm.; patella, 1.44 mm.; tibia, 3.20 mm.; metatarsus 2.88 mm.; tarsus 1.44 mm. Fourth femur, 4.00 mm.; patella, 2.08 mm.; tibia, 3.84 mm.; metatarsus, 4.64 mm.; tarsus, 1.76 mm.

Description. Anterior eyes one-half their diameter apart. Posterior median eyes separated by two and a half times their diameter, closer to the larger laterals. Chelicerae robust with four teeth on posterior margin, one nearest base of fang the largest. Carapace reddish brown, chelicerae dark brown, coloration otherwise like other *Clubionoides.* Epigynum illustrated by Figure 37.

Comments. The general structure and coloration indicate a close relationship with *C. tigrina* (Cambridge). The epigynum of *kohlsi* has the free median scape much broader and more rounded than is the case in *tigrina.*

Distribution. This species is known only from a single specimen taken in Montana.

CLUBIONOIDES MULAIKI (Gertsch)
Figures 20, 24-26, 207

Clubiona mulaiki Gertsch, 1935, Amer. Mus. Novitates, no. 805, p. 11, figs. 22-24. (♀ type from 7 mi. E. of Edinburg, Texas, in the American Museum of Natural History.)

Measurements. Female: Length 3.45-5.46 mm.; average 4.26 mm. Carapace 1.98 mm. long, 1.44 mm. wide. First femur, 1.50 mm.; patella, 0.60 mm.; tibia, 1.20 mm.; metatarsus, 0.74 mm.: tarsus, 0.54 mm. Fourth femur, 1.82 mm.; patella, 0.84 mm.; tibia, 1.26 mm.; metatarsus, 1.38 mm.; tarsus, 0.54 mm.

Male: Length 3.18-4.20 mm.; average 3.81 mm. Carapace 2.13 mm. long, 1.50 mm. wide. First femur, 1.70 mm.; patella, 0.83 mm.; tibia, 1.37 mm.; metatarsus, 1.03 mm.; tarsus, 0.63. Fourth femur, 2.10 mm.; patella, 0.83 mm.; tibia, 1.43 mm.; metatarsus, 1.70 mm.; tarsus, 0.53 mm.

Description. Anterior median eyes separated by one-half to almost one diameter, closer to the larger laterals. Posterior medians almost two of their diameter apart, closer to laterals. Chelicerae of female armed with 3 or 4 contiguous teeth on lower margin, those of male with 5 small teeth. Epigynum illustrated by Figure 26, palpus by Figures 24-25.

Comments. The general structure and coloration are in close agreement with *C. dorothea;* only the genitalia differ.

Records. Texas: 7 mi. E. of Edinburg, ♀; Edinburg, ♂; 15 mi. SW. of Harlingen, ♀; Rio Grande City, ♀; Cameron Co., ♂, ♀; 5 mi. NW. of Hidalgo, ♂; 1 mi. NW. of Rio Hondo, ♀, ♂; N. of McCook, ♀.

CLUBIONOIDES TEXANA (Gertsch)

Figures 23, 27-30, 210

Clubiona texana Gertsch, 1933, Amer. Mus. Novitates, no. 637, p. 7, fig. 16 (♀ type from Brownsville, Texas, in the American Museum of Natural History).

Measurements. Female: Length 9.20-11.66 mm.; average 10.07 mm. Carapace 4.64 mm. long, 3.04 mm. wide. First femur, 3.04 mm.; patella, 1.76 mm.; tibia, 2.40 mm.; metatarsus, 2.04 mm.; tarsus, 1.00 mm. Fourth femur, 4.24 mm.; patella, 1.72 mm.; tibia, 2.80 mm.; metatarsus, 3.92 mm.; tarsus, 1.04 mm.

Male: Length 7.60-10.48 mm.; average 8.81 mm. Carapace 4.28 mm. long, 2.84 mm. wide. First femur, 3.36 mm.; patella, 1.60 mm.; tibia, 2.64 mm.; metatarsus, 2.16 mm.; tarsus, 1.08 mm. Fourth femur, 4.00 mm.; patella, 1.52 mm.; tibia, 2.80 mm.; metatarsus, 3.60 mm.; tarsus, 1.12 mm.

Description. Anterior median eyes their radius apart, closer to slightly smaller laterals. Posterior medians twice their diameter apart, closer to laterals. Chelicerae of female armed with 4 teeth, those of male with 5 teeth on lower margin. Epigynum illustrated by Figure 30, palpus by Figures 27-29.

Comments. This species is closest to *C. sericea* (Cambridge).

Distribution. Texas: Laguna Madre, ♂, ♀; N. of McCook, ♂, ♀; Corpus Christi ♀; S. of Pharr, ♀; Edinburg, ♂, ♀ (many records); NW. of Hidalgo, ♀; Rio Grande City, ♂; *Brownsville, ♀.

CLUBIONOIDES DOROTHEA (Gertsch)
Figures 22, 34-36, 208

Clubiona dorothea Gertsch, 1935, Amer. Mus. Novitates, no. 805, p. 12, fig. 25. (♀ type from Edinburg, Texas, in the American Museum of Natural History).

Measurements. Female: Length 3.24-4.32 mm.; average 3.70 mm. Carapace 1.80 mm. long, 1.38 mm. wide. First femur, 1.20 mm.; patella, 0.66 mm.; tibia, 0.84 mm.; metatarsus, 0.72 mm.; tarsus, 0.42 mm. Fourth femur, 1.74 mm.; patella, 0.63 mm.; tibia, 1.14 mm.; metatarsus, 1.41 mm.; tarsus, 0.39 mm.

Male: Length 4.14-4.74 mm.; average 4.50 mm. Carapace 2.10 mm. long, 1.50 mm. wide. First femur, 1.50 mm.; patella, 0.70 mm.; tibia, 1.20 mm.; metatarsus, 0.78 mm.; tarsus, 0.42 mm. Fourth femur, 1.82 mm.; patella, 0.75 mm.; tibia, 1.28 mm; metatarsus, 1.71 mm.; tarsus, 0.48 mm.

Description. Anterior median eyes separated by three-fourths their diameter, closer to the larger, oval laterals. Posterior medians two diameters apart, closer to the slightly larger laterals. Chelicerae with 3 teeth on lower margin in female, with two contiguous teeth in male.

Comments. The pale palpus (Figs. 34-35) resembles *C. mulaiki;* the epigynum (Fig. 36) is very distinct.

Records. Texas: *Edinburg, ♀; S. of Pharr, ♂, ♀ (sev. collections).

CLUBIONA Latreille

Clubiona Latreille, 1804, Nouv. Dict. Hist. Nat., vol. 24, p. 134. Type species: *Clubiona pallidula* (Clerck).

Elaver Cambridge, 1898, Biologia Centrali Americana, Araneidea, vol. 1, p. 238. Type species: *Elaver tigrina* Cambridge.

Description. Small or medium size, usually pale or tawny with darker brown coloration at the anterior end of carapace and on chelicerae. Abdomen clothed with silky white or pale yellow pubescent hairs which give it a soft silky appearance without hiding color of surface. Most are without distinct markings, although a few have abdomen marked with a median stripe or with a series of posteriorly directed chevrons.

Carapace wide in front, especially in females. Thoracic groove present. Posterior row of eyes wider than anterior row; eyes of posterior row nearly equidistant, or medians farther from each other than from laterals. Chelicerae of females usually robust and swollen at base. Males, chelicerae generally longer, attenuated, sometimes with keels along antero-median face, lateral face, or both. Lower margin of furrow of chelicerae armed with two to five teeth, although number is variable even in same species. Upper margin of furrow of chelicerae usually with five teeth, but number may vary from three to six. Posterior pair of legs longer than first pair; all tarsi armed with pair of long claws. First two tibiae and metatarsi with paired spines beneath (see comparisons in preceding genus); usually two pairs but sometimes one beneath tibia, and a single pair beneath metatarsus. Abdomen truncated at base, tapering behind.

Natural History. These spiders live in flat tubular nests of silk, with an opening at either end, which they spin under bark or stones or in rolled leaves. Most species are sedentary in habit.

Misplaced and doubtful species: Species misplaced in *Clubiona* and not now in genera revised in this paper are: *C. albens* Hentz (*Anyphaenella*); *C. celer* Hentz (*Anyphaena*); *C. fallens* Hentz (*Anyphaena*); *C. gracilis* Hentz (*Aysha*); *C. sublurida* Hentz (*Anyphaena*); *C. tranquilla* Hentz (*Trachelas*); *Clubiona immatura* Hentz is not recognizable, the types having been lost. *Clubiona frigidula* Thorell described from Labrador cannot be recognized; the deposition of the type is not known.

Comments. In this paper, the genus *Clubiona* is divided into four groups. Groups I-III are made up of species the details of whose genitalia indicate that they form natural units. Group IV is set up as a convenience, containing two species which do not appear to be closely related, either between themselves or with members of the first three groups. Group I is further divided into two divisions.

Group I: Males with single heavy retrolateral carpoblem on tibia of palpus. The relatively short embolus lies in a shallow groove on median division of tegulum. Females of Group I have epigyna which are usually broader than long, oval or rounded sperm duct openings being either lateral in position near posterior edge of epigynum, or else ducts open by a common opening which is medial in position at posterior edge of epigynum. In *C. mimula*, the sperm duct openings are separate, although close together near midline at posterior edge of epigynum. Females of this species are readily distinguished from those of Group III since the sperm ducts travel directly back to the openings instead of curving around near lateral edges of epigynum. Division A: *C. moesta, C. pygmaea, C. trivialis, C. janae.* Division B: *C. praematura, C. furcata, C. obesa, C. mixta, C. chippewa, C. bryantae, C. mimula, C. spiralis, C. rileyi*).

Group II. Darker in color than other groups; dorsum of abdomen marked by characteristic patterns. Retrolateral apophysis of tibia of male palpus with two or three divisions; the ventral division always longest, sharply pointed distally, and with a notch on dorsal edge at varying distances from tip. Embolus, unlike other species of *Clubiona*, has tip extending distally and not curving toward base of palp and lying in a groove on tegulum. Epigyna of females broader than long, and sperm duct openings usually obscured by posterior edge of epigynum. (*C. canadensis, C. californica, C. norvegica, C. kulczynskii.*)

Group III. With broad pars cephalica; posterior eyes farther apart; ocular quadrangle much broader than high, usually greatly narrowed in front; species small. This group is quite readily separated from other species of *Clubiona* by characteristics of the genitalia.

Male palpus with long, shallow groove on median division of tegulum in which the thin embolus lies. Two elements make up distal division of embolic portion of palpus: the embolus, and a characteristic well-developed distal apophysis. Distal apophysis is a fold covering basal portion of embolus where it is attached, expanding to a point near or even beyond middle of the tegulum. The apophysis is expanded into a conspicuous lobe distally on prolateral side. Inner portion of distal division of embolus in a few species is also expanded into a distinct apophysis (*C. abbotii, C. newnani,* and *C. adjacens*). Tibia of male palpus with two strong apophyses which are very close together, sometimes overlapping. One apophysis retrolateral, the other nearly dorsal or dorso-retrolateral.

Epigyna of females very similar, all longer than broad; the oval or spherical sperm duct openings usually located close together near notched posterior edge. Sperm receptacles located anteriorly, sperm ducts curving laterally near edge of epigynum to sperm duct openings. (*C. abbotii, C. adjacens, C. alachua, C. bishopi, C. catawba, C. dyasia, C. estes, C. gertschi, C. johnsoni, C. kagani, C. kastoni, C. kiowa, C. littoralis, C. mutata, C. newnani, C. nicholsi, C. odelli, C. oteroana, C. pikei, C. plumbi, C. pomoa, C. procteri, C. rhododendri, C. saltitans*).

Group IV. The two species placed in this group are not closely related, however they differ from the preceding groups. (*C. maritima, C. riparia.*)

Key to males of Clubiona

1. Tibia of palpus with a single, relatively simple, heavy retrolateral apophysis . . . . . . Group 1
1. Tibia with two or more apophyses 2
2. Two simple tibial apophyses very close together, relatively heavy; bulb of palpus with a cusp-like distal division of embolus; tegulum with a long, shallow groove in which lies the long, thin embolus Group III
2. Tibial apophyses not very close together; distal division of embolus without a cusp-like apophysis 3
3. Tibial apophyses consisting of a short dorsal element and a longer ventral element and with a median element in some forms, the ventral element always sharply pointed distally and notched (as in Fig. 150); embolus short and directed distally, not lying in a shallow groove on the tegulum . . . . . . Group II
3. Male palpus not as above . . . . . . Group IV

Group 1

1. Tibial apophysis of palpus spatulate and very simple, without notches and processes (Division A) 2
1. Tibial apophysis not spatulate, with notches, hooks on processes (Division B) 4
2. Carpoblem broad and truncate (Fig. 99) . . . *C. moesta*
2. Carpoblem with distal point gently rounded (Figs. 97, 101) . . . 3
3. Distal division of embolic portion of palpus with three small dark distal lobes (Fig. 102) . . . . . . *C. trivialis*
3. Distal division of embolic portion without any distal lobes (Fig. 98) . . . *C. pygmaea*
4. Carpoblem with a dorsal division and a ventral division 5
4. Carpoblem a single stout process 6
5. Tibial apophysis of palpus with a heavy notched ventral division and a thin pointed dorsal division (Fig. 111) *C. spiralis*

5. Tibial apophysis with both divisions sharply pointed and turned in same direction toward tarsus (Fig. 114-115) *C. bryantae*
6. Carpoblem terminating in a hook turned toward tarsus 8
6. Carpoblem not terminating in a hook turned toward tarsus 7
7. Carpoblem with a ventral, distally projected narrow finger-like process; carpoblem relatively thin as seen in ventral view (Figs. 103-104) *C. mimula*
7. Carpoblem thick as seen in ventral view and with a short, narrow, dorsally projected ectal process (Figs. 116-118) *C. chippewa*
8. Carpoblem longer than broad as seen from the side 9
8. Carpoblem broader than long and with a long, sharp, prolaterally directed process as seen in dorsal view (Figs. 105-106, 124) *C. praematura*
9. Carpoblem terminating in a single point 10
9. Carpoblem terminating dorsally in two short points (Figs. 109-110) *C. furcata*
10. Carpoblem as seen from the side deeply notched just below tip; embolus shorter (Figs. 119-120) *C. mixta*
10. Carpoblem as seen from the side gently curved dorsally and not deeply notched; embolus longer (Figs. 121-123) *C. obesa*

Group II

1. Tibial apophysis of palpus with only two distinct divisions 2
1. Tibial apophysis with a distinct bluntly rounded median division (Fig. 149) *C. kulczynskii*
2. Tibial apophysis with dorsal and ventral divisions extended ventrally; ventral division very much longer than dorsal (Fig. 146) *C. norvegica*
2. The two divisions of tibial apophysis extended distally; ventral division at most slightly more than twice as long as dorsal division 3
3. Ventral division of tibial apophysis at least twice as long as dorsal division and much heavier than dorsal division (Fig. 150) *C. canadensis*
3. Ventral division of tibial apophysis less than twice as long as dorsal division and about as narrow as dorsal division (Fig. 152) *C. californica*

Group III

1. Retrolateral tibial apophysis bifid (Fig. 74) *C. dyasia*
1. Retrolateral tibial apophysis not bifid 2
2. Embolus with an enlargement near base 3
2. Embolus without enlargement near base 4

3. Dorsal and retrolateral tibial apophyses nearly the same length (Figs. 68, 69) . . . . . *C. nicholsi*
3. Retrolateral tibial apophysis much longer than dorsal (Fig. 72) . . . . . *C. pomoa*
4. Retrolateral tibial apophysis essentially straight, without an enlargement at base of apex (Fig. 76) . . . . . *C. catawba*
4. Retrolateral tibial apophysis curved or with an enlargement at base of apex 5
5. Retrolateral tibial apophysis with an enlargement at apex (Fig. 54) . . . *C. adjacens*
5. Retrolateral tibial apophysis without an apical enlargement 6
6. Chelicerae very robust and protruding; posterior eyes widely separated *C. littoralis*
6. Chelicerae normal, not protruding; posterior eyes not as widely separated 7
7. Distal half of retrolateral tibial apophysis bent sharply dorsad (Fig. 66) . . . . . *C. procteri*
7. Distal half of retrolateral apophysis not bent sharply dorsad 8
8. Retrolateral tibial apophysis distinctly longer than dorsal apophysis . 9
8. Retrolateral tibial apophysis at most but slightly longer than dorsal apophysis 13
9. Chelicerae with distinct ridges above; dorsal tibial apophysis broad and truncate (Fig. 58) . . . . . *C. saltitans*
9. Chelicerae without ridges above; dorsal tibial apophysis not as broad 10
10. Dorsal tibial apophysis terminating in a ventrally directed point (Fig. 64) . . . . . *C. mutata*
10. Dorsal tibial apophysis not as in *C. mutata* . . . 11
11. Retrolateral tibial apophysis with a truncate apex (Fig. 62) *C. kiowa*
11. Retrolateral tibial apophysis thinner, apex pointed . . . 12
12. Posterior median eyes separated by one and a half times the diameter of one of them . . . . . *C. plumbi*
12. Posterior median eyes separated by more than twice the diameter of one of them . . . . . *C. pikei*
13. Distal apophysis of the embolic portion of bulb with inner fold produced into a distinct spur 18
13. Distal apophysis of embolic portion of bulb without distinct spur produced from inner fold 14
14. Apex of retrolateral tibial apophysis produced into a sharp, ventrally curved point (Fig. 50) . . . . . *C. gertschi*
14. Apex of the retrolateral tibial apophysis not pointed 15
15. Apex of the dorsal tibial apophysis bluntly rounded (Fig. 40) . . . . . *C. bishopi*

15. Apex of the dorsal tibial apophysis pointed 16
16. Dorsal tibial apophysis at most no longer than ventral apophysis; embolus comparatively long 17
16. Dorsal tibial apophysis somewhat longer than ventral; embolus comparatively short (Fig. 39) . . . . *C. rhododendri*
17. Retrolateral tibial apophysis about as long as its width at the base (Fig. 46) . . . . *C. kastoni*
17. Retrolateral tibial apophysis considerably longer than its width at the base (Fig. 48) . . . . *C. johnsoni*
18. Retrolateral tibial apophysis longer than broad 19
18. Retrolateral tibial apophysis about as long as broad (Fig. 52) . . . . . . *C. newnani*
19. Dorsal point of the apex of the retrolateral tibial apophysis longer than the ventral point; retrolateral apophysis widest at the base (Fig. 42) . . . . *C. abbotii abbotii*
19. Dorsal point of the apex of the retrolateral tibial apophysis no longer than ventral point; retrolateral apophysis widest at middle (Fig. 45) *C. abbotii abbotoides*

Group IV

1. Tibial apophysis of palpus mainly dorsal in position, very heavy and complex; the very long thin embolus lying in a shallow groove on tegulum (Figs. 132-133) . . . . *C. maritima*
1. The comparatively small retrolateral tibial apophysis with two divisions; the spiraled embolus enclosed in a heavy conductor and not lying in a groove on tegulum (Figs. 125, 127) *C. riparia*

Key to females (except *C. rhododendri*)

A short immersion in clove oil may be necessary to reveal the internal characters of some species. Individual variation in different species is very great, thus individual specimens may at times not key out.

1. Epigynum with openings not visible or with paired openings three or more diameters apart 6
1. Epigynum with one median opening or paired openings close together, two diameters or less apart 2
2. Openings hidden by a transverse dark mark, which may be broken (Figs. 143, 212) . . . . *C. spiralis*
2. Openings otherwise 3

3. Epigynum with openings in an indistinct depression which is divided by a posterior pointing septum; sides of depression white in color; (Figs. 145, 219); size 5-10 mm. *C. riparia*
3. Epigynum otherwise, mostly smaller species 4
4. Epigynum with a single median opening 16
4. Epigynum with two separate openings 5
5. Openings separated by a V-shaped division, a pair of depressions anterior to openings (Figs. 138, 229) *C. mimula*
5. Epigynum otherwise *abbotii* group
6. Less than 3 mm. long, one central opening present (Fig. 244), but difficult to discern *C. catawba*
6. More than 3.5 mm. long 7
7. Openings visible as slits or depressions in a plate 11
7. Openings on the posterior margin of a plate 8
8. Epigynum covering most of width of abdomen, openings far apart (Figs. 139, 214) *C. maritima*
8. Epigynum not exceptionally wide, openings relatively close together 9
9. Epigynum with a posterior median notch, margin sclerotized (Figs. 156, 215) *C. norvegica*
9. Epigynum with margin not sclerotized 10
10. Epigynum with a characteristic median darker raised area which is narrower anteriorly (Figs. 155, 216) *C. canadensis*
10. Epigynum with a median posterior lobe (Figs. 158, 217 and 153, 218) *C. kulczynskii, C. californica*
11. Openings connected to margin (Figs. 157, 213 and 214) *C. rileyi, C. maritima*
11. Openings not touching margin 12
12. Openings indistinct slits (Figs. 161, 220) *C. furcata*
12. Openings circular on oval depression 13
13. Openings minute, several diameters from margin (Figs. 137, 221) *C. bryantae*
13. Openings, their diameter or less from posterior margin 14
14. Openings more than 10 diameters apart, or if less, posterior receptacles more than their length from margin (Figs. 136, 222); eastern mountain summits *C. praematura*
14. Openings less than 8 diameters apart, oval in shape; posterior receptacles close to posterior margin, visible without clearing 15
15. Indentation in posterior margin as wide as length of 3 openings, posterior receptacles small, about their length from openings (Figs. 141, 223) *C. mixta*
15. Indentation in posterior margin less than length of two openings; posterior receptacles large, less than their length from openings (Figs. 140, 224) *C. obesa*

16. Depression bordered all around or ducts running parallel entering opening from anterior (Figs. 225-228) (if posterior margin missing, seminal receptacles in two rows forming square, Fig. 226; if only lateral margins present, receptacles in one line (Fig. 228) 17

16. Depression not bordered all around, ducts entering at sides or at a 45 degree angle, usually less than 5 mm. long, rarely more than 6 mm. *Not* like Figures 144, 226, 228 . . . . *abbotii* group

17. Seminal receptacles in one row (Figs. 134, 227 and 144, 228) . . . . *C. janae*, *C. moesta*

17. Seminal receptacles in two rows 18

18. Anterior receptacles about their diameter from posterior margin of plate (Figs. 135, 226) . . . . . . *C. pygmaea*

18. Anterior receptacles more than their diameter from posterior margin (Figs. 142, 225) . . *C. trivialis*

Key to females of *abbotii* group (Group III)

1. Openings their radius or more from end of lobe, area around openings sclerotized (Figs. 79, 82, 83, 231, 236) 2

1. Openings closer to margin . . 3

2. Margin flaring out in two large lobes (Figs. 82, 231); Colorado . . *C. odelli*

2. Lobes not flared (Figs. 79, 83, 236) . . . *C. abbotii*

3. Opening without septum, very difficult to see, a pair of black transverse patches visible (Figs. 92, 244); usually less than 3 mm. long, eastern United States . . . . *C. catawba*

3. Openings visible (after removing hairs) 4

4. Receptacles in one row, or median ones slightly anterior (Figs. 93, 239 and 94, 238); southwestern states, California . . . . *C. pomoa*, *C. oteroana*

4. Receptacles in two rows, or median ones posterior to laterals . . . 5

5. Posterior border of median receptacles forming a straight line (Fig. 235); Lake states, New England . . . *C. johnsoni*

5. Posterior border of median receptacles not forming a straight line . . 6

6. Anterior receptacles more than twice as long as wide, openings more than 3 times as long as wide (Figs. 88, 240); southeastern states . . *C. procteri*

6. Receptacles or openings otherwise 7

7. Openings joined, the anterior margin of each side pointing anterior and becoming parallel (Figs. 86, 234) . . *C. opeonga*

7. Openings otherwise 8

8. Epigynum sclerotized, ducts with 2 right angles (Figs. 84, 232); eastern mountain summits . . . . *C. gertschi*

8. Ducts lacking angles, usually not on mountain summits 9
9. Ducts approaching openings in a V-shape, lacking elbows; anterior receptacles longer than wide, with their axes at right angles (Figs. 81, 233) widespread .... *C. kastoni*
9. Ducts either having a slight angle or strongly curved 10
10. Openings joined, depression having an anterior median lobe (Fig. 87, 242); Atlantic coast states .... *C. littoralis*
10. Openings not joined, or if joined not having an anterior lobe 11
11. Anterior receptacles at least twice as long as wide, hiding posterior receptacles, a pair of transverse black marks on epigynum (Figs. 89, 243) and posterior median eyes only two diameters apart; Texas .... *C. kagani*
11. Anterior receptacles otherwise or eyes farther apart 12
12. Anterior receptacles at least twice as long as wide and ducts having an angle (Figs. 85, 241). Atlantic coast states, probably found only in beach vicinity .... *C. nicholsi*
12. Anterior receptacles or ducts otherwise 13
13. Ducts with slight angles, area between ducts less than twice the width of combined openings (Figs. 90, 245); posterior median eyes only two diameters apart; probably eastern states .. . . *C. kiowa*
13. Ducts otherwise 14
14. Openings two parallel grooves, more than twice as long as wide (Fig. 248); posterior median eyes only two diameters apart; Atlantic coast states on shore; doubtful on shore of Gt. Lakes ...... *C. saltitans*
14. Openings more rounded or eyes farther apart 15
15. Posterior median eyes two diameters or less apart; Atlantic coast states in dune grass; (Genitalia Figs. 95, 250) .... *C. plumbi*
15. Posterior median eyes about three diameters apart 16
16. Area surrounded by ducts about three diameters the combined width of openings (Fig. 249). Atlantic coast states .... *C. pikei*
16. Area surrounded by ducts about two diameters combined width of openings 17
17. Size 2.4-3.8 mm. long, widespread .... *C. mutata*
17. Size 4 mm. long, Colorado .. .. *C. estes*

CLUBIONA TRIVIALIS C. Koch
Figures 101-102, 142, 170, 225

Clubiona trivialis C. Koch, 1843, Die Arachniden, vol. 10, p. 132, figs. 844-845 (Types from southern Germany). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 502. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1161.

Clubiona obtusa Emerton, 1915, Trans. Connecticut Acad. Sci., vol. 20, p. 153, pl. 3, fig. 4 (♂ and ♀ syntypes from Banff, Canada, in the Museum of Comparative Zoology). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 516. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1138. NEW SYNONYMY.

Measurements. Female. Length 3.18-5.34 mm.; average 4.15 mm. Carapace 1.74 mm. long, 1.14 mm. wide. First femur. 1.20 mm.; patella, 0.60 mm.; tibia, 0.96 mm.; metatarsus, 0.68 mm.; tarsus, 0.42 mm. Fourth femur, 1.44 mm.; patella, 0.54 mm.; tibia, 1.14 mm.; metatarsus, 1.26 mm.; tarsus, 0.46 mm.

Male. Length 3.00-4.26 mm.; average 3.55 mm. Carapace 1.40 mm. long, 0.96 mm. wide. First femur, 1.08 mm.; patella, 0.48 mm.; tibia, 0.96 mm.; metatarsus, 0.66 mm.; tarsus, 0.42 mm. Fourth femur, 1.38 mm.; patella, 0.51 mm.; tibia, 1.00 mm.; metatarsus, 1.08 mm.; tarsus, 0.42 mm.

Description. Anterior median eyes their radius apart, half as far from laterals. Posterior medians separated by three diameters, two diameters from laterals in female, slightly closer in male. Epigynum and palpus (Figs. 101-102) separate it from *C. pygmaea*.

Natural History. This species has been collected from grass and bushes along a beach, from under bark and in ground debris.

Distribution. Common in northern Europe and the British Isles, southern Canada, northern United States, in the West south to Arizona.

Records. Arizona: Scotsdale, ♂. *Maine:* Bass Harbor, ♂; Eastbrook, ♂. *Michigan:* *Wilderness Park, ♂. *New York:* Brittons, ♂; Little Pond, Orange Co., ♂, ♀. *Washington:* Friday Harbor, ♀. *Wisconsin:* Manitowoc Co., ♀. *Wyoming:* Bridge Bay, Yellowstone Natl. Pk., ♂, ♀.

Alberta: *Banff, ♂, ♀; Carthew Lk., Waterton Natl. Pk., ♀, ♂. *British Columbia:* Manning Park, ♂; Ross Lk., Yoho Natl. Pk., ♀. *Labrador:* ♀. *Newfoundland:* St. Fintans, ♀. *Ontario:* Smoky Falls, Mattagami River, ♀; Providence Bay, Manitoulin Isl., ♂, ♀; 8 mi. N. of Temagami, ♀; Fort Severn, ♀. *Saskatchewan:* Wallaston Lake, ♂, ♀.

CLUBIONA PYGMAEA Banks
Figures 97-98, 135, 173, 226

Clubiona minuta Emerton, 1890, Trans. Connecticut Acad. Sci., vol. 8, p. 121, pl. 5, fig. 4 (♂ type from Readville, Massachusetts, in the Museum of Comparative Zoology). Name preoccupied by *C. minuta* Nicolet.

Clubiona pygmaea Banks, 1892, Proc. Acad. Nat. Sci. Philadelphia, p. 21, pl. 1, fig. 64 (♀ type from Fall Creek, Ithaca, New York, in the Museum of Comparative Zoology). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 516. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1148.

Clubiona minutissima Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 461. New name for *C. minuta* Emerton, preoccupied. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1135.

Clubiona lenta Banks, 1916, Proc. Acad. Nat. Sci. Philadelphia, p. 69 (♀ type from Fall Creek, Ithaca, New York, in the Museum of Comparative Zoology).

Measurements. Female. Length 2.94-4.02 mm.; average 3.43 mm. Carapace 1.56 mm. long, 1.08 mm. wide. First femur, 1.08 mm.; patella, 0.48 mm.; tibia, 0.78 mm.; metatarsus, 0.57 mm.; tarsus, 0.36 mm. Fourth femur, 1.32 mm.; patella, 0.54 mm.; tibia, 0.99 mm.; metatarsus, 1.08 mm.; tarsus, 0.39 mm.

Male. Length 2.70-3.78 mm.; average 3.07 mm. Carapace 1.35 mm. long, 0.96 mm. wide. First femur, 0.86 mm.; patella, 0.42 mm.; tibia, 0.72 mm.; metatarsus, 0.60 mm.; tarsus, 0.30 mm. Fourth femur, 1.08 mm.; patella, 0.42 mm.; tibia, 0.80 mm.; metatarsus, 0.84 mm.; tarsus, 0.36 mm.

Description. Anterior median eyes two-thirds to one diameter apart, half that distance from laterals. Posterior medians three diameters apart, half as far from laterals. Epigynum illustrated by Figure 135, palpus by Figures 97-98.

Natural History. This species has been collected on tall marsh grass and from low bushes.

Distribution. Southeastern Canada, eastern United States, as far west as Colorado.

Records. Colorado: Denver. *Connecticut:* Norwalk; *Amston; *New Haven; *North Haven; *Simsbury; *South Meriden. *District of Columbia. Florida:* St. Petersburg; Keuka; Marianna; Eustis. *Illinois:* Nr. Chicago; Urbana. *Indiana:* Vawter Park; Arlington. *Maine:* *Portland. *Maryland:* *Prince Georges Co. *Massachusetts:* Sharon; *Readville; Wellfleet. *Michigan:* Quincy.

Mississippi: Humphreys Co. *New Jersey:* Ramsey. *New York:* Sea Cliff, L. I.; Cold Spring Harbor, L. I.; Ithaca; Yonkers: Beaver River Flow; Mendon Ponds, Monroe Co.; Enfield Glen; West Kilns. *North Carolina:* Canton. *Ohio:* Gambler; *Columbus; *Delaware; *Rockbridge. *Texas:* Edinburg. *Virginia:* Falls Church. *West Virginia:* Aurora. *Wisconsin:* Madison.

Ontario: Humber, Toronto; Newmarket. *Quebec.*

CLUBIONA MOESTA Banks

Figures 99-100, 130, 144, 228

Clubiona pusilla Emerton, 1890, Trans. Connecticut Acad. Sci., vol. 8, p. 181-182, pl. 15, fig. 5 (♂ types from Salem, Massachusetts, in the Museum of Comparative Zoology). Name preoccupied by *C. pusilla* Nicolet.

Clubiona moesta Banks, 1896, Trans. Amer. Ent. Soc., vol. 23, p. 64 (♂ and ♀ syntypes from Chicago, Illinois, in the Museum of Comparative Zoology). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 515.

Clubiona emertoni Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., vol. 29, p. 460. New name for *C. pusilla* Emerton, preoccupied.

Clubiona orinoma Chamberlin, 1919, Ann. Ent. Soc. Amer., vol. 12, p. 225, pl. 14, fig. 4 (♀ type from Chalk Creek, Uintah Mts., Utah, in the Museum of Comparative Zoology).

Clubiona maesta, Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1133.

Measurements. Female. Length 4.32-6.48 mm.; average 5.42 mm. Carapace 2.32 mm. long, 1.76 mm. wide. First femur, 1.60 mm.; patella, 0.76 mm.; tibia, 1.28 mm.; metatarsus, 0.84 mm.; tarsus, 0.52 mm. Fourth femur, 2.00 mm.; patella, 0.80 mm.; tibia, 1.36 mm.; metatarsus, 1.69 mm.; tarsus, 0.52 mm.

Male. Length 3.68-6.00 mm.; average, 4.84 mm. Carapace 2.24 mm. long, 1.62 mm. wide. First femur, 1.68 mm.; patella, 0.72 mm.; tibia, 1.41 mm.; metatarsus, 1.02 mm.; tarsus, 0.57 mm. Fourth femur, 1.86 mm.; patella, 0.72 mm.; tibia, 1.32 mm.; metatarsus, 1.62 mm.; tarsus, 0.54 mm.

Description. Anterior eyes separated by their radius in female, by their diameter in male. Posterior medians separated by three diameters, one diameter from laterals. In the female the chelicerae are stout, in the male attenuated with their anterior surfaces concave. Epigynum illustrated by Figure 144, palpus by Figures 99-100.

Natural History. This species is very common under bark of standing aspen in the West.

Distribution. Northern United States to Alaska.

Records. Colorado: Fort Collins; Gunnison Co.; La Plata Co. *Connecticut:* Black Hall. *Idaho:* Thousand Springs; Crow Creek. *Illinois:* Chicago. *Maine:* Mount Desert Isl. *Massachusetts:* Saugus; Holliston; *Salem; *Beverly. *Michigan:* *Southern Peninsula. *Minnesota:* Minneapolis; Itasca Park. *Montana:* Beaverhead Co.; Ravalli Co. *Nebraska:* *Lincoln. *New Hampshire:* 3 Mile Island, Lake Winnepesaukee. *New York:* Juanita Isl., Lake George; Lake Bluff; Freeville; Little Pond, Orange Co.; Long Isl.; McLean; Hunter; Labrador Pond, Cortland Co.; Oswego; Lotus Point; Adirondack Lodge; Honeoye Falls. *Oregon:* Eugene; Scappoose; Portland. *Pennsylvania:* *Western part. *South Dakota:* Grizzly Bear Cr., Black Hills. *Utah:* Salt Lake City; Rear Lake; *Chalk Creek, Raft River Mtns.; *Clear Cr., Raft River Mtns.; *South fork of the Raft River; *Dove Creek, Raft River Mtns.; *Park Valley. *Wisconsin:* Manitowoc Co. *Wyoming:* Mount Afton.

Alaska: *College.

Manitoba: Le Pas. *Ontario:* Port Credit; Toronto; Wellington; Haliburton; Long Point; Elmhurst Beach; Huyks Bay; Little Vermillion Lake; High Park, Toronto; Garrott Island; Picton; Mindemoya, Manitoulin Lake; Providence Bay, Manitoulin Lake; Hogs Hollow, Toronto; Beamsville; Lake Opeonga, Algonquin Park; Point Pelee. *Saskatchewan:* Lac La Rouge.

CLUBIONA JANAE, new species

Figures 134, 177, 227

Type. Female holotype from Pilarcitas Creek, San Mateo County, California, April 27, 1947 (W. Tilden), in the American Museum of Natural History.

Measurements. Female. Total length 6.30 mm. Carapace 2.64 mm. long, 1.80 mm. wide. Abdomen 3.84 mm. long, 2.40 mm. wide. First femur, 1.38 mm.; patella, 0.60 mm.; tibia, 1.08 mm.; metatarsus, 0.84 mm.; tarsus, 0.48 mm. Fourth femur, 1.74 mm.; patella, 0.68 mm.; tibia, 1.50 mm.; metatarsus, 1.78 mm.; tarsus, 0.56 mm.

Description. Anterior median eyes separated by nearly the diameter of one, nearer the equal laterals. Posterior medians separated by two and a half diameters of one, nearer the slightly sub-equal laterals. Chelicerae armed with two small teeth on lower margin.

Carapace light brown, unmarked except for dark median groove and black rings surrounding the eyes. Sternum light yellow, margined by darker yellow-brown, and with dark spots at margin in regions of coxae. Chelicerae reddish-brown. Endites and labium light brown except for the lighter distal margin of the labium. Coxae light yellow-brown, legs slightly darker. First and second tibia with a mid-ventral heavy band of long hairs on the distal half and two ventro-lateral bands extending the length of the tibia. Dorsum of abdomen light yellow-brown with a red-brown stripe and five or six indistinct posteriorly directed chevrons, darker red-brown behind. Venter of abdomen light yellow-brown and clothed in same manner as dorsum.

Diagnosis. Epigynum (Fig. 134) much like that of *C. trivialis.* Details of it distinguish it from the latter species.

Record. California: Berkeley, ♀ paratype, Dec. 1919 (H. Dietrich), in the Cornell Univ. Collection.

CLUBIONA FURCATA Emerton
Figures 108-110, 161-162, 220

Clubiona furcata Emerton, 1917, Canadian Ent., vol. 49, p. 107, pl. 7, fig. 8 (♂ type from Saskatoon, Saskatchewan, lost).

Clubiona rowani Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 17, fig. 13 (♀ type from Seba, Alberta, in the American Museum of Natural History). NEW SYNONYMY.

Measurements. Female: length 4.07 mm. Carapace 1.86 mm. long, 1.32 mm. wide. First femur, 1.14 mm.; patella, 0.54 mm.; tibia, 1.08 mm.; metatarsus, 0.72 mm.; tarsus, 0.48 mm. Fourth femur, 1.62 mm.; patella, 0.56 mm.; tibia, 1.26 mm.; metatarsus, 1.35 mm.; tarsus, 0.50 mm.

Male: Length, 3.88 mm. Carapace 1.76 mm. long, 1.33 mm. wide.

Description. Anterior median eyes two-thirds diameter apart, closer to laterals. Posterior medians separated by two diameters, closer to laterals. Epigynum illustrated by Figure 161, palpus by Figures 108-110.

Records. Utah: Lakota Beach, Bear Lake, ♂ (W. J. Gertsch). *Alberta:* Lac la Rouge; Seba Beach. *Manitoba:* Birtle.

CLUBIONA PRAEMATURA Emerton

Figures 105, 106-107, 124, 136, 222

Clubiona praematura Emerton, 1909, Trans. Connecticut Acad. Sci., vol. 14, p. 219, pl. 10, fig. 7 (♂, ♀ syntypes from summit of Mt. Washington, New Hampshire, in the Museum of Comparative Zoology). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 516. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1147.

Measurements. Female. Length 4.86-6.84 mm.; average 5.73 mm. Carapace 2.40 mm. long, 1.63 mm. wide. First femur, 1.33 mm.; patella, 0.77 mm.; tibia, 1.07 mm.; metatarsus, 0.80 mm.; tarsus, 0.60 mm. Fourth femur, 1.73 mm.; patella, 0.80 mm.; tibia, 1.33 mm.; metatarsus, 1.67 mm.; tarsus, 0.63 mm.

Male. Length, 4.38-5.04 mm.; average, 4.75 mm. Carapace 2.13 mm. long, 1.50 mm. wide. First femur, 1.32 mm.; patella, 0.72 mm.; tibia, 1.20 mm.; metatarsus, 0.84 mm.; tarsus, 0.57 mm. Fourth femur, 1.68 mm:; patella, 0.78 mm.; tibia, 1.44 mm.; metatarsus, 1.68 mm.; tarsus, 0.66 mm.

Description. Anterior median eyes separated by two-thirds diameter in female, by radius in male, closer to laterals. Posterior medians more than two diameters apart in female, one and one-half in male, closer to laterals. Epigynum illustrated by Figure 136, palpus by Figures 105-107, 124.

Natural History. This species has been collected from under stones and in ground debris.

Distribution. Eastern mountain tops, Canada, Alaska.

Records. Kentucky: Tableland Mtn., ♂, ♀. *Maine:* Mt. Katahdin summit, ♂, ♀. *New Hampshire:* Mt. Washington, ♂, ♀. *Alaska:* Eklutna, ♀; Eklutna Flats, ♀; Anaktuvuk Pass, ♀. *Mackenzie:* Ft. Resolution, Great Slave Lake, ♀.

CLUBIONA MIMULA Chamberlin

Figures 103-104, 129, 138, 178, 229

Clubiona mimula Chamberlin, *in* Chamberlin and Gertsch, 1928, Proc. Biol. Soc. Washington, vol. 41, p. 184 (♂ type from Fruita, Wayne Co., Utah, in the University of Utah collection). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 515. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1135.

Measurements. Female. Length 4.86-6.00 mm.; average 5.36 mm. Carapace 2.37 mm. long, 1.62 mm. wide. First femur, 1.28 mm.; patella, 0.68 mm.; tibia, 0.99 mm.; metatarsus, 0.72 mm.; tarsus, 0.50 mm. Fourth femur, 1.86 mm.; patella 0.72 mm.; tibia, 1.32 mm.; metatarsus, 1.59 mm.; tarsus, 0.54 mm.

Male. Length 4.20-5.22 mm.; average 4.65 mm. Carapace 2.16 mm. long, 1.38 mm. wide. First femur, 1.56 mm; patella, 0.75 mm.; tibia, 1.32 mm.; metatarsus, 0.96 mm.; tarsus, 0.54 mm. Fourth femur, 2.01 mm.; patella, 0.78 mm.; tibia, 1.38 mm.; metatarsus, 1.68 mm.; tarsus, 0.60 mm.

Description. Anterior median eyes separated by three-quarters diameter in female, by radius in male, closer to laterals. Posterior medians separated by two and a half diameters in female, by two diameters in male, closer to laterals. Epigynum illustrated by Figure 138, palpus by Figures 103-104. The sperm ducts (Fig. 229) go directly back to the openings, not curving as they do in the *C. abbotii* group.

Records. California: Lake Tahoe, ♀, ♂; Yosemite Falls, ♂. *Idaho:* Snake River; Ferncroft. *Oregon:* Spencer Butte, ♂. *Utah:* Beaver Canyon, ♂, ♀; *Clear Creek, Raft River Mtns., ♂, ♀.

CLUBIONA CHIPPEWA Gertsch

Figures 116-118

Clubiona chippewa Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 16, figs. 50-51 (♂ type from St. Croix Falls, Wisconsin, in the American Museum of Natural History). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 514.

Measurements. Male. Length 4.50 mm. Carapace 2.10 mm. long, 1.44 mm. wide. First femur, 1.98 mm.; patella, 0.81 mm.; tibia, 1.83 mm.; metatarsus, 1.26 mm.; tarsus, 0.81 mm. Fourth femur, 2.40 mm.; patella, 0.78 mm.; tibia, 1.86 mm.; metatarsus, 2.55 mm.; tarsus, 0.75 mm.

Description. Anterior median eyes separated by two-thirds diameter, closer to slightly larger laterals. Posterior medians two diameters apart, closer to laterals. Palpus illustrated by Figures 116-118. The female is not known.

Record. Wisconsin: Tipler, Florence Co., ♂. *Ontario:* Wiarton, Bruce Co., ♂.

CLUBIONA OBESA Hentz

Figures 121-123, 140, 172, 224

Clubiona obesa Hentz, 1847, Proc. Boston Soc. Nat. Hist., vol. 5, p. 450, pl. 22, fig. 14. (Types from "Massachusetts, North Carolina, Alabama", lost.) Roewer, 1955, Katalog der Araneae, vol. 2a, p. 516. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1138.

Clubiona crassipalpis Keyserling, 1887, Verh. zool. bot. Gesell. Wien, vol. 37, p. 438, fig. 13 (♂ type from near Cambridge, Massachusetts, in the Museum of Comparative Zoology).

Clubiona triloba Banks, 1906, Ann. Rept. Indiana Geol. Nat. Hist. Surv., p. 737, fig. 19 (♀ syntypes from Wyandotte, Indiana, in the Museum of Comparative Zoology). Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1161. NEW SYNONYMY.

Measurements. Female. Length 6.48-10.32 mm.; average 8.28 mm. Carapace 3.92 mm. long, 2.80 mm. wide. First femur, 3.20 mm.; patella, 1.36 mm.; tibia, 2.60 mm.; metatarsus, 1.92 mm.; tarsus, 1.12 mm. Fourth femur, 3.52 mm.; patella, 1.22 mm.; tibia, 2.68 mm.; metatarsus, 3.52 mm.; tarsus, 1.04 mm.

Male. Length 5.52-8.64 mm.; average 6.84 mm. Carapace 3.16 mm. long, 2.22 mm. wide. First femur, 3.18 mm.; patella, 1.32 mm.; tibia, 3.06 mm.; metatarsus, 2.22 mm.; tarsus, 1.02 mm. Fourth femur, 3.48 mm.; patella, 1.20 mm.; tibia, 2.58 mm.; metatarsus, 3.36 mm.; tarsus, 0.88 mm.

Description. Anterior median eyes their diameter apart; in female an equal distance from laterals, in male slightly closer to laterals. Posterior medians two and one half diameters apart in female, two diameters in male, a little closer to laterals. Chelicerae robust in female, keeled on their lateral and anteromedial faces in male.

Diagnosis. The carpoblem of the palpus of *C. mixta* is more deeply notched than that of *C. obesa* (Figs. 121-123) and the embolus is shorter. The openings in the epigynum are larger in *C. obesa* (Fig. 140) than in *C. mixta.*

Natural History. This spider has usually been found on leaves and branches of low bushes in deciduous woods, although it also occurs in tall grass and overwinters under logs, stones, bark and debris. Hibernation usually occurs in the penultimate instar. Mature males have been collected from April to August, and females through September. Egg sacs have been found in June and July. Kaston observed that eggs laid on June 21, hatched July 11. An egg sac attached under a leaf was 6.9 mm. in diameter and 3.9 mm. high and contained 79 yellow, non-agglutinate, oval eggs each measuring about 0.95 mm. by 1.05 mm. Emerton found 33 eggs in one sac and observed that eggs laid July 5, hatched August 5, but the spiderlings did not leave the cocoon until August 26. A male and female have been found enclosed together in a silk cocoon May 24. On June 16, a male and immature females were found together in a cocoon. On the same date a young female was found with cast skins in a cocoon.

Distribution. Southeastern Canada and eastern United States.

Records. Alabama: Hatchet Creek, Coosa Co. *Connecticut:* Riverton; Norwalk; Westville; Woodmont, Southbury; Morris; South Meriden; Bethany; Salisbury; Branford; Simsbury; Granby; *New Haven. *District of Columbia:* Washington. *Illinois:* Urbana; Peoria; Elgin; *Waukegan; *Waukegan Flats. *Indiana:* *Wyandotte; *Richmond; *Valparaiso; *Ogden Dunes; *Smith. *Iowa:* Sioux City; Dickinson Co. *Maine:* South Casco, Lake Sebago. *Maryland:* *Prince Georges Co. *Massachusetts:* Ipswich River; Natick; Salem; Holliston; *Brookline; *Milton; *Sharon. *Michigan:* Douglas Lake; Roscommon Co.; New Baltimore; *Ann Arbor; *Saugatuck; *Lakeside. *Minnesota:* Itasca Park; Albert Lea. *Mississippi:* Camp Shelby; Centreville. *Nebraska:* Plattsmouth; Murdock; Weeping Water; Fremont; Lincoln; Ainsworth. *New Hampshire:* Three Mile Island, Lake Winnepesaukee; *Franconia. *New Jersey:* Ramsey; Oakland; Moorestown. *New York:* McLean; Van Cortland Swamp, Bronx; Valcour Island; East Hampton, L. I.; Cold Spring Harbor, L. I.; Jamaica, L. I.; Orient, L. I.; Webster; Ithaca; Enfield Gorge; Lake George; New Rochelle; Huyck Preserve, Albany Co.; *Sacandaga River; Lake Bluff; *Youngstown; *Crosby; *Newfield; Albany; Thacher Park; Cossayuna Lake; Coy Pt., Canandaigua Lake; *Queechy Lake; *Juanita Island, Lake George; Cragsmoor; Oakland Valley; *Sea Cliff; *Roslyn. *North Carolina:* Raleigh; Transylvania Co.; *Swannanoa Valley. *Ohio:* Sandusky; *Columbus; *Rockbridge. *Pennsylvania:* *"Western Pennsylvania". *Rhode Island:* *Providence. *Vermont:* Newfare. *Virginia:* Falls Church. *West Virginia:* *near Charleston. *Wisconsin:* Grant Co.; Racine Co.; St. Croix.

Manitoba: *Lake Winnipeg. *Ontario:* Port Credit; Portland; Wellington; West Hill, September; Fonde Bay, Lake Nipigon; Holst Point, Minaki; Point Pelee; Humber, Toronto.

CLUBIONA MIXTA Emerton

Figures 119-120, 141, 165, 223

Clubiona mixta Emerton, 1890, Trans. Connecticut Acad. Sci., vol. 8, p. 180, pl. 5, fig. 2 (♀, ♂ syntypes from Marblehead, Massachusetts, in the Museum of Comparative Zoology). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 515. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1135.

Measurements. Female: length, 6.70-9.76 mm.; average 8.30 mm. Carapace 3.60 mm. long, 2.40 mm. wide. First femur, 2.72 mm.; patella, 1.28 mm.; tibia, 2.24 mm.; metatarsus, 1.68 mm.; tarsus, 0.96 mm. Fourth femur, 3.44 mm.; patella, 1.28 mm.; tibia, 2.40 mm.; metatarsus, 2.96 mm.; tarsus, 0.96 mm.

Male: Length, 5.20-8.48 mm.; average 6.63 mm. Carapace 2.80 mm. long, 2.00 mm. wide. First femur, 2.48 mm.; patella, 1.00 mm.; tibia, 2.10 mm.; metatarsus, 1.52 mm.; tarsus, 0.66 mm. Fourth femur, 2.80 mm.; patella, 1.00 mm.; tibia, 2.72 mm.; metatarsus, 2.40 mm.; tarsus, 0.66 mm.

Description. The structure of this species is similar to that of *C. obesa* except for details of the genitalia. The carpoblem of *C. obesa* is less deeply notched and the embolus is comparatively longer. The sperm duct openings of *C. mixta* (Fig. 141) are smaller than in *C. obesa.*

Natural History. This species has been found on bushes and trees and under stones in silken retreats. The habits resemble those of *C. obesa.*

Distribution. Southeastern Canada, northeastern and north central United States.

Records. Connecticut: *Mount Carmel, *Portland; *Sandy Hook. *Maine:* *Portland; Long Island. *Massachusetts:* Lexington; Sharon; Holliston; *Salem; *Marblehead. *Michigan:* Macomb Co.; Oceana Co. *Minnesota:* Itasca Park. *New Hampshire:* West Ossippee. *New Jersey:* Ramsey. *New York:* Youngstown; Crosby; Chautauqua Co.; Lake Bluff. *Ohio:* Germantown; Sandusky. *Oklahoma:* Enid. *Pennsylvania:* Arentsville. *Wisconsin:* Dane Co.; Grant Co.; Racine Co.

Ontario: Haliburton.

CLUBIONA SPIRALIS Emerton
Figures 111-113, 143, 175, 212

Clubiona spiralis Emerton, 1909, Trans. Connecticut Acad. Sci., vol. 14, pl. 10, fig. 10 (♂ type from Magnolia, Massachusetts, in the Museum of Comparative Zoology). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 517. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1153.

Measurements. Female: Length 4.74-7.62 mm.; average 6.12 mm. Carapace 2.70 mm. long, 1.98 mm. wide. First femur, 1.80 mm.; patella, 0.90 mm.; tibia, 1.44 mm.; metatarsus, 1.08 mm.; tarsus, 0.66 mm. Fourth femur, 2.40 mm.; patella, 0.90 mm.; tibia, 1.81 mm.; metatarsus, 2.34 mm.; tarsus, 0.66 mm.

Male: Length 4.38-5.70 mm.; average 5.16 mm. Carapace 2.46 mm. long, 1.62 mm. wide. First femur, 1.86 mm.; patella, 0.72 mm.; tibia, 1.56 mm.; metatarsus, 1.02 mm.; tarsus, 0.63 mm. Fourth femur, 2.34 mm.; patella, 0.84 mm.; tibia, 1.83 mm.; metatarsus, 2.22 mm.; tarsus, 0.69 mm.

Description. Anterior median eyes separated by their diameter in female, two-thirds diameter in male, closer to laterals. Posterior medians separated by three and one-half diameters in female, by two diameters in male, closer to laterals. The distinctive epigynum with sperm duct openings transverse slits on a median ridge (Fig. 143); palpus illustrated by Figures 111-113.

Distribution. Northeastern states and southeastern Canada.

Records. Connecticut: Salisbury, ♀. *Maine:* Orono, ♀. *Massachusetts:* West Gloucester, ♀; *Ipswich, ♀; *Blue Hills, ♀. *New Hampshire:* Meredith, ♀; Jackson, ♂. *New Jersey:* Ramsey, ♂, ♀. *New York:* Brant Lake, ♂; Lake Keuka, ♂; Elizabethtown, ♂; Newfane, ♂, ♀; Ithaca, ♂; Chesire, ♀; Sea Cliff, ♀. *Pennsylvania:* Potters Mills, ♀; Johnstown, ♂.

Ontario: Newmarket, ♀; Fort Severn, ♀.

CLUBIONA BRYANTAE Gertsch
Figures 114-115, 137, 174, 221

Clubiona agrestis Emerton, 1924, Psyche, vol. 31, p. 144, Fig. 6 (♂ syntypes from Holliston, Massachusetts, in the Museum of Comparative Zoology). Name preoccupied by *C. agrestis* Hentz.

Clubiona bryantae Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 16. New name for *C. agrestis,* preoccupied. Roewer, 1955, Katalog der Araneae, vol. 2a, p. 513.

Measurements. Female: Length 5.10-7.20 mm.; average 6.26 mm. Carapace 2.85 mm. long, 2.16 mm. wide. First femur, 1.80 mm.; patella, 0.69 mm.; tibia, 1.56 mm.; metatarsus, 1.11 mm.; tarsus, 0.63 mm. Fourth femur, 2.28 mm.; patella, 0.90 mm.; tibia, 1.20 mm.; metatarsus, 1.38 mm.; tarsus, 0.57 mm.

Male. Length 4.40-5.70 mm.; average 4.98 mm. Carapace 2.46 mm. long, 1.76 mm. wide. First femur, 1.90 mm.; patella, 0.97 mm.; tibia, 1.67 mm.; metatarsus, 1.20 mm.; tarsus, 0.66 mm. Fourth femur, 2.10 mm.; patella, 0.97 mm.; tibia, 1.67 mm.; metatarsus, 2.46 mm.; tarsus, 0.77 mm.

Description. Anterior median eyes more than their diameter apart, as far from larger laterals in female, closer in male. Posterior medians separated by more than three diameters in female, two and a half diameters in male, closer to slightly larger lateral eyes. Epigynum illustrated by Figure 137, palpus by Figures 114-115.

Records. Illinois: nr. Chicago, ♀. *Maine:* Mount Desert Isl., ♀. *Massachusetts:* Holliston, ♂, ♀; Blue Hills, ♂. *Michigan:* *Conway, ♂, ♀. *New York:* Lake Sebago, ♀. *Wyoming:* 13 mi. N. of Old Faithful, Yellowstone Natl. Park, ♀.

Ontario: Fort Albany, ♀.

CLUBIONA RILEYI Gertsch
Figures 157, 213

Clubiona rileyi Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 17, fig. 47 (♀ type from Itasca Park, Minnesota, in the American Museum of Natural History). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 517.

Clubiona elizabethae Kaston, 1945, Amer. Mus. Novitates, no. 1290, p. 4, fig. 43, ♀ (juv. ♀ type from Riverton, Connecticut in the American Museum of Natural History). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 514. NEW SYNONYMY.

Measurements. Female: Length 7.42 mm. Carapace 3.24 mm. long, 2.28 mm. wide. First femur, 2.64 mm.; patella, 1.26 mm.; tibia, 2.34 mm.; metatarsus, 1.80 mm.; tarsus, 1.02 mm. Fourth femur, 3.18 mm.; patella, 1.26 mm.; tibia, 2.58 mm.; metatarsus, 3.06 mm.; tarsus, 1.02 mm.

Description. Anterior median eyes their diameter apart. Posterior medians three diameters apart, closer to laterals. Epigynum illustrated by Figure 157. The male is not known.

Comment. The type of *C. elizabethae* lacks internal genitalia, thus is an immature.

Records. Connecticut: Meriden, ♀ (H. L. Johnson).

CLUBIONA KULCZYNSKII de Lessert
Figures 148-149, 158, 168, 217

Clubiona kulczynskii de Lessert, 1905, Rev. Suisse Zool., vol. 13, p. 647, fig. 13 (♂ type from Schuls, Graubünden, Switzerland at 1250 m. elev.). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 495. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1130.

Clubiona intermontana Gertsch, 1933, Amer. Mus. Novitates, no. 637, p. 9, figs. 10, 13 (♂ type from Slough Creek, Yellowstone National Park, Wyoming, in the American Museum of Natural History). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 515. NEW SYNONYMY.

Clubiona altana Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 16, fig. 54 (♀ type from Seba, Alberta, in the American Museum of Natural History). NEW SYNONYMY.

Measurements. Female: Length 4.80-7.75 mm.; average 5.71 mm. Carapace 2.64 mm. long, 1.86 mm. wide. First femur, 2.04 mm.; patella, 0.90 mm.; tibia, 1.50 mm.; metatarsus, 1.02 mm.; tarsus, 0.60 mm. Fourth femur, 2.52 mm.; patella, 0.96 mm.; tibia, 1.92 mm.; metatarsus, 2.40 mm.; tarsus, 0.72 mm.

Male: Length 4.35-5.04 mm.; average 4.72 mm. Carapace 2.34 mm. long, 1.65 mm. wide. First femur, 1.92 mm.; patella, 0.84 mm.; tibia, 1.50 mm.; metatarsus, 1.26 mm.; tarsus, 0.82 mm. Fourth femur, 2.66 mm.; patella, 0.90 mm.; tibia, 1.80 mm.; metatarsus, 2.34 mm.; tarsus, 0.82 mm.

Description. Anterior median eyes a little more than their diameter apart in female, by their radius in males, two thirds as far from larger lateral eyes. Posterior median eyes separated by two and a half times their diameter in female, by two diameters in male, closer to laterals. Epigynum illustrated by Figure 158, palpus by Figures 148-149.

Natural History. This species has been collected from lodgepole pine forest in the Rocky Mountains, and females with egg sac in a rolled up *Sambucus* leaf.

Distribution. Switzerland, Scandinavia, Kamchatka; Rocky Mountains, northern United States to Alaska.

Records. Colorado: 4 mi. N. of Allenspark, Boulder Co.; Crystal, Gunnison Co. *New York:* Summit of Mt. MacIntyre. *North Carolina:* Summit of Roan Mt. *Vermont:* Burke Mtn. *Wyoming:* Two Ocean Lk.; Emma Matilda Lake, Teton Co. *Alaska:* Tnoko; *Juneau; *5 mi. S. of Rapids, on Richardson Highway; *Matanuska.

Alberta: Banff, Seba Beach; Edmonton. *Newfoundland:* Spruce Brook. *Ontario:* Mattagami River, Smoky Falls. *Saskatchewan:* Lac La Rouge. *Yukon*: Marsh Lake.

CLUBIONA CALIFORNICA FOX

Figures 152-154, 167, 218

Clubiona californica Fox, 1938, Iowa State College Jour. Sci., vol. 12, p. 239, pl. 2, fig. 4 (♀ type from San Francisco, California, in the United States National Museum).

Measurements. Female: Length 4.62-6.06 mm.; average 5.53 mm. Carapace 2.37 mm. long, 1.62 mm. wide. First femur, 1.50 mm.; patella, 0.78 mm.; tibia, 1.11 mm.; metatarsus, 0.72 mm.; tarsus, 0.54 mm. Fourth femur, 1.68 mm.; patella, 0.78 mm.; tibia, 1.98 mm.; metatarsus, 1.68 mm.; tarsus, 0.60 mm.

Male: Length 3.78-4.80 mm.; average 4.27 mm. Carapace 1.98 mm. long, 1.44 mm. wide. First femur, 1.38 mm.; patella, 0.63 mm.; tibia, 1.26 mm.; metatarsus, 0.96 mm.; tarsus, 0.60 mm. Fourth femur, 1.62 mm.; patella, 0.66 mm.; tibia, 1.26 mm.; metatarsus, 1.56 mm.; tarsus, 0.60 mm.

Description. Anterior median eyes their diameter apart, slightly closer to laterals. Posterior medians separated by three diameters in female, by two in male. Epigynum illustrated by Figure 218.

Diagnosis. The dorsal division of the palpal apophysis is nearly the same thickness as the ventral division, and the ventral division is less than twice as long as the dorsal. (Figs. 152, 154) while in *C. canadensis* the ventral division is heavier and at least twice as long as the dorsal.

Records. California: Bodega Bay, ♀, ♂; Yosemite Natl. Park, ♀, ♂ (W. J. Gertsch).

CLUBIONA NORVEGICA Strand

Figures 146-147, 156, 164, 215

Clubiona norvegica Strand, 1900, Norske Vid. Selsk. Skrift, p. 30, fig. e (♂ type from Rösvandsholmen, Hatfjelddalen, Norway). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 497. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1138.

Clubiona canadensis, Emerton, 1909, Trans. Connecticut Acad. Sci., vol. 14, pl. 10, fig. 8 (err. det.). Kaston, 1948, Bull. Connecticut Geol., Nat. Hist. Surv., no. 70 (in part) fig. 1345. Not *C. canadensis* Emerton.

Clubiona carpenterae Fox, 1938, Iowa State College Jour. Sci., vol. 12, p. 240, pl. 2, fig. 7 (♀ type from Labrador in the United States National Museum). NEW SYNONYMY.

Measurements. Female: Length 4.65-7.26 mm.; average 6.70 mm. Carapace 2.82 mm. long, 1.98 mm. wide. First femur, 1.92 mm.; patella, 0.99 mm.; tibia, 1.62 mm.; metatarsus, 1.14 mm.; tarsus, 0.74 mm. Fourth femur, 2.52 mm.; patella, 0.92 mm.; tibia, 1.68 mm.; metatarsus, 2.24 mm.; tarsus, 0.74 mm.

Male. Length 4.86-5.28 mm.; average 5.07 mm. Carapace 2.35 mm. long, 1.59 mm. wide. First femur, 1.98 mm.; patella, 0.90 mm.; tibia, 1.74 mm.; metatarsus, 1.02 mm.; tarsus, 0.78 mm. Fourth femur, 2.16 mm.; patella, 0.78 mm.; tibia, 1.74 mm.; metatarsus, 2.04 mm.; tarsus, 0.72 mm.

Description. Anterior eyes their radius apart in female, anterior medians slightly more separated in male. Posterior medians separated by three diameters, closer to laterals, those of male closer together. The male has a prolateral ridge on the attenuated chelicerae. The ventral division of the palpal apophysis of the palpus is very much longer than the dorsal division and both divisions extend ventrally (Figs. 146-147). The epigynum (Fig. 156) is distinct.

Distribution. England, Scandinavia, Finland, Northern United States, Canada.

Records. Minnesota: Itasca Park. *New York:* Long Lake, Adirondack Mountains. *Oregon:* Scappoose. *Utah:* W. 111°55′: N. 40°15′. *Washington:* Lupez Island. *Alaska:* College; Kobuk Riv., between Shunguak and Kiana; 86 mi. N. of Fairbanks, nr. Alaska Lodge.

Labrador: Butte Harbor; Battle Harbor. *Mackenzie:* Reindeer Station; Pearson Point, Great Slave Lake. *Manitoba:* Churchill; Manitoba; Victoria Beach. *Newfoundland:* NE. of Belle Island. *Ontario:* Weller Bay; Hallowell; Cape Henrietta Maria; Mindemoya, Lake Manitoulin.

CLUBIONA CANADENSIS Emerton

Figures 150-151, 155, 163, 216

Clubiona canadensis Emerton, 1890, Trans. Connecticut Acad. Sci., vol. 8, p. 181, pl. 5, fig. 4 (♂, ♀ syntypes from Mt. Washington, New Hampshire, in the Museum of Comparative Zoology). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 514. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1115.

Clubiona pacifica Banks, 1896, Trans. Amer. Ent. Soc., vol. 23, p. 65 (♀ syntypes from Olympia, Washington, in the Museum of Comparative Zoology). Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1139. NEW SYNONYMY.

Measurements. Female: Length 6.00-11.50 mm.; average 7.76 mm. Carapace, 2.92 mm. long, 2.08 mm. wide. First femur, 2.16 mm.; patella, 1.04 mm.; tibia, 1.52 mm.; metatarsus, 1.16 mm; tarsus, 0.76 mm. Fourth femur, 2.56 mm.; patella, 1.04 mm.; tibia, 1.76 mm.; metatarsus, 2.24 mm.; tarsus, 0.76 mm.

Male: Length 4.80-8.00 mm.; average 6.07 mm. Carapace 2.82 mm. long, 2.07 mm. wide. First femur, 2.52 mm.; patella, 1.14 mm.; tibia, 2.10 mm.; metatarsus, 1.59 mm.; tarsus, 0.93 mm. Fourth femur, 3.00 mm.; patella, 1.14 mm.; tibia, 2.40 mm.; metatarsus, 2.88 mm.; tarsus, 0.98 mm.

Description. Anterior median eyes one-half to two-thirds their diameter apart, slightly farther (in female), closer (in male) to lateral eyes. Posterior medians three and a half diameters apart in female, two and a quarter in male, two-thirds as far from laterals. Epigynum illustrated by Figure 155, often margin disappearing in genital groove; male palpus illustrated by Figures 150-151 differentiate it from *C. californica*.

Natural History. This species has been collected from trees and shrubs, from under loose bark, under stones, fallen leaves and moss. Individuals mature from June to September. It usually hibernates in the immature stage, and immature specimens may be found as late as July 16, with mature individuals appearing after the middle of June. A female from Nova Scotia was collected with her egg sac in September. The egg sac was a flat oval measuring 18 by 14 mm.

Distribution. Western Mountains, northern United States, Canada to Alaska.

Records. California: Yosemite; Echo Lake; Ben Lomond; Mount Shasta; Marin Co. *Colorado:* Crater Lk., Pitkin Co.; Crystal and Gothic, Gunnison Co. *Connecticut:* *New Haven; *Riverton; *Salisbury. *Idaho:* Crow Creek. *Maine:* South Harpswell; Baxter St. Park. *Michigan:* Crawford Co. *Minnesota:* Minneapolis. *Montana:* Numa Ridge, Glacier Natl. Park. *New Hampshire:* Pike, nr. Gorham; Randolph; *Mt. Washington, *Franconia; *Lake Winnepesaukee. *New Jersey:* Kittatinny Mtn., Warren Co. *New York:* Callicoon; Snyder Lake; Hunter; Point Breeze; Artist's Brook; Trout Pond; Slide Mountain, Adirondack Lodge; Mt. McIntyre; Ithaca; Speculator; Hunter Mtn., Mt. Whiteface; Lake Keuka; *Wilmington; *Lake Cinnamon; Riders Mills; Stamford. *North Carolina:* Frying Pan Gap; *Linville. *Oregon:* McCredie Springs; Mary's Peak; Salt Creek Pass; Oak Ridge; Lake of the Woods; McKenzie Bridge; Cave City; Bandon; Mt. Hood; Spencer Butte; Fossil Point; Marshfield; Eugene; Medford; Colton; Corvallis; Portland; McMinnville, Hood River Co. *Pennsylvania:* Laurenceville. *Tennessee:* Great Smoky Mtns. Natl. Park. *Utah:* Silver Lake; Fish Lake; Salt Lake City; 15 m. N. of Boulder; Pine Isl. Lake. *Vermont:* Rutland; Mt. Mansfield. *Virginia:* Mountain Lake; Siles Co. *Washington:* Mt. Ranier; *Olympia; *Camp Umatilla; *Chihalis; Seattle; *Olympic Peninsula; *Lopez Isl.; *San Juan Isl.; *Cypress Isl.; *Shaw Isl.; *Orcas Isl.; *Blakely Isl.; *Spieden Isl.; Walla Walla. *Wisconsin:* Calumet Co.; Door Co.; Manitowoc Co. *Wyoming:* Grand Teton Natl. Park.

Alaska: Shagway; Admiralty Islands; Nakutat; Aleutian Island; *Juneau; Kuhak Bay; *Haines.

Alberta: Seba Beach; Fitzgerald; Devils Lake; Lake Louise; Lembrich Falls. *British Columbia:* Wellington; Vancouver; *Kaslo; *Bear Lake; *Kaslo Creek; *Glacier; *Balfour; *Ainsworth; *Metlakatla. *Labrador:* Paradise River; *Battle Harbor. *Manitoba:* La Pas; Ohnr; Victoria Beach; Lockhead; Horse Shoe Lake. *New Brunswick:* Fredricton. *Newfoundland:* Humber River; Stephenville Crossing, Bay of Saint George. *Nova Scotia:* Digby; Barrington. *Ontario:* Nipigon; Mindemoya, Manitoulin; Wellington: Silver Inlet, Thunder Bay; Deux Rivières; Port Arthur; Island 1008, Lake Temagami; Kakinor; Algonquin Park; Costello Creek, Algonquin Park; Smoke Lake, Algonquin Park; Little Vermilion Lake; Kagawong, Manitoulin; Pobler Island; Hollowalk; Eva L. Quetico Park; Altonapeskat; Grimthop, Manitoulin; Smoky Falls, Mattagami Riv.; Beaver Riv., Grey Co.; *Shea's Bay, Anticosti. *Quebec:* *Montreal; Gaspé; Ellis Bay, Anticosti. *Saskatchewan:* Lac La Rouge; Waterton; Waskesiu.

CLUBIONA ADJACENS Gertsch and Davis

Figures 54-55, 160

Clubiona adjacens Gertsch and Davis, 1936, Amer. Mus. Novitates no. 881, p. 19, figs. 35 (♂ type from Cameron Co., Texas, in the American Museum of Natural History). Gertsch, 1941, *ibid.*, no. 1148, p. 8, figs. 30, 31. Roewer, 1955, Katalog der Araneae, vol. 2a, p. 513.

Measurements. Male: Total length 2.30 mm. Carapace 1.05 mm. long, 0.75 mm. wide. First femur, 0.72 mm.; patella, 0.38 mm.; metatarsus, 0.48 mm.; tarsus, 0.30 mm.

Description. Anterior median eyes their radius apart, half as far from laterals. Posterior medians two diameters apart, one from laterals. Figures 54, 55, 160 were made after drawings by Gertsch and Davis (1936) and Gertsch (1941). The female is not known.

CLUBIONA GERTSCHI, new species

Figures 50-51, 84, 195, 232

Type. Male holotype from under stone on Mt. Washington, New Hampshire, July 4, 1907 (J. H. Emerton) in the Museum of Comparative Zoology.

Measurements. Female: Length 4.93 mm. Carapace 2.23 mm. long, 1.50 mm. wide. Abdomen, 2.83 mm. long, 1.70 mm. wide. First femur, 1.29 mm.; patella, 0.67 mm.; tibia, 1.02 mm.; metatarsus, 0.73 mm.; tarsus, 0.42 mm. Fourth femur, 1.53 mm.; patella, 0.75 mm.; tibia, 1.33 mm.; metatarsus, 1.33 mm.; tarsus, 0.52 mm.

Male: Length 4.14 mm. Carapace 1.92 mm. long, 1.26 mm. wide. Abdomen 2.22 mm. long, 1.35 mm. wide. First femur, 1.20 mm.; patella, 0.60 mm.; tibia, 1.08 mm.; metatarsus, 0.75 mm.; tarsus, 0.48 mm. Fourth femur, 1.47 mm.; patella, 0.59 mm.; tibia, 1.26 mm.; metatarsus, 1.47 mm.; tarsus, 0.55 mm.

Description. Female: Clypeus equal in height to one-fourth diameter of an anterior median eye. First row of eyes slightly recurved as seen from front and narrower than second row, the median eyes separated by less than one diameter, nearer larger laterals. Second row of eyes slightly procurved, the medians separated by slightly more than two diameters, nearer the somewhat larger laterals. Chelicerae armed with three small teeth on lower margin of furrow, the first two being close together and smallest.

Carapace red-brown, unmarked except for dark median groove and black rings surrounding eyes, clothed with fine sub-erect dark hairs and scattered dark bristles which are longest and most numerous in ocular area. Sternum light yellow-brown, margins darker brown with prominent dark spots at coxae. Chelicerae dark red-brown, provided with conspicuous lateral condyles. Endites light brown, as is the distal margin of labium, the rest of the labium being dark brown. Coxae and legs light yellow-brown, clothed with sub-erect long hairs and scattered black bristles. Dorsum of abdomen light red-brown with many scattered fine light yellow spots shading to a darker color in posterior regions. There is a faint indication of posteriorly directed chevrons on the distal third of abdomen. Dorsum is clothed with fine recumbent pubescent hairs and scattered sub-erect dark bristles which are coarser and most numerous at base. Venter of abdomen light yellow-brown with two longitudinal lines of small dark spots near the midline. Epigynum as illustrated in Figure 84.

Male. Clypeus equal in height to one-fifth of diameter of an anterior median eye. First row of eyes straight as seen from front and narrower than the second row, median eyes separated by nearly two-thirds diameter, nearer equal laterals. Median ocular area broader than long, narrowed in front; eyes equal in size. Chelicerae with well developed lateral condyles armed with three small teeth on lower margin of furrow, the tooth nearest base of fang the smallest. Coloration similar to that of female. Palpus as illustrated in Figures 50-51.

Diagnosis. The character of palpi and epigynum shows that this species is most closely related to *C. johnsoni* and *C. kastoni*. *Clubiona gertschi* is easily distinguished from *C. kastoni* in that the posterior median eyes are separated by two diameters. The larger size and coloration of the abdomen readily distinguish *C. gertschi* from *C. johnsoni*.

Distribution. It is interesting to note that this species has been taken only on mountain tops in Vermont, New Hampshire and Maine, where it has been found under stones.

Records. Maine: Mount Katahdin, ♀ allotype, July (J. H. Emerton). *New Hampshire:* Mount Moosilauke, ♀ paratype, July (E. B. Bryant); Mount Washington, ♂ holotype, July (J. H. Emerton). *Vermont:* Mt. Mansfield, ♂, ♀ (H. and L. Levi).

Clubiona rhododendri Barrows

Figures 38, 39, 230

Clubiona rhododendri Barrows, 1945, Ann. Ent. Soc. Amer., vol. 38, p. 72, pl. 1, figs. 2, 4 (♂ and ♀ types from New Found Gap, Great Smoky Mountain National Park, Tennessee).

Measurements. Male: Length, 3.48 mm. Carapace 1.74 mm. long, 1.26 mm. wide. First femur, 1.38 mm.; patella, 0.60 mm.; tibia, 1.32 mm.; metatarsus, 0.93 mm.; tarsus, 0.51 mm. Fourth femur, 1.62 mm.; patella, 0.60 mm.; tibia, 1.38 mm.; metatarsus, 1.59 mm.; tarsus, 0.54 mm.

Description. Male: Anterior median eyes their radius apart, half as far from slightly larger lateral eyes. Posteror medians two diameters apart, closer to smaller laterals. Palpus illustrated by Figures 38-39. The female specimens have apparently been lost.

Diagnosis. This species is most closely related to *C. abbotii,* but is readily distinguished from *abbotii* in that the tibial apophyses of *rhododendri* are directed ventrad and the retrolateral apophysis is nearly as broad as long, whereas in *abbotii* the tibial apophyses are directed distad and the retrolateral apophysis is distinctly longer than broad.

Natural History. This species has been taken from rhododendron bushes and from the leaves under these bushes along streams from 2,550 feet up to 5,000 feet elevation. *Clubiona abbotii* has not been collected in the locality in which *rhododendri* has been collected.

CLUBIONA PLUMBI Gertsch

Figures 60-61, 95, 250

Clubiona plumbi Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 12, figs. 21-22 (♂ type from Long Island, New York, in the American Museum of Natural History). Barnes, 1953, Amer. Mus. Novitates, no. 1632, p. 16.

Measurements. Female: Length 3.6 mm. Carapace 1.79 mm. long, 1.20 mm. wide. First femur, 0.94 mm.; patella, 0.52 mm.; tibia, 0.78 mm.; metatarsus, 0.63 mm.; tarsus, 0.39 mm. Fourth femur, 1.40 mm.; patella, 0.66 mm.; tibia, 1.17 mm.; metatarsus, 1.33 mm.; tarsus, 0.42 mm.

Male: Length: 2.95-4.1 mm. One male length 2.95 mm. Carapace, 1.36 mm. long, 0.93 mm. wide.

Description. Anterior median eyes their radius apart, half as far from laterals. Posterior median eyes one and one half (Massachusetts) to two diameters (North Carolina) apart, less than a diameter from laterals.

Diagnosis. This species is closely related to *C. pikei* Gertsch, but is smaller, and the eyes are spaced closer.

Natural History. Found in dry beach habitats such as dune grass and dry beach drift (Barnes, 1953).

Records. Massachusetts: Wellfleet, ♀, ♂ (N. Banks). *North Carolina:* Carrot Isl., Carteret Co., ♀, ♂ (R. Barnes).

CLUBIONA OPEONGO, new species
Figures 86, 234

Type. Female holotype from Lake Opeongo, Algonquin Park, Ontario, July 20, 1943, in the American Museum of Natural History.

Measurements. Female: Length 3.60 mm. Carapace 1.82 mm. long, 1.30 mm. wide. First femur, 1.05 mm.; patella, 0.51 mm.; tibia, 0.79 mm.; metatarsus, 0.59 mm.; tarsus, 0.38 mm. Fourth femur, 1.35 mm.; patella, 0.57 mm.; tibia, 1.00 mm.; metatarsus, 1.33 mm.; tarsus, 0.45 mm.

Description. Anterior median eyes their diameter apart, less than their diameter from laterals. Posterior median eyes a little more than three diameters apart, two from laterals. The color is yellow-white except for the black eye-rings.

Diagnosis. The openings of the epigynum (Fig. 86) are similar to that of *C. littoralis,* but the ducts and receptacles are closer to each other.

CLUBIONA LITTORALIS Banks
Figures 70-71, 87, 201, 242

Clubiona littoralis Banks, 1895, Jour. New York Ent. Soc., vol. 3, p. 79 (♂, ♀ syntypes from Sea Cliff, Long Island, New York, in the Museum of Comparative Zoology). Barnes, 1953, Amer. Mus. Novitates, no. 1632, p. 15. Roewer, 1955, Katalog der Araneae, vol. 2a, p. 515. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1131.

Clubiona latifrons Emerton, 1913, Trans. Connecticut Acad. Sci., vol. 18, p. 220, pl. 2, fig. 12 (♂, ♀ syntypes from Plum Island, Ipswich, Massachusetts, in the Museum of Comparative Zoology).

Measurements. Female: Length 4.44-7.80 mm.; average 6.20 mm. Carapace 2.76 mm. long, 1.86 mm. wide. First femur, 1.62 mm.; patella, 0.96 mm.; tibia, 1.50 mm.; metatarsus, 1.14 mm.; tarsus, 0.66 mm. Fourth femur, 2.01 mm.; patella, 0.96 mm.; tibia, 1.65 mm.; metatarsus, 2.22 mm.; tarsus, 0.66 mm.

Male: Length 4.26-5.46 mm.; average 5.06 mm. Carapace 2.40 mm. long, 1.56 mm. wide. First femur, 1.32 mm.; patella, 0.72 mm.; tibia, 1.26 mm.; metatarsus, 1.08 mm.; tarsus, 0.60 mm. Fourth femur, 1.56 mm.; patella, 0.72 mm.; tibia, 1.35 mm.; metatarsus, 1.71 mm.; tarsus, 0.60 mm.

Description. Anterior median eyes three-fourths diameter apart, twice as far from larger lateral eyes. Posterior medians three and a half diameters apart in female, less than three in male, closer to laterals.

Diagnosis. This is one of the most readily distinguished species of the *abbotii* group because of its larger size, the very broad cephalic part of the cephalothorax, the more widely spaced eyes, and the heavy and protruding chelicerae. The male palpus (Figs. 70-71) is distinct as is shown in the figures. The epigynum of the female somewhat resembles that of *Clubiona kastoni*, but differs in several details as shown in Figure 87.

Natural History. This species has been collected from salt marsh grass (Barnes, 1953).

Distribution. Ontario, Atlantic coast states to Florida.

Records. Florida: Cedar Keys, ♀. *Massachusetts:* Martha's Vineyard, ♂, ♀; *Plum Isl., Ipswich, ♂, ♀; *Dighton, ♂, ♀: *Nantucket, ♀, ♂. *New Jersey:* Cape May, ♀. *North Carolina:* Beaufort, Carteret Co. *New York:* Sea Cliff, L. I., ♂, ♀; Amagansett, L. I., ♀; Gardiners Isl., ♂.

Ontario: Barrie Isl., Manitoulin Lake, ♀.

CLUBIONA BISHOPI, new species

Figures 40-41

Type. Male holotype from Cheat Range, Durbin, West Virginia, August 1, 1943, in the American Museum of Natural History.

Measurements. Male: Length 4.36 mm. Carapace 2.02 mm. long, 1.52 mm. wide. Abdomen 2.40 mm. long, 1.52 mm. wide. First femur, 1.44 mm.; patella, 0.60 mm.; tibia, 1.35 mm.; metatarsus, 0.90 mm.; tarsus, 0.48 mm. Fourth femur, 1.68 mm.; patella, 0.69 mm.; tibia, 1.38 mm.; metatarsus, 1.62 mm.; tarsus, 0.51 mm.

Description. Clypeus equal in height to one-fourth diameter of an anterior median eye. First row of eyes straight as seen from front and narrower than the second row, median eyes separated by radius of one of them, an equal distance from slightly larger oval laterals. Second row of eyes straight, median eyes separated by one and a half times diameters, two-thirds as far from smaller laterals. Eyes subequal in size. Chelicerae armed with four small teeth on lower margin of the furrow; teeth nearest base of fang very small. Leg spines robust and brown in color.

Carapace pale yellow-brown and unmarked except for the dark median groove and the black rings surrounding the eyes. Chelicerae attenuated, orange-brown, clothed sparsely with long erect black bristles on anterior faces. Labium and endites light yellow-brown except for pale yellow distal margins. Sternum pale yellow with light yellow-brown margins. Coxae and proximal segments of the legs concolorous with sternum, distal segments of legs light yellow-brown. Dorsum of abdomen light rusty-brown flecked with small spots of pale yellow. An indistinct median stripe of light brown extends from base of abdomen to a point about half-way back on dorsum. Venter of abdomen unmarked pale yellow-brown.

Diagnosis. This species is closely related to *C. rhododendri*, but may be readily distinguished from that species in that the dorsal tibial apophysis of *C. bishopi* (Figs. 40, 41) is bluntly rounded, whereas in *C. rhododendri* it is sharply pointed.

Records. Maine: Katahdin Stream Camp, Piscataquis Co. *New York:* Jordanville, ♂ paratype, November (C. Crosby and H. Dietrich). *West Virginia:* Cheat Range, Durbin, ♂, August. *Ontario:* Mindemoya, Manitoulin, ♂ paratype, July (T. Kurata); Lake Archamboult, ♂ paratype, August (Kurata).

Clubiona kastoni Gertsch
Figures 46-47, 81, 196, 233

Clubiona kastoni Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 14, figs. 37-39 (♂ type from Norwalk, Connecticut, in the American Museum of Natural History). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 515.

Measurements. Female: Length 3.12-5.22 mm.; average 4.21 mm. Carapace 1.86 mm. long, 1.26 mm. wide. First femur, 1.08 mm.; patella, 0.54 mm.; tibia, 0.86 mm.; metatarsus, 0.66 mm.; tarsus, 0.38 mm. Fourth femur, 1.35 mm.; patella, 0.54 mm.; tibia, 1.14 mm.; metatarsus, 1.44 mm.; tarsus, 0.42 mm.

Male: Length 3.06-4.02 mm.; average 3.65 mm. Carapace 1.80 mm. long, 1.32 mm. wide. First femur, 1.32 mm.; patella, 0.54 mm.; tibia, 1.14 mm.; metatarsus, 0.84 mm.; tarsus, 0.48 mm. Fourth femur, 1.62 mm.; patella, 0.60 mm.; tibia, 1.20 mm.; metatarsus, 1.56 mm.; tarsus, 0.50 mm.

Description. Anterior median eyes two-thirds diameter apart, closer to slightly larger laterals. Posterior eyes two and a half diameters apart, one and a quarter diameters from laterals.

Diagnosis. The tibial apophyses of the palpus of *C. kastoni* (Figs. 46, 47) are more robust and the retrolateral apophysis is much broader at the base than is the case in closely related *C. saltitans,* and the cheliceral keels found in *saltitans* are missing in the males of *kastoni.* The sperm receptacles of the epigynum of *C. kastoni* (Fig. 81) are widely separated and the sperm duct openings are oval in shape, whereas in *C. saltitans,* the sperm receptacles are closer together and the sperm duct openings are nearly round.

Distribution. Most parts of the United States and southern Canada.

Records. California: Weed. *Connecticut:* Columbia; Norwalk, ♂ holotype, ♀ allotype, ♀ paratypes; Cheshire, ♀ paratype; *Macedonia; *Portland; *Watertown; *Wilton; New Haven. *District of Columbia:* Washington. *Maine:* Wales; Orono, ♀ paratype. *Massachusetts:* Boston; Holliston; Cambridge. *Nebraska:* nr. Lincoln. *New Hampshire:* Gilmantown; Mt. Washington. *New Jersey:* Ramsey. *New York:* Lake Sebago, Interstate Park, ♂ paratype; Ithaca, ♂, Sea Cliff; Flushing; Black Brook; Long Pond; Cheshire; Bolton; Lake George; Stamford; Yonkers; Wappingers Falls; Cragsmoor. *North Carolina:* Mt. Graybeard. *Ohio:* Cantwell Cliffs, Hocking Co. *Oregon:* Goble, ♂ paratypes; Scappoose, ♂, ♀ paratypes; Portland; nr. McMinnville. *Tennessee:* Kingston, ♂ paratype. *Vermont:* South Newfane. *Wisconsin:* St. Croix Falls.

Alberta: Edmonton. *British Columbia:* Wellington. *Ontario:* Toronto; South Tea Lake, Algonquin Park; Wellington; Sproule Bay, Lake Opeongo; Port Credit. *New Brunswick:* Newburg.

CLUBIONA ESTES, new species

Figures 78, 197, 247

Type. Female holotype from 10 miles west of Estes Park, Rocky Mountain National Park, Colorado, July 8, 1949 (W. J.

and J. W. Gertsch) in the American Museum of Natural History.

Measurements. Female: Length 4.23 mm. Carapace 1.70 mm. long, 1.27 mm. wide. Abdomen 2.73 mm. long, 1.73 mm. wide. First femur, 0.77 mm.; patella, 0.47 mm.; tibia, 0.70 mm.; metatarsus, 0.50 mm.; tarsus, 0.40 mm. Fourth femur, 1.33 mm.; patella, 0.47 mm.; tibia, 0.87 mm.; metatarsus, 1.07 mm.; tarsus, 0.43 mm.

Description. Clypeus equal in height to one-sixth diameter of an anterior median eye. First row of eyes straight as seen from front. Eyes separated by radius of one of them. Second row of eyes very slightly procurved, median eyes separated by three times the diameter of one of them, nearer the equal lateral eyes. Eyes unequal in size. Chelicerae armed with four teeth on lower margin of furrow; first two being close together and very small.

Carapace very light yellow-brown, unmarked except for very short dark median groove and black eye rings. Sternum pale yellow with a light brown border and two light brown spots on margin at third coxae and two dark brown spots on margin at fourth coxae. Sternum clothed with long and dark sub-erect hairs in median portion and erect dark bristles at margins. Chelicerae brown and clothed on anterior faces with scattered pubescent hair and long black bristles. Endites and labium light brown except for a thin band of light yellow at distal margins, and clothed with scattered black bristles. Coxae and femora very pale yellow, with remainder of legs a very light yellow-brown. Dorsum of abdomen a very pale yellow, unmarked, slightly darker posteriorly, sides and venter concolorous with dorsum and likewise unmarked.

Diagnosis. This species is closely related to *C. mutata,* but is larger. The anterior median eyes of *C. estes* are separated by the radius of one of them, whereas in *C. mutata,* the anterior medians are separated by a diameter. The shape of the sperm duct openings of the epigyna (Fig. 78) differ slightly in shape, as do other details.

Clubiona odelli, new species

Figures 82, 190, 231

Type. Female holotype from North Creede, Colorado, July 1934 (F. M. Carpenter) in the Museum of Comparative Zoology.

Measurements. Female. Length 6.12 mm. Carapace 2.16 mm. long, 1.53 mm. wide. Abdomen 4.08 mm. long, 2.25 mm. wide. First femur, 1.20 mm.; patella, 0.66 mm.; tibia, 1.02 mm.; metatarsus, 0.72 mm.; tarsus, 0.42 mm. Fourth femur, 1.50 mm.; patella, 0.72 mm.; tibia, 1.26 mm.; metatarsus, 1.47 mm.; tarsus, 0.54 mm.

Description. Clypeus equal in height to one-sixth diameter of an anterior median eye. First row of eyes very slightly procurved as seen from front, the median eyes separated by one-half diameter, slightly farther from larger laterals. Second row of eyes nearly straight, medians separated by approximately two and a half diameters, less than one and a half diameters from subequal laterals; the eyes equal in size. Chelicerae armed on lower margin with three teeth, the first being the smallest.

Carapace light yellow-brown, unmarked except for dark median groove and black eye rings. Sternum pale yellow with darker margins and distinct dark spots on margin at fourth coxae. Chelicerae red-brown with scattered long black bristles on anterior face. Endites and labium brown, except for light yellow distal margins. Legs and coxae pale yellow and clothed with long dark hairs and scattered bristles. Dorsum of abdomen pale yellow with scattered light gray spots, a little darker at posterior end. A faint, light yellow lanceolate stripe extends along midline. Venter of abdomen pale yellow.

Diagnosis. The epigynum (Fig. 82) has the same general characteristics as that of *C. abbotii abbotoides*, but may be distinguished from that species by its larger size, and by differences in details.

Natural History. Found under rocks and logs in dry areas.

Record. Colorado: Piedra, 7000 ft., Archuleta Co. (H. and L. Levi).

CLUBIONA ABBOTII ABBOTII L. Koch

Figures 42-43, 83, 181-182, 236

Clubiona abbotii L. Koch, 1866, Die Arachniden-Familie der Drassiden, p. 303, pl. 12, fig. 193 (♀ type from North America: Baltimore). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 513. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1107.

Clubiona rubra Keyserling, 1887, Verhandl. Zool. Bot. Gesell. Wien, vol. 37, p. 436, pl. 6, fig. 12 (♂ type from Cambridge, Massachusetts, in the Museum of Comparative Zoology).

Clubiona bufonis Chamberlin, 1925, Bull. Mus. Comp. Zool., vol. 67, p. 220 (♂ type from Upper Missouri River in the Museum of Comparative Zoology). NEW SYNONYMY.

Clubiona procteri, Bryant, 1944, Psyche, vol. 52, p. 187, fig. 9 (♀, err. det.).

Measurements. Female: Length 3.66-5.70 mm.; average 4.54 mm. Carapace 2.35 mm. long, 1.32 mm. wide. First femur, 1.32 mm.; patella, 0.60 mm.; tibia, 0.90 mm.; metatarsus, 0.69 mm.; tarsus, 0.39 mm. Fourth femur, 1.74 mm.; patella, 0.60 mm.; tibia, 1.20 mm.; metatarsus, 1.38 mm.; tarsus, 0.43 mm.

Male: Length 3.24-4.40 mm.; average 3.76 mm. Carapace 1.74 mm. long, 1.20 mm. wide. First femur, 1.43 mm.; patella, 0.67 mm.; tibia, 1.20 mm.; metatarsus, 0.90 mm.; tarsus, 0.52 mm. Fourth femur, 1.83 mm.; patella, 0.67 mm.; tibia, 1.30 mm.; metatarsus, 1.67 mm.; tarsus, 0.52 mm.

Description. Anterior median eyes their diameter apart in female, less than the radius apart in male, closer to larger laterals. Posterior medians separated by two and a half diameters in female, by more than two diameters in male, closer to laterals. Epigynum illustrated by Figure 83, palpus by Figures 42-43.

Comments. This species is a very common and widespread clubionid which shows considerable variation throughout its range. *C. abbotii* has been divided by the author into two subspecies, *C. a. abbotii* and *C. a. abbotoides.* Chamberlin and Ivie originally described *C. abbotoides* as a new species, but since these spiders show constant minor differences from *C. abbotii,* and since *C. abbotii* has not been found in the range of *abbotoides,* it is logical to assume that *abbotoides* is a geographic race of *abbotii.* There are indications that with further study other subspecies will be found to exist.

Diagnosis. C. abbotii is most closely related to *C. newnani,* but is readily distinguished from that species. In *C. newnani,* the tooth on the middle of the bulb is distinctly longer than in *abbotii* and the retrolateral apophysis of *newnani* is greatly swollen ventrally.

Distribution. Southern Canada and most parts of the United States, rare on Pacific coast and the Southwest.

Records. Alabama: *Andalusia; Hatchet Creek; Auburn, S. of Ariton; Mobile. *Colorado:* Fountain Valley. *Connecticut:* Norwalk; *Branford; *Burnet Corners; Cheshire; Hadlyme; *Jordan; New Haven; *Portland; Sandy Hook. *District of Columbia:* Washington. *Florida:* Orlando; Lake Co.; Alachua Co. *Georgia:* 5 mi. N. of Macon; *Okefenokee Swamp; *S. of Lake Park; *4 mi. NE. of Sylvania. *Illinois:* Fox Lake; Havana; Urbana. *Indiana:* *Richmond; *Valparaiso; *Arlington. *Kentucky:* Nr. Louisville; Summit. *Louisiana:* Shreveport; Tallulah; Baton Rouge; Sorrento. *Maine:* Falmouth. *Maryland:* College Park; Baltimore; Smithsburg. *Massachusetts:* Amherst; *Nantucket; Cambridge; Windsor; Holliston; Clarendon. *Michigan:* Ann Arbor; *Grand Marshes; Douglas Lake; Pawpaw; Selfridge Field. *Minnesota:* Fort Snelling, Albert Lea; Minneapolis, Lake Co.; Lake Pepin. *Mississippi:* Lucedale; Agricultural College. *Montana:* Canyon Creek. *Nebraska:* Badlands. *New Hampshire:* Randolph; Hollis; Fitzwilliam; Moosilauke; Squam Lake. *New Jersey:* Pine Brook; Ramsey. *New York:* Plattsburg; Onondaga Co.; Bergen Beach; Lake Sebago, Interstate Park; Staten Isl.; Long Isl.; Ithaca; Poughkeepsie; Sea Cliff; Ringwood; Renwick; Flushing; Shelter Island; Orient; Mendon Ponds, Monroe Co.; Spencer; Gardiners Isl.; McLean; Winthrop Beach; New Rochelle; Old Forge; Mt. Marcey; Black Brook, Clinton Co.; Freeville; Raquette Lake; Letchworth Park; Wawbeek; Jordanville; Labrador Pond, Tompkins Co.; Slide Mtn.; Sodus Point; Cinnamon Lake; Rochester; Wilminton Notch; *Gloversville; *Lake Bluff; Juanita Isl.; Albany; Kingston; *Cragsmoor; *Maratanza Lake; *Pine Isl.; *Hunter. *North Carolina:* *Belsam; *Mt. Graybeard; *Clay Co.; Raleigh. *Ohio:* *Columbus; Springfield; Gambier; Sandusky. *Oklahoma:* Texas Co. *Oregon:* Eugene. *Pennsylvania:* North Wales; *Pittsburgh; Schenley Park, Pittsburgh; Allegheny Co. *Tennessee:* Knoxville, Newfound Gap; Kingston. *Texas:* Orange; Liberty; Dallas; Port Arthur; Brazos Co.; Kerrville; New Braunfels; Houston. *Utah:* *Clear Creek, Raft River Mtns.; Salt Lake City; W. side Utah Lake; *Moab. *Virginia:* Glencarlyn; Falls Church. *Wisconsin:* Dane Co.; Lincoln Co.; Marathon Co.; Monroe Co.; Racine Co.; Taylor Co.

Alberta: Beaver Lake. *Ontario:* Galsnear Point; Owen Point; Point Pelee; 1 mi. E. of Kingston; Wellington; North Bay; Huyks Bay; Huyks Point; 3 mi. N. of Newburg; 1 mi. W. of Newburg, Newmarket; Brown Hill; Toronto; Elmhurst Beach; Port Credit; Ottawa; Warner; Lake Archamboult. *Manitoba:* Horseshoe Lake; Le Pas.

CLUBIONA ABBOTII ABBOTOIDES Chamberlin and Ivie

Figures 44-45, 79, 183, 237

Clubiona abbotoides Chamberlin and Ivie, 1946, Bull. Univ. Utah, vol. 36, no. 13, p. 10, figs. 13-14 (♂ type from 1.5 mi. NE. of Fruitland, Idaho, in the University of Utah Collection).

Measurements. Female: Length 3.78-5.20 mm.; average 4.33 mm. Carapace 1.86 mm. long, 1.26 mm. wide. First femur, 1.14 mm.; patella, 0.54 mm.; tibia, 0.90 mm.; metatarsus, 0.60 mm.; tarsus, 0.52 mm. Fourth femur, 1.50 mm.; patella, 0.60 mm.; tibia, 1.14 mm.; metatarsus, 1.32 mm.; tarsus, 0.54 mm.

Male: Length 3.48-4.10 mm.; average 3.76 mm. Carapace 1.83 mm. long, 1.26 mm. wide. First femur, 1.26 mm.; patella, 0.54 mm.; tibia, 1.02 mm.; metatarsus, 0.78 mm.; tarsus, 0.39 mm. Fourth femur, 1.50 mm.; patella, 0.60 mm.; tibia, 1.20 mm.; metatarsus, 1.38 mm.; tarsus, 0.45 mm.

Diagnosis. Only careful comparison of the genitalia (Figs. 44-45, 79) distinguishes this from *C. a. abbotii.*

Records. Idaho: 2 mi. NE. of Fruitland; 1.5 mi. NE. of Fruitland (many records).

CLUBIONA PIKEI Gertsch

Figs. 56-57, 91, 189, 249

Clubiona pikei Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 10, figs. 25-27 (♂ type from Long Island, New York, in the American Museum of Natural History). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 516.

Clubiona plumbi, Kaston, 1948, Bull. Connecticut Geol. Nat. Hist. Surv., no. 70, p. 379 (in part; err. det.).

Measurements. Female: Length 3.54-5.50 mm.; average 4.34 mm. Carapace 1.80 mm. long, 1.14 mm. wide. First femur, 0.96 mm.; patella, 0.58 mm.; tibia, 0.74 mm.; metatarsus, 0.57 mm; tarsus, 0.36 mm. Fourth femur, 1.38 mm.; patella, 0.63 mm.; tibia, 0.96 mm.; metatarsus, 1.20 mm.; tarsus, 0.39 mm.

Male: Length 3.18-4.75 mm.; average 3.94 mm. Carapace 1.86 mm. long, 1.32 mm. wide. First femur, 1.20 mm.; patella, 0.54 mm.; tibia, 0.96 mm.; metatarsus, 1.02 mm.; tarsus, 0.42 mm. Fourth femur, 1.56 mm.; patella, 0.54 mm.; tibia, 1.14 mm.; metatarsus, 1.38 mm.; tarsus, 0.48 mm.

Description. Anterior median eyes their radius or less apart, as far from laterals in female, half the distance in male. Posterior medians separated by three diameters in female, two and a half in male.

Diagnosis. C. pikei is closely related to *C. plumbi*, the main differences being the larger size of *pikei*, the details of the palpus (Figs. 56-57) and the more widely spaced posterior median eyes.

Kaston (1948) placed *C. pikei* in the synonymy of *C. plumbi*. I have examined the holotype of *plumbi* and compared it with paratypes of *C. pikei*, and am in agreement with Gertsch that these are two distinct species.

Distribution. Atlantic coast states from Maine to Florida.

Records. Connecticut: Norwalk, ♀ paratype; *Orange; *Shelton; *Wallingford; *West Haven; *Westville. *Florida:* Dunedin; Cocoa Beach, ♂; Alachua Co., ♀. *Maine:* Orono, ♀. *Massachusetts:* Provincetown, ♂, ♀; Woods Hole, ♀ paratypes; Duxbury, ♂, ♀; Ipswich, ♀; Winthrop, ♀; Gloucester, Eastern Point, ♂, ♀; James Brewster's Isl., Boston Harbor, ♀. *New Jersey:* Lakewood, ♀ paratype. *New York:* Long Isl., ♀ allotype, ♀, ♂ paratypes; Onondaga Co., ♂, ♀; Lloyd's Neck, L. I., ♀; Sea Cliff, L. I., ♀; Riverhead, L. I., ♂, ♀; Tottenville, L. I., ♂, ♀; Orient, L. I., ♂; Watermill, ♂, ♀; Cold Spring Harbor, L. I., ♀; Montauk Point, L. I., ♂, ♀; Canoe Place, L. I., ♂, ♀. *Pennsylvania:* Roxbury, ♂. *Vermont:* South Newfane, ♂. *Virginia:* Falls Church. *Georgia:* *NW. of Elberton, ♂.

CLUBIONA POMOA Gertsch

Figures 72-73, 93, 192, 239

Clubiona pomoa Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 6, figs. 7-9 (♂ type from Oakland, Alameda Co., California, in the American Museum of Natural History).

Measurements. Female: Length 4.08-5.22 mm.; average 4.50 mm. Carapace 1.98 mm. long, 1.44 mm. wide. First femur, 1.14 mm.; patella, 0.60 mm.; tibia, 0.84 mm.; metatarsus, 0.63 mm.; tarsus, 0.42 mm. Fourth femur, 1.50 mm.; patella, 0.60 mm.; tibia, 1.08 mm.; metatarsus, 1.26 mm.; tarsus, 0.45 mm.

Male: Length 3.48-4.86 mm.; average 4.08 mm. Carapace 1.92 mm. long, 1.26 mm. wide. First femur, 1.20 mm.; patella, 0.60 mm.; tibia, 1.08 mm.; metatarsus, 0.76 mm.; tarsus, 0.45 mm. Fourth femur, 1.50 mm.; patella, 0.63 mm.; tibia, 1.08 mm.; metatarsus, 1.34 mm.; tarsus, 0.46 mm.

Description. Anterior median eyes two-thirds their diameter apart in female, one-half in male. Posterior median eyes two and a half diameters apart in female, two diameters in male, about half as far from laterals.

Diagnosis. Although *C. pomoa* has the general characteristics of the group, it is quite distinct. The male palpus (Figs. 72-73) is characterized by the well defined bulb on the embolus at the base, and by the fact that the retrolateral apophysis of the tibia is much longer than the dorsal apophysis. Unlike other members of Group III, the epigynum of *pomoa* has the sperm receptacles contiguous (Fig. 93).

Records. California: Oakland, ♀ allotype, ♂, ♀ paratypes; San Francisco, ♂ paratype; Gaviota, ♂, ♀; Santa Barbara, ♂.

CLUBIONA JOHNSONI Gertsch

Figures 48-49, 96, 187, 235

Clubiona johnsoni Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 14, figs. 43-45 (♂ type from Norwalk, Connecticut, in the American Museum of Natural History). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 515.

Measurements. Female: Length 3.06-4.44 mm.; average 3.66 mm. Carapace 1.81 mm. long, 1.17 mm. wide. First femur, 0.96 mm.; patella, 0.50 mm.; tibia, 0.78 mm.; metatarsus, 0.55 mm.; tarsus, 0.39 mm. Fourth femur, 1.25 mm.; patella, 0.54 mm.; tibia, 0.96 mm.; metatarsus, 1.14 mm.; tarsus, 0.43 mm.

Male: Length 2.58-3.36 mm.; average 3.02 mm. Carapace 1.47 mm. long, 1.05 mm. wide. First femur, 1.08 mm.; patella, 0.48 mm.; tibia, 0.86 mm.; metatarsus, 0.63 mm.; tarsus, 0.38 mm. Fourth femur, 1.38 mm.; patella, 0.48 mm.; tibia, 1.02 mm.; metatarsus, 1.14 mm.; tarsus, 0.39 mm.

Description. Anterior median eyes four-fifths diameter apart in female, one-third diameter in male. Posterior medians separated by three diameters in female, by two in male, about half as far from slightly larger laterals. Epigynum illustrated by Figure 96, palpus by Figures 48-49.

Natural History. Mature specimens of both sexes have been collected from debris brought down by spring floods, indicating that this species overwinters, at least to a certain extent, in the adult stage. A female was collected on August 3, with an egg sac containing 22 eggs.

Distribution. Southeastern Canada, New England and Great Lake states.

Records. Connecticut: Norwalk, ♀ allotype; ♂, ♀ paratypes; Shelton, ♀ paratypes; Watertown, ♂ paratype; *Greenwich; *Orange; *Sandy Hook. *Illinois:* nr. Chicago, ♀ paratype. *Massachusetts:* Duxbury, ♂; Allston, ♂; Holliston, ♂; Sharon, ♂. *Michigan:* Dunes nr. Sawyer, ♂. *New Hampshire:* Randolph, ♂; Intervale, ♂; Dublin, ♂; Mt. Washington, ♀. *New York:* Cold Spring Harbor, ♂; Peru, ♂; Sea Cliff, ♂; Long Island, ♀. *New Jersey:* Ramsey, ♂ paratype. *Rhode Island:* Portsmouth, ♂. *Vermont:* South Newfane, ♂.

Nova Scotia: Greenwich, ♀. *Ontario:* Port Credit, ♂. *Saskatchewan:* Saskatoon, ♂ paratype.

CLUBIONA NEWNANI Ivie and Barrows, emend.

Figures 52-53

Clubiona newmani Ivie and Barrows, 1935, Bull. Univ. Utah, vol. 26, no. 6, p. 20, pl. 7, figs. 57-58 (♂ type from Lake Newman [*sic* = Newnans Lake] Gainesville, Florida in the University of Utah collection). Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 15.

Measurements. Male: Length 3.24-3.66 mm.; average 3.52 mm. Carapace 1.74 mm. long, 1.26 mm. wide. First femur, 1.20 mm.; patella, 0.60 mm.; tibia, 1.20 mm.; metatarsus, 0.84 mm.; tarsus, 0.51 mm. Fourth femur, 1.62 mm.; patella, 0.60 mm.; tibia, 1.20 mm.; metatarsus, 1.50 mm.; tarsus, 0.53 mm.

Description. Anterior median eyes their radius apart, slightly closer to laterals. Posterior medians separated by two diameters, one diameter from larger laterals. The female is not known.

Diagnosis. This species is closely related to *C. abbotii*, differing mainly in the much broader retrolateral tibial apophysis of the male palpus (Figs. 52-53).

Records. Florida: Silver Springs, ♂; Highland Hammock, nr. Sebring, ♂; Alachua Co., ♂; *Newnans Lake, Gainesville, ♂; Sebastian, ♂. *Pennsylvania:* North Wales, ♂. *Virginia:* Siles Co., ♂.

CLUBIONA NICHOLSI Gertsch

Figures 68-69, 85, 199, 241

Clubiona nicholsi Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 8, figs. 5-6 (♂ type from Mastic, Long Island, New York, in the American Museum of Natural History). Barnes, 1953, Amer. Mus. Novitates, no. 1632, p. 16, fig. 19. Roewer, 1955, Katalog der Araneae, vol. 2a, p. 516.

Measurements. Female: Length 4.86 mm. Carapace 2.34 mm. long, 1.50 mm. wide. First femur, 1.41 mm.; patella, 0.72 mm.; tibia, 1.14 mm.; metatarsus, 0.80 mm.; tarsus, 0.56 mm. Fourth femur, 1.74 mm.; patella, 0.78 mm.; tibia, 1.26 mm.; metatarsus, 1.62 mm.; tarsus, 0.56 mm.

Male: Length 4.02-4.50 mm.; average 4.23 mm. Carapace 2.22 mm. long, 1.50 mm. wide. First femur, 1.62 mm.; patella, 0.81 mm.; tibia, 1.20 mm.; metatarsus, 1.02 mm.; tarsus, 0.63 mm. Fourth femur, 1.80 mm.; patella, 0.81 mm.; tibia, 1.38 mm.; metatarsus, 1.74 mm.; tarsus, 0.57 mm.

Description. Anterior median eyes separated by less than a radius, about the same distance from smaller lateral eyes. Posterior medians about three diameters apart, half as far from larger laterals.

Diagnosis. The relatively short, heavy tibial apophysis and the enlargement at the base of the embolus (Figs. 68-69) and the epigynum (Fig. 85) distinguishes this species.

Natural History. This species is found abundant in "thick moist drift straw in the intertidal marshes" (Barnes, 1953).

Records. Massachusetts: Lynn, ♀, ♂. *North Carolina:* Beaufort (R. Barnes).

CLUBIONA PROCTERI Gertsch

Figures 66-67, 88, 198, 240

Clubiona procteri Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 10, figs. 17-18 (♂ type from Indian Town, Florida, in the American Museum of Natural History).

Clubiona hilltonia Chamberlin and Ivie, 1944, Bull. Univ. Utah, vol. 35, no. 9, p. 182, fig. 201 (♂ type from Briar Creek, 7 miles north of Sylvania, Georgia, in the University of Utah collection). NEW SYNONYMY.

Measurements. Female: Length 3.5 mm. Carapace, 1.42 mm. long, 0.96 mm. wide. First femur, 0.90 mm.; patella, 0.42 mm.; tibia, 0.72 mm.; metatarsus, 0.48 mm.; tarsus, 0.30 mm. Fourth femur, 1.08 mm.; patella, 0.48 mm.; tibia, 0.78 mm.; metatarsus, 0.90 mm.; tarsus, 0.30 mm.

Male: Length 3.16 mm. Carapace 1.52 mm. long, 0.98 mm. wide. First femur, 1.11 mm.; patella, 0.56 mm.; tibia, 1.06 mm.; metatarsus, 0.74 mm.; tarsus, 0.40 mm. Fourth femur, 1.37 mm.; patella, 0.52 mm.; tibia, 0.95 mm.; metatarsus, 1.20 mm.; tarsus, 0.43 mm.

Description. Anterior median eyes separated by one-third diameter in female, by radius in male. Posterior medians separated by two and one-half diameters in female, two diameters in male; half as far from lateral eyes.

Diagnosis. The male is characterized by the retrolateral tibial apophysis of the palpus which bends sharply dorsad and the dorsal apophysis which is a short, sharply pointed process (Figs. 66-67). The epigynum has very large, distinctively shaped sperm duct openings (Fig. 88).

Comments. Miss E. B. Bryant described the female of *Clubiona procteri* in 1945 (Psyche, vol. 52, p. 3). Two of her specimens examined were found to be *C. abbotii.*

Records. Alabama: Silver Hill, ♂. *Florida:* Lake Placid, ♂; Port Mayaca, ♀; 0.5 mi. N. of Archbold Biol. Sta., ♀; *Indiantown, ♂; *Wabasco, ♂. *Georgia:* *7 mi. N. of Sylvania, Briar Creek, ♂. *North Carolina:* *Raleigh, ♂.

CLUBIONA KAGANI Gertsch

Figures 89, 200, 243

Clubiona kagani Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 6, fig. 6 (♀ type from Riesel, Texas, in the American Museum of Natural History).

Measurements. Female: Length 3.06 mm. Carapace 1.35 mm. long, 0.97 mm. wide. First femur, 0.52 mm.; patella, 0.40 mm.; tibia, 0.55 mm.; metatarsus, 0.42 mm.; tarsus, 0.28 mm. Fourth femur, 1.00 mm.; patella, 0.45 mm.; tibia, 0.75 mm.; metatarsus, 0.96 mm.; tarsus, 0.31 mm.

Description. Anterior median eyes their radius apart, closer to the laterals. Posterior median eyes two diameters apart, a diameter from laterals. Epigynum illustrated by Figure 200. Only the female is known.

Record. Texas: Houston, ♀.

CLUBIONA CATAWBA Gertsch

Figures 76-77, 92, 194, 244

Clubiona catawba Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 10, figs. 10-11 (♂ type from Kingston, Tennessee, in the American Museum of Natural History).

Clubiona alachua Gertsch, 1941, Amer. Mus. Novitates, no. 1148, pp. 4, 6, fig. 4 (♀ type from Alachua County, Florida, in the American Museum of Natural History). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 513. NEW SYNONYMY.

Measurements. Female: Length 2.76-3.06 mm.; average 2.91 mm. Carapace 1.40 mm. long, 0.93 mm. wide. First femur, 0.80 mm.; patella, 0.40 mm.; tibia, 0.63 mm.; metatarsus, 0.41 mm.; tarsus, 0.28 mm. Fourth femur, 1.08 mm.; patella, 0.42 mm.; tibia, 0.80 mm.; metatarsus, 0.95 mm.; tarsus, 0.32 mm.

Male: 2.34-3.36 mm.; average 2.90 mm. Carapace 1.50 mm. long, 1.00 mm. wide. First femur, 0.90 mm.; patella, 0.50 mm.; tibia, 0.87 mm.; metatarsus, 0.58 mm.; tarsus, 0.32 mm. Fourth femur, 1.20 mm.; patella, 0.53 mm.; tibia, 0.90 mm.; metatarsus, 1.17 mm.; tarsus, 0.40 mm.

Description. Anterior median eyes their radius apart. Posterior medians two and one-half diameters apart, about a diameter or more from laterals.

Diagnosis. This species is distinguished by the straight retrolateral tibial apophysis of the palpus and the ventrally directed sharply pointed dorsal apophysis (Figs. 76-77).

Records. Florida: Nr. Sebring, ♀ paratype; Blountstown, ♀ paratype, ♂; Sebastian, ♀; *Alachua Co., ♀; *Jasper, ♀.

Georgia: *Millen, ♀; *S. of Lake Park, ♀; Nr. Waycross, ♂ paratypes; *Lyone. *Michigan:* Stony Lake, Oceana Co., ♂. *Mississippi:* Centreville. *North Carolina:* Durham. *Ohio:* Gambier. *Tennessee:* *Kingston. *Texas:* Austin; Victoria; 5 mi. E. of Rio Grande City. *Virginia:* Falls Church.

CLUBIONA SALTITANS Emerton
Figures 58-59, 188, 248

Clubiona saltitans Emerton, 1919, Canadian Ent., vol. 51, p. 107, fig. 14 (♂ syntypes from Ipswich, Massachusetts, in the Museum of Comparative Zoology). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 517. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1152.

Measurements. Female: Length 4.13 mm. Carapace 1.74 mm. long, 1.10 mm. wide. First femur, 1.02 mm.; patella, 0.54 mm.; tibia, 0.78 mm.; metatarsus, 0.54 mm.; tarsus, 0.34 mm. Fourth femur, 1.38 mm.; patella, 0.54 mm.; tibia, 0.96 mm.; metatarsus, 1.20 mm.; tarsus, 0.36 mm.

Male: Length 3.00-3.46 mm. Carapace 1.63 mm. long, 1.13 mm. wide. First femur, 1.07 mm.; patella, 0.50 mm.; tibia, 0.97 mm.; metatarsus, 0.70 mm.; tarsus, 0.40 mm. Fourth femur, 1.43 mm.; patella, 0.53 mm.; tibia, 1.03 mm.; metatarsus, 1.20 mm.; tarsus, 0.40 mm.

Description. Anterior median eyes one-third diameter apart in female, their radius apart in male. Posterior medians separated by less than two diameters in female, two and a half diameters in male.

Diagnosis. This species is closely related to *C. pikei*, but differs from it in that the retrolateral tibial apophysis of the male palpus is shorter and broader and the dorsal apophysis is broader (Figs. 58-59). The chelicerae of the male are marked with a shallow groove on the medial edge of the dorsal surface, this groove being bordered by low ridges. The epigyna of the two species differ in that the openings of *C. saltitans* are much longer than wide and closer together (Fig. 248) than those of *C. pikei.*

Comments. The series of specimens which Emerton used as the type material includes some specimens of *Clubiona pikei.* The male described and figured by Emerton I have now designated lectotype. A vial containing two females of *C. pikei* in the

Cornell University collection is labeled in handwriting "*Type, Clubiona saltitans*"; presumably it is the allotype of the female described at a later date.

Records. Connecticut: *Hadlyme, ♂; *New Haven, ♂; *Orange, ♂. *District of Columbia:* Washington, ♂. *Florida:* Wabasso, ♂. *?Illinois:* *Kankakee Co., ♂. *Massachusetts:* Holliston, ♂; *Ipswich, ♂; *Plum Isl., ♂; *Wellfleet, ♂; *Nantucket. *New York:* Bergen Beach, Ontario Co., ♂; Onondaga Co., ♂; Tottenville, L. I., ♂.

CLUBIONA KIOWA Gertsch

Figures 62-63, 90, 186, 245

Clubiona kiowa Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 12, figs. 23-24 (♂ type from Dallas, Texas, in the American Museum of Natural History).

Measurements. Female: Length 3.72 mm. Carapace 1.50 mm. long, 0.86 mm. wide. First femur, 1.00 mm.; patella, 0.40 mm.; tibia, 0.70 mm.; metatarsus, 0.53 mm.; tarsus, 0.33 mm. Fourth femur, 1.33 mm.; patella, 0.53 mm.; tibia, 0.90 mm.; metatarsus, 1.07 mm.; tarsus, 0.40 mm.

Male: Length 2.76-3.30 mm. Carapace 1.56 mm. long, 1.00 mm. wide. First femur, 0.95 mm.; patella, 0.48 mm.; tibia, 0.86 mm.; metatarsus, 0.62 mm.; tarsus, 0.40 mm. Fourth femur, 1.30 mm.; patella, 0.48 mm.; tibia, 1.00 mm.; metatarsus, 1.19 mm.; tarsus, 0.40 mm.

Description. Anterior median eyes their radius apart, closer to laterals. Posterior medians slightly more than two diameters apart.

Diagnosis. The genitalia (Figs. 62-63, 90) distinguish this species from *C. pikei.*

Records. Michigan: Ann Arbor, ♀, ♂. *Texas:* Edinburg, ♂, ♀; La Gringa Resaca, ♀; Dallas, ♂. *Mexico:* Monterrey, ♀.

CLUBIONA MUTATA Gertsch

Figures 64-65, 80, 185, 246

Clubiona mutata, Gertsch 1941, Amer. Mus. Novitates, no. 1148, p. 14, figs. 19-20 (♂ type from Salt Lake City, Utah, in the American Museum of Natural History).

Clubiona screveni Chamberlin and Ivie, 1944, Bull. Univ. Utah, vol. 35, p. 184, figs. 204-206 (♂ type from Millen, Georgia, in the University of Utah collection). NEW SYNONYMY.

Measurements. Female: Length 2.40-3.83 mm.; average 3.20 mm. Carapace 1.37 mm. long, 0.97 mm. wide. First femur, 0.77 mm.; patella, 0.33 mm.; tibia, 0.51 mm.; metatarsus, 0.40 mm.; tarsus, 0.30 mm. Fourth femur, 1.03 mm.; patella, 0.37 mm.; tibia, 0.73 mm.; metatarsus, 0.87 mm.; tarsus, 0.37 mm.

Male: Length 2.60-3.56 mm.; average 2.91 mm. Carapace 1.40 mm. long, 1.00 mm. wide. First femur, 0.90 mm.; patella, 0.40 mm.; tibia, 0.63 mm.; metatarsus, 0.50 mm.; tarsus, 0.35 mm. Fourth femur, 1.17 mm.; patella, 0.47 mm.; tibia, 0.77 mm.; metatarsus, 0.93 mm.; tarsus, 0.34 mm.

Description. Anterior median eyes their diameter apart, closer to the slightly larger laterals. Posterior median eyes nearly three diameters apart in female, more than two diameters in male.

Diagnosis. The dorsal tibial apophysis of the male palpus of *C. mutata* (Figs. 64, 65) is sharply pointed and comparatively narrow, whereas in *C. pikei,* the dorsal tibial apophysis is broad and truncate. The sperm duct openings of the epigynum of *C. mutata* (Fig. 80) are more rounded and farther spaced than in *C. pikei.*

Records. Colorado: Boulder. *Georgia:* *Millen, ♂, ♀; *N. of Sylvania, ♂. *Kansas:* Manhattan, ♂. *Nebraska:* 9 mi. NW. of Lincoln, ♂, ♀. *North Carolina:* Durham, ♂. *Utah:* Salt Lake City, ♂. *Washington:* Spokane, ♂. *Wyoming:* Bridge Bay, Yellowstone Natl. Park, ♂, ♀.

Saskatchewan: Saskatoon, ♂ paratype.

CLUBIONA OTEROANA Gertsch

Figures 94, 193, 238

Clubiona oteroana Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 6, fig. 3 (♀ type from Camp Mary White, Otero County, New Mexico, in the American Museum of Natural History).

Measurements. Female: Length, 4.20 mm. Carapace 2.04 mm. long, 1.32 mm. wide. First leg missing. Fourth femur, 1.42 mm.; patella, 0.70 mm.; tibia, 1.10 mm.; metatarsus, 1.32 mm.; tarsus, 0.45 mm.

Description. Anterior median eyes a little more than a diameter apart. Posterior median eyes two and a half times their diameter apart, a little more than a diameter from subequal lateral eyes. The sperm duct openings are large circles close together at the posterior edge of the epigynum (Fig. 94). The male is not known.

CLUBIONA DYASIA Gertsch
Figures 74-75

Clubiona dyasia Gertsch, 1941, Amer. Mus. Novitates, no. 1148, p. 4, figs. 1-2 (♂ type from Dyas Creek, Baldwin County, Alabama, in the American Museum of Natural History).

Measurements. Male: Length 3.02 mm. Carapace 1.50 mm. long, 0.99 mm. wide. First femur, 0.92 mm.; patella, 0.42 mm.; tibia, 0.81 mm.; metatarsus, 0.66 mm.; tarsus, 0.39 mm. Fourth femur, 1.22 mm.; patella, 0.54 mm.; tibia, 0.90 mm.; metatarsus, 1.14 mm.; tarsus, 0.42 mm.

Description. Anterior median eyes their radius apart, about half as far from slightly larger laterals. Posterior median eyes more than their diameter apart, slightly less than a diameter from laterals. Retrolateral tibial apophysis of palpus bifid (Figs. 74-75). The female is not known.

CLUBIONA RIPARIA L. Koch
Figures 125-128, 145, 219

Clubiona riparia L. Koch, 1866, Die Arachniden Familie der Drassiden, p. 294, pl. 12, fig. 187 (♀ type from Baltimore, North America). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 517. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1151.

Clubiona ornata Emerton, 1890, Trans. Connecticut Acad. Sci., vol. 8, p. 183, pl. 5, fig. 9 (3 juv. ♀ syntypes from Dublin, New Hampshire, in the Museum of Comparative Zoology). Name preoccupied by *C. ornata* Thorell, 1875.

Clubiona americana Banks, 1892, Proc. Acad. Nat. Sci. Philadelphia, p. 22. New name for *C. ornata* Emerton.

Measurements. Female: 5.44-10.16 mm.; average 7.72 mm. Carapace 2.64 mm. long, 1.92 mm. wide. First femur, 2.28 mm.; patella, 1.02 mm.; tibia, 1.80 mm.; metatarsus, 1.35 mm.; tarsus, 0.75 mm. Fourth femur, 2.58 mm.; patella, 1.02 mm.; tibia, 1.80 mm.; metatarsus, 2.28 mm.; tarsus, 0.78 mm.

Male: Length 4.56-6.00 mm.; average length 5.37 mm. Carapace 2.28 mm. long, 1.62 mm. wide. First femur, 2.10 mm.; patella, 0.96 mm.; tibia, 2.04 mm.; metatarsus, 1.59 mm.; tarsus, 0.90 mm. Fourth femur, 2.34 mm.; patella, 0.90 mm.; tibia, 1.74 mm.; metatarsus, 2.22 mm.; tarsus, 0.80 mm.

Description. Anterior median eyes almost their diameter apart in female, three-fourths diameter apart in male. Posterior median eyes two and a half diameters apart, two-thirds as far from the laterals. Chelicerae slender, but attenuated in male. Abdomen with a dark lanceolate mark on dorsum; on each side of it is a yellow-brown stripe with irregular edges. Epigynum with a median lobe (Fig. 145) which may be very short, palpus illustrated by Figures 125-127.

Natural History. The habits of *C. riparia* are similar to those of its European relative, *C. grisea* L. Koch. This spider has been collected mainly from tall grass near streams and ponds. During the breeding season the female folds a blade of grass together with silk to form a three-sided nest which is lined with silk. The nest is used as a place of concealment for the egg sac, serving later as a nursery for the spiderlings and a coffin for the parents. A female was taken on June 18, guarding her egg sac. The egg sac was a flat packet containing 114 light yellow eggs, each of which was approximately 0.76 mm. in diameter. Another egg mass in the form of a flattened oval was collected in June, the egg sac measuring 5.4 by 1.8 mm. There were 36 oval eggs in the sac, each measuring about 0.80 by 0.70 mm. *C. riparia* overwinters in the penultimate instar under bark and debris on the ground and individuals mature as early as April.

Distribution: Alaska, eastern Canada, eastern United States, west to Utah.

Records. Connecticut: Colebrook; Shelton; Sandy Hook; East Putnam; Branford; *Barkhamsted; *Salisbury; *Watertown; *Windsor; Windsor Locks. *Illinois:* *Waukegan. *Maine:* Mount Desert Isl.; Lincoln; Moosehead Lake; Milbridge; *Bayville; *Portland. *Massachusetts:* East Gloucester; *Sharon; *Brookline; Holliston. *Michigan:* Douglas Lake; New Baltimore; Sanford; Lexington. *Minnesota:* Ramsey Co. *New Hampshire:*

Shelburne; *Mt. Washington; *Dublin; *Franconia. *New Mexico:* Beulah (N. Banks). *New York:* McLean; Sport Isl., Sacandaga Park; Long Lake; Black Brook, Clinton Co.; nr. Oswego; Point Breeze, Orleans Co.; Labrador Pond, Cortland Co. Crusoe Lake; Ithaca; Lake Erie Beach, Chautauqua Co.; Junius Bog, Seneca Co.; Trenton Falls; Oak Orchard Swamp; Tunasasa; Rochester; Huyck Preserve, Albany Co.; *Onondaga Co.; Scotia; Albany; *Delmar; Riders Mills; *Poughkeepsie; *Long Isl. *Ohio:* *Wooster. *Pennsylvania:* President; *"Western Pennsylvania." *South Dakota:* Blue Bell, Black Hills; Game Lodge, Black Hills. *Utah:* Fish Lake. *Wisconsin:* St. Croix Falls. *Alaska:* *Homer.

Alberta: Seba Beach; Gull Lake; Fawcett. *Manitoba:* Victoria Beach; N. of Victoria Beach; Owen. *New Brunswick:* Woodstock; Grand Manan Isl. *Nova Scotia:* Weymouth; Truro. *Ontario:* Port Credit; Highland Creek; Newmarket; Toronto; Franks Bay, Lake Nipigon; MacLennon; Tanamakoon, Algonquin Park; Goose Isl., Lake Nipissing; Holst Point; Mindemoya, Lake Manitoulin; Attowapiskat; Red Rock, James Bay; Turkey Point; Hollowell; Wellington; Spruce Bank; Elmhurst Beach, Lake Simcoe; Sproule Bay, Lake Opeongo; N. of Camp Laird; Port Arthur; Pottageville; Lake Opeongo; nr. Minaki; Gananoque. *Quebec:* Ellis Bay, Anticosti; *Gaspé; *Montreal; *Ha-Ha Bay, Bagotville.

CLUBIONA MARITIMA L. Koch

Figures 131-133, 139, 180, 214

Clubiona maritima L. Koch, 1866, Die Arachniden-Familie der Drassiden, p. 310, pl. 12, fig. 198 (♀ type from St. Thomas, Virgin Islands). Roewer, 1955, Katalog der Araneae, vol. 2a, p. 511. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1134.

Clubiona tibialis Emerton, 1890, Trans. Connecticut Acad. Sci., vol. 8, p. 180, pl. 5, fig. 3 (♂ and ♀ syntypes from Cambridge, Massachusetts, in the Museum of Comparative Zoology). Roewer 1955, Katalog der Araneae, vol. 2a, p. 517. Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1160. NEW SYNONYMY.

Clubiona transversa Bryant, 1936, Psyche, vol. 43, p. 97, pl. 3, fig. 8 (♀ type from White Rock Lake, Dallas, Texas, in the Museum of Comparative Zoology). Bonnet, 1956, Bibliographia Araneorum, vol. 2, p. 1161. NEW SYNONYMY.

Measurements. Female: Length 5.84-8.88 mm.; average 7.33 mm. Carapace 3.09 mm. long, 2.16 mm. wide. First femur, 2.28 mm.; patella, 1.08 mm.; tibia, 1.86 mm.; metatarsus, 1.41 mm.; tarsus, 0.78 mm. Fourth femur, 2.70 mm.; patella, 1.02 mm.; tibia, 2.10 mm.; metatarsus, 2.52 mm.; tarsus, 0.76 mm.

Male: Length 5.04-7.12 mm.; average 6.26 mm. Carapace 3.12 mm. long, 2.08 mm. wide. First femur, 2.52 mm.; patella, 1.12 mm.; tibia, 2.40 mm.; metatarsus, 1.82 mm.; tarsus, 0.96 mm. Fourth femur, 2.88 mm.; patella, 1.12 mm.; tibia, 2.28 mm.; metatarsus, 2.82 mm.; tarsus, 0.98 mm.

Description. Anterior median eyes two-thirds diameter apart in female, less than radius in male, slightly farther or an equal distance from laterals. Posterior medians three diameters apart in female, two and a half diameters in male. The chelicerae of the male have a shallow concavity on the median surface, bordered by low ridges. The epigynum (Fig. 139) takes up the entire width of the epigastric plate, the palpus is much larger and more complex than found in other members of this genus (Figs. 131-133).

Natural History. This spider has been collected from under stones and debris on the ground. The female makes a cocoon consisting of two sheets of silk connecting the edges of a large blade of grass, and the eggs are placed in an inner case between the two sheets of silk. An egg sac has been taken in June containing 70 eggs. *Clubiona maritima* hibernates usually in the mature stage.

Distribution. Greater Antilles, eastern United States, southeastern Canada.

Records. Alabama: Colbert Co. *Connecticut:* South Meriden; Cheshire; Portland; Union; *Mount Carmel; *Shelton. *District of Columbia:* Washington. *Florida:* Pinecrest; Lake Co.; Newnans Lake, Alachua Co.; Volusia Co.; Port Mayaca, Lake Okeechobee; Sebastian; *Runnymede. *Georgia:* Atlanta; Okefinokee Swamp; *Briar Creek, 7 mi. N. of Sylvania; *16 mi. S. of Cordele. *Massachusetts:* *Nantucket; *Cambridge; *Franklin

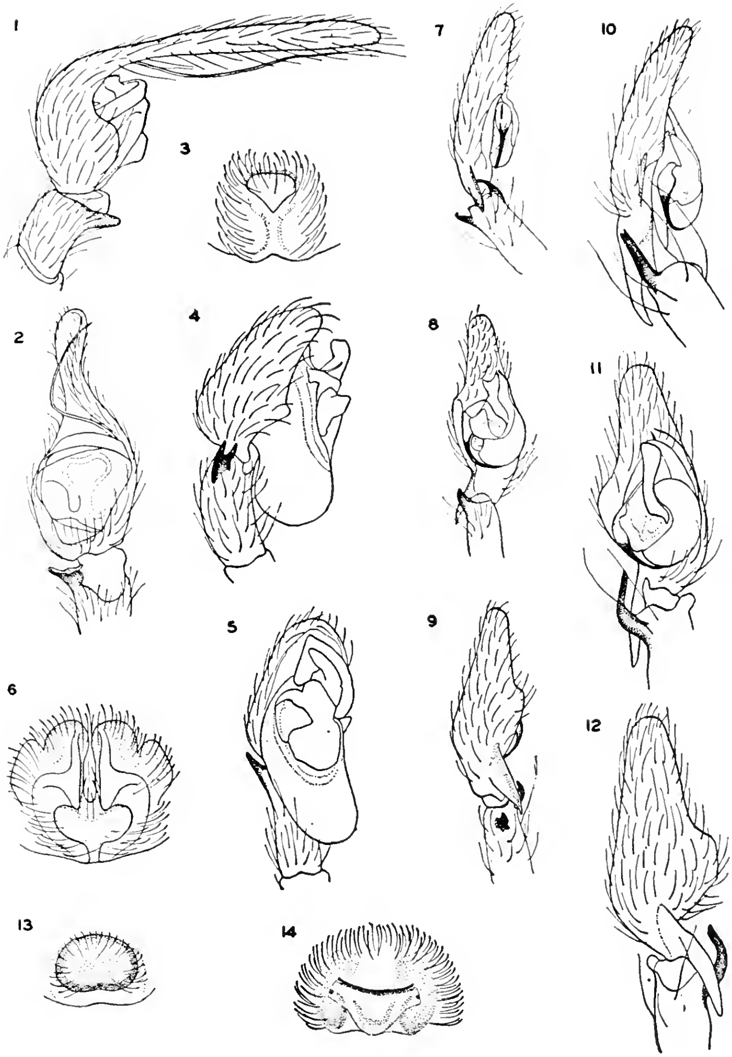
Park. *Michigan:* *Calhoun Co. *Minnesota:* St. Paul. *Mississippi:* Humphreys Co. **Nebraska.* *New Jersey:* Ramsey. *New York:* Southampton, L. I.; Orient, L. I.; Ithaca; Lakeside; Flushing, L. I. *Ohio:* *Ceder Point. *Pennsylvania:* *"Western Pennsylvania." *Tennessee:* Reelfoot Lake; Knoxville. *Texas:* Brownsville; *White Rock Lake, Dallas. *Wisconsin:* Madison; Marathon Co.

Ontario: 4 mi. S. of Carrying Place; East Beach, Pt. Pelee; Hollowell.

Index to Scientific Names

Names used for Clubioninae north of Mexico, valid as well as synonymous, are listed. Valid names are printed in italics.

FIGURES



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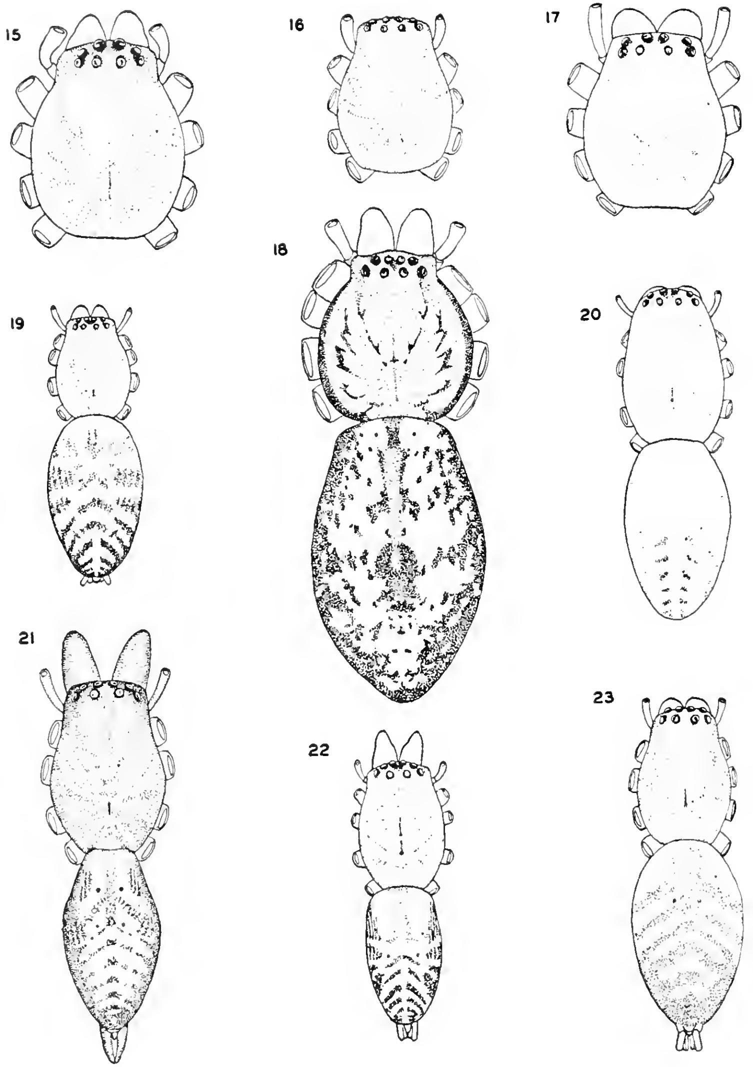

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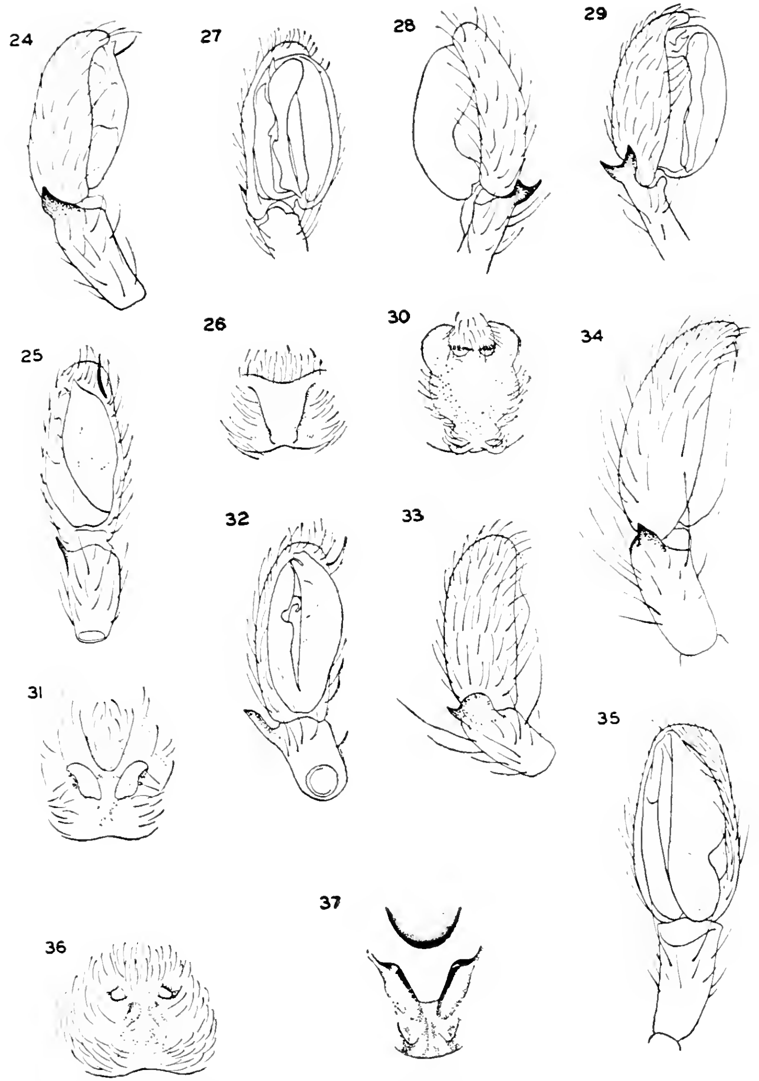

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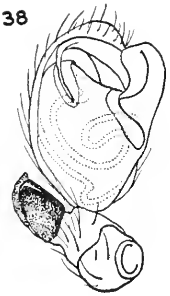

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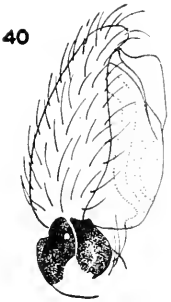

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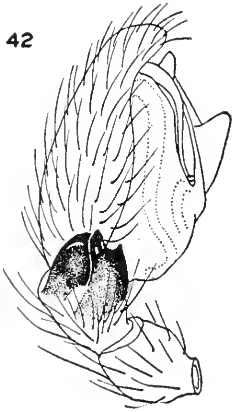

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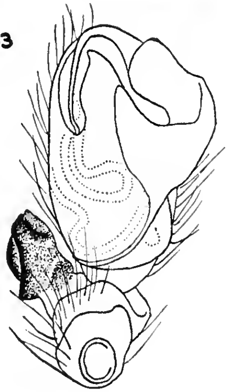

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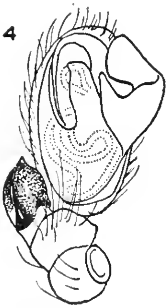

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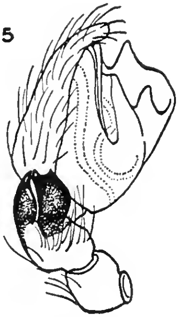

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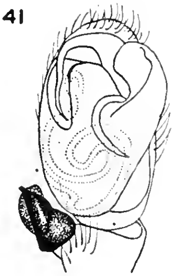

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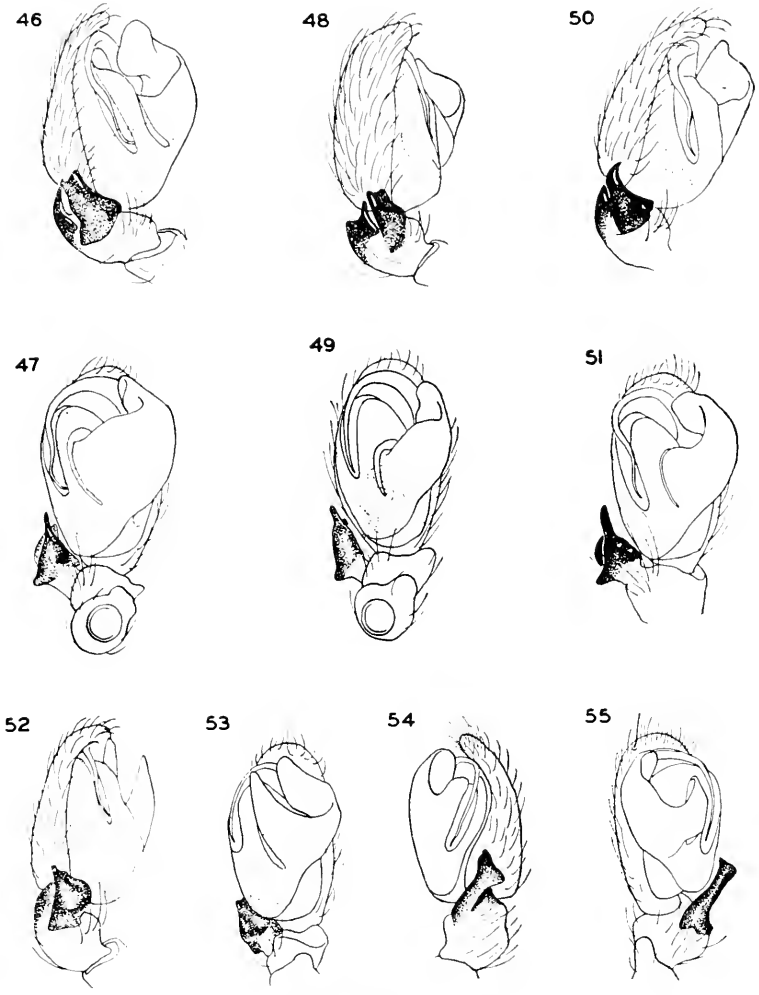

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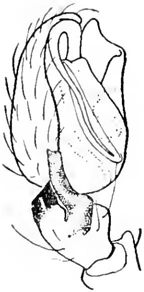

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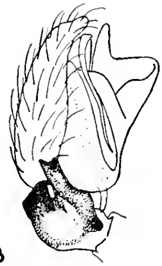

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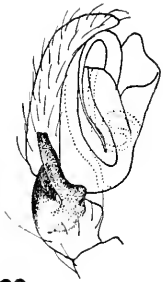

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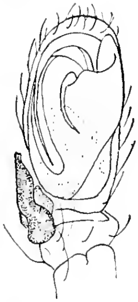

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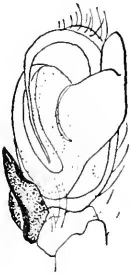

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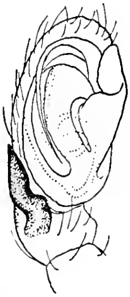

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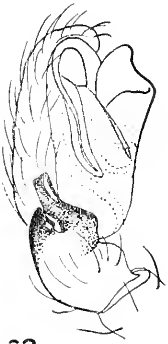

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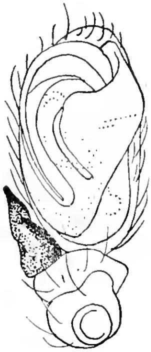

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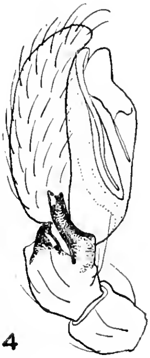

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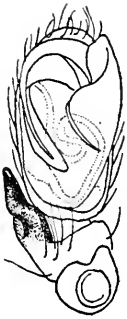

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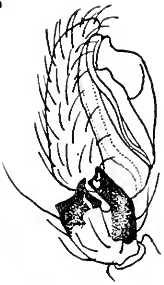

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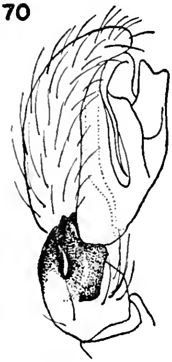

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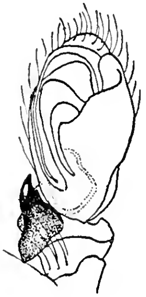

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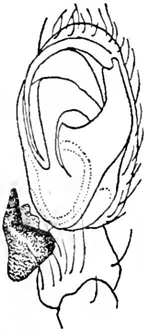

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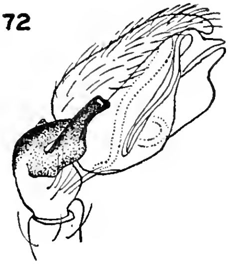

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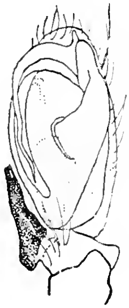

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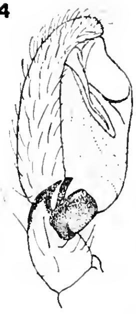

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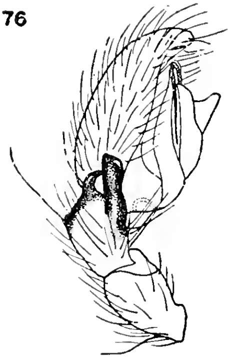

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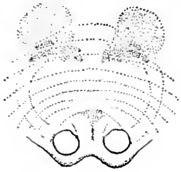

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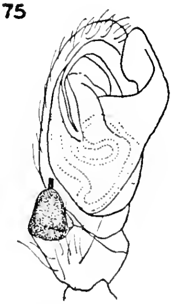

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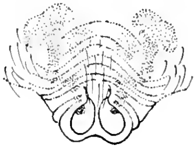

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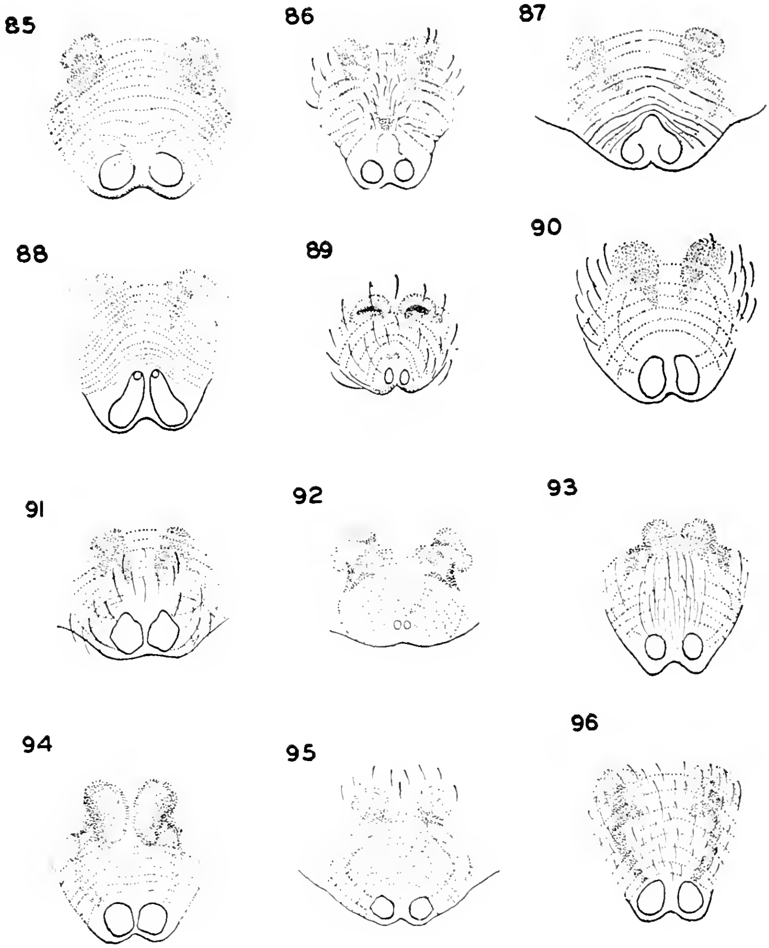

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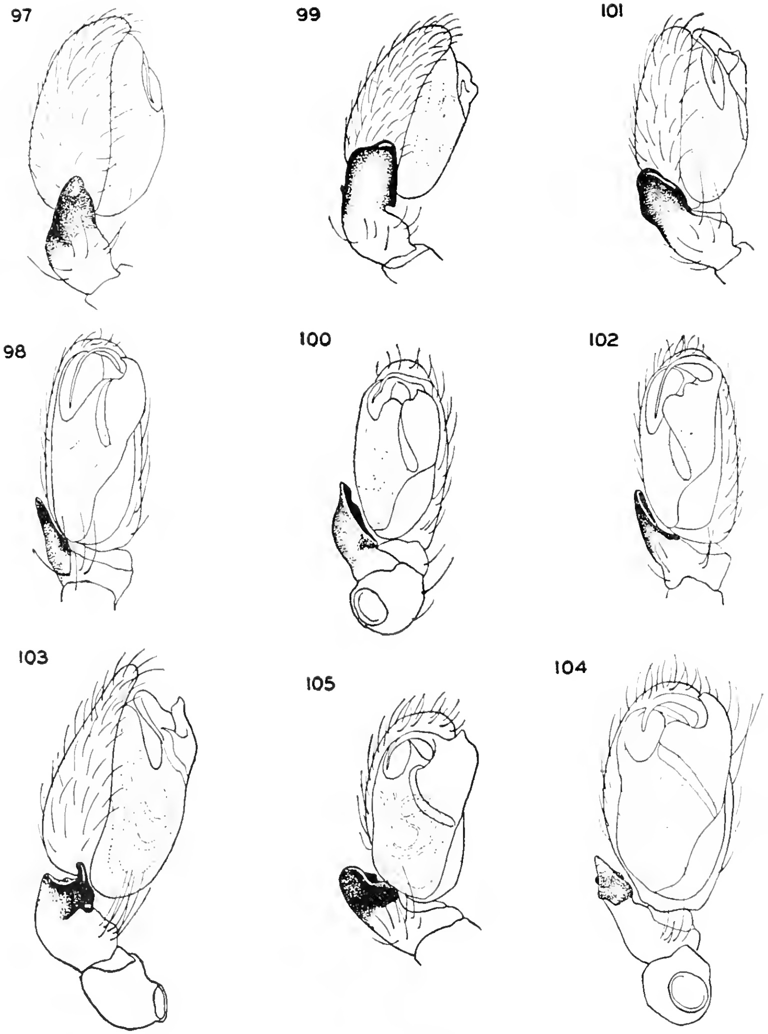

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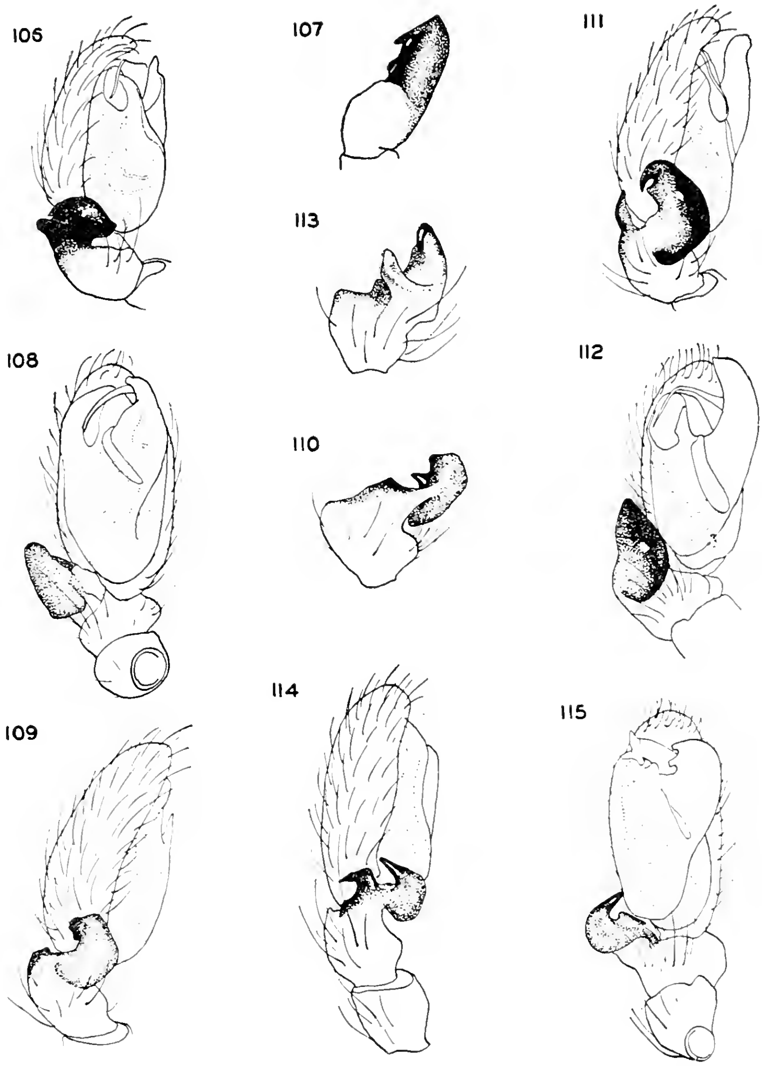

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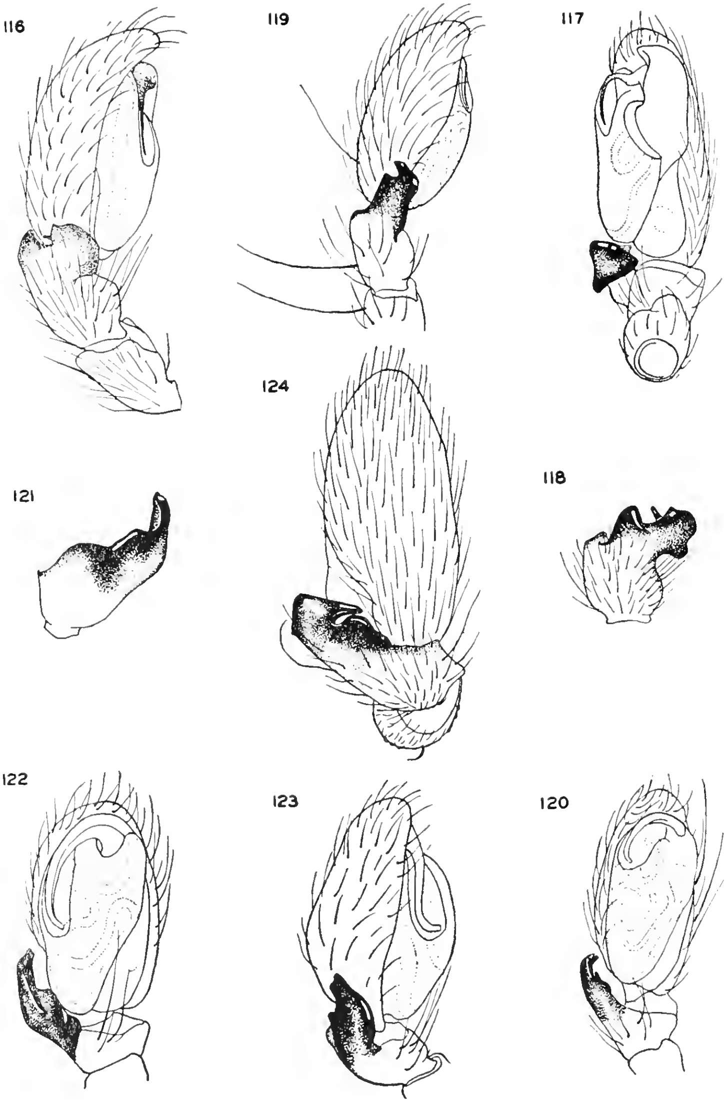

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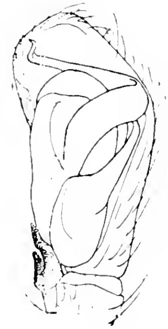

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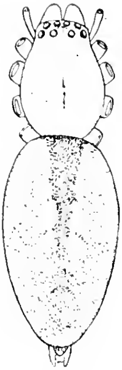

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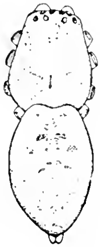

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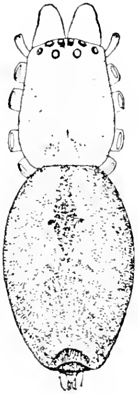

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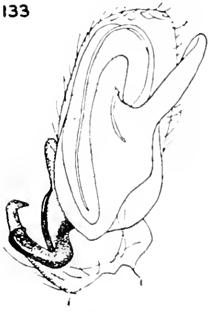

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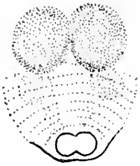

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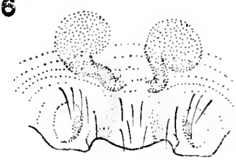

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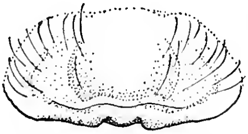

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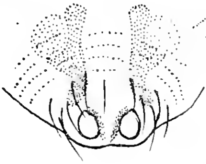

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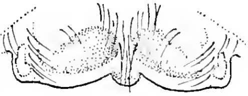

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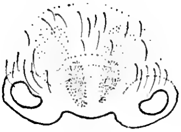

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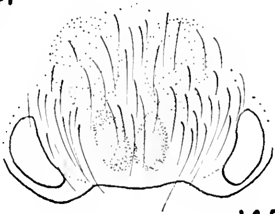

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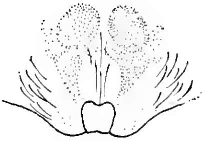

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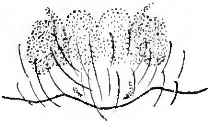

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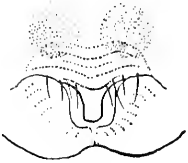

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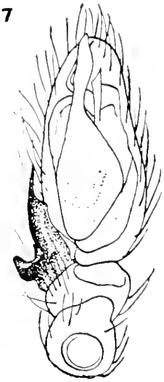

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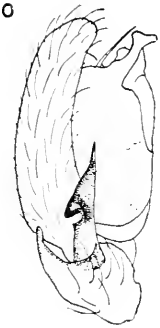

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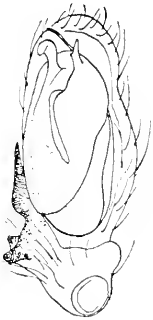

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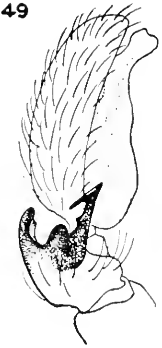

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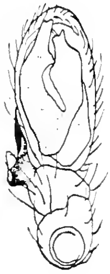

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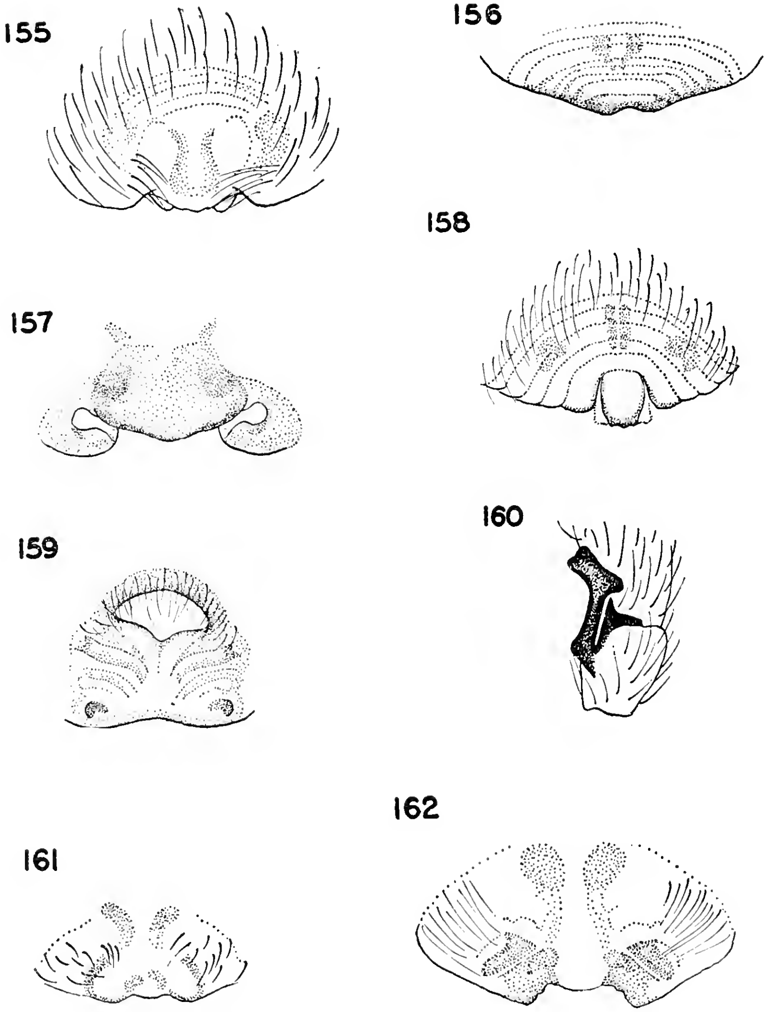

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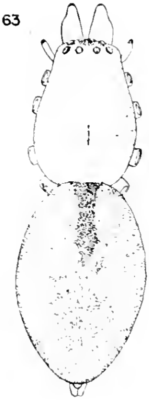

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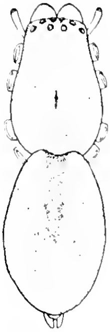

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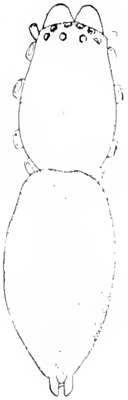

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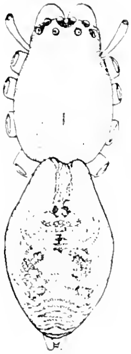

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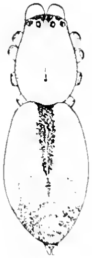

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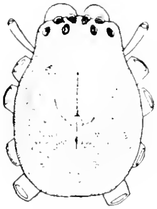

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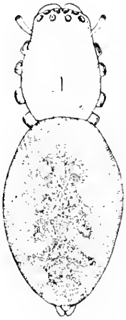

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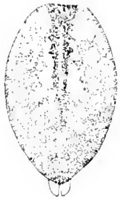

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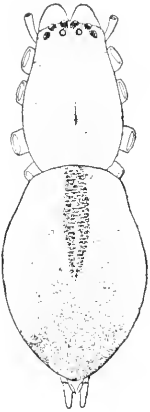

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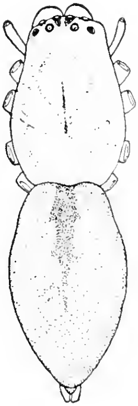

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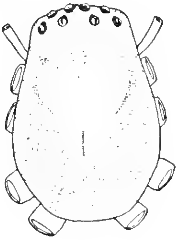

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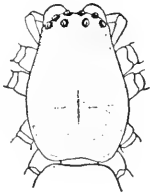

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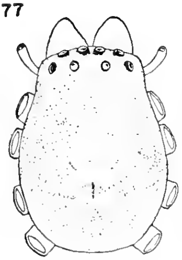

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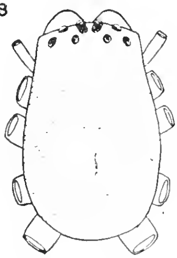

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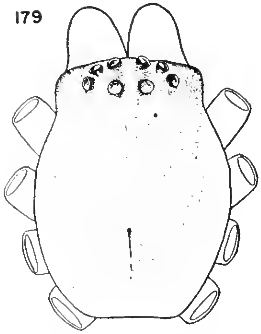

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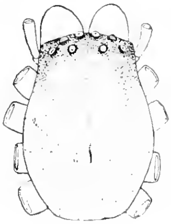

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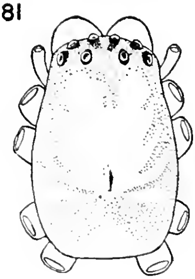

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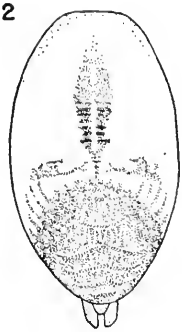

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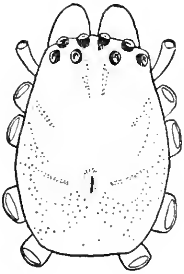

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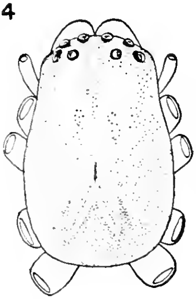

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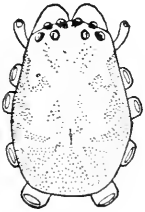

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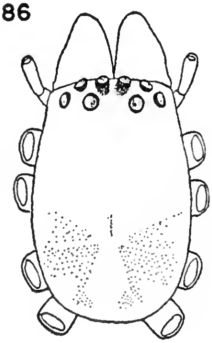

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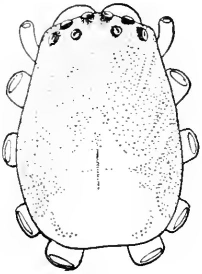

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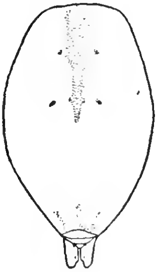

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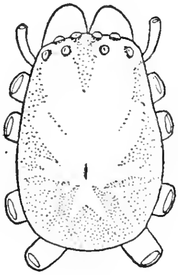

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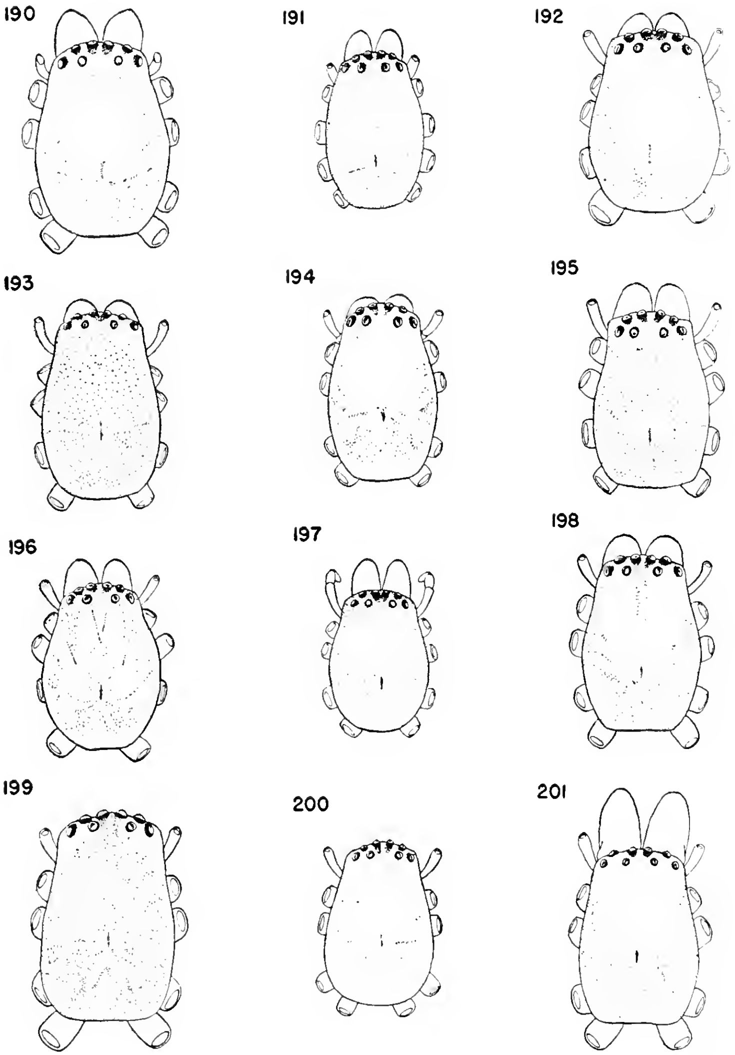

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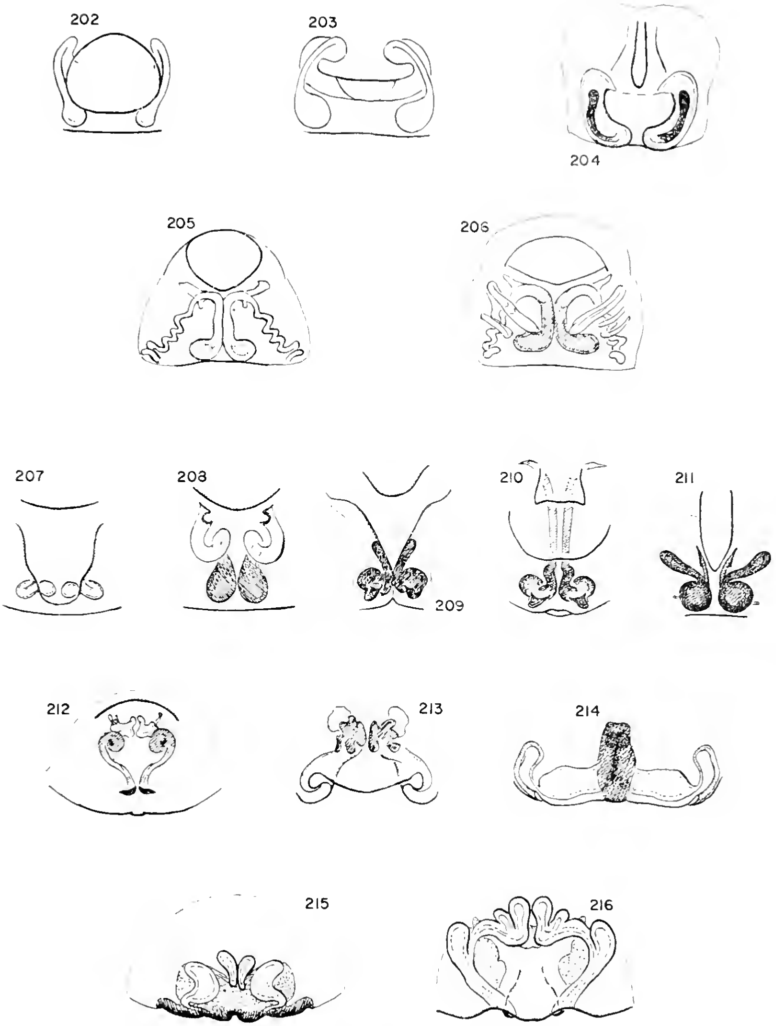

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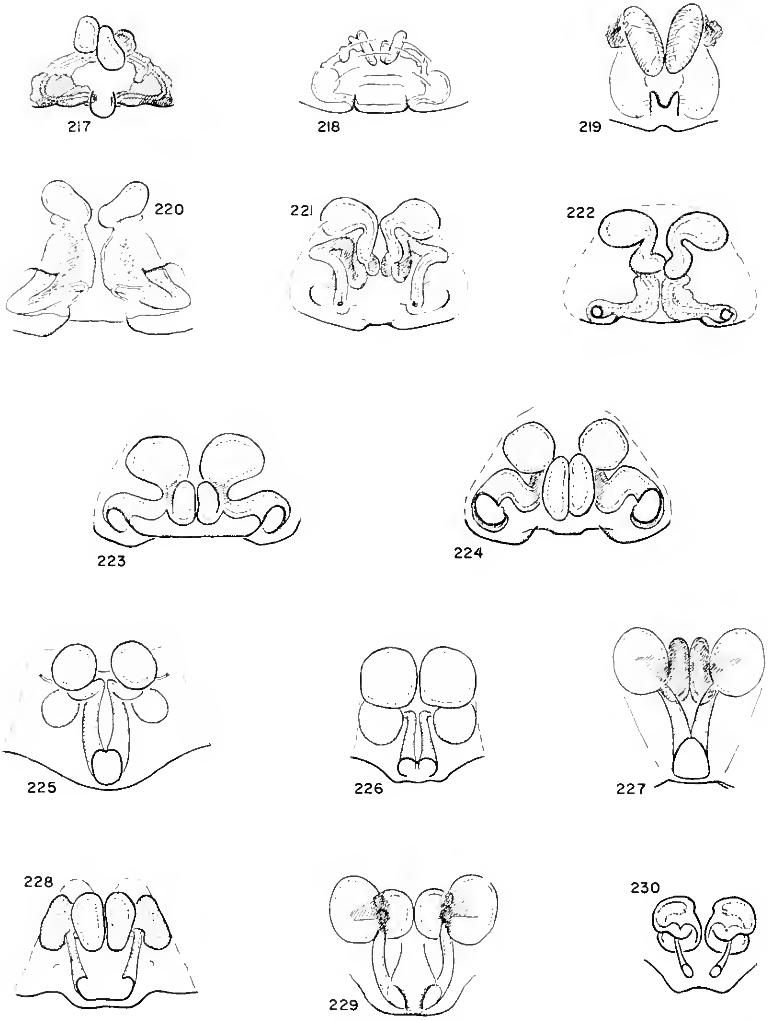

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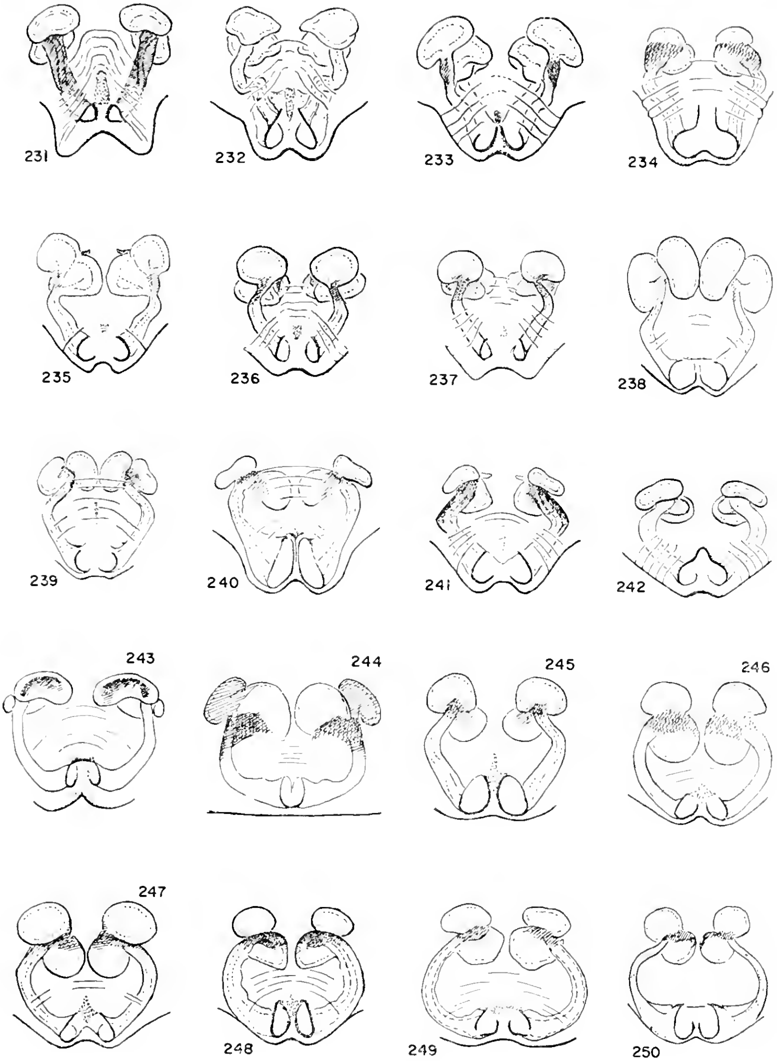

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AT HARVARD COLLEGE
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THE NEARCTIC MEMBERS OF THE GENUS *ENTOMOBRYA* (COLLEMBOLA)

By Kenneth Christiansen
Grinnell College

With Twenty-Four Plates

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
June, 1958

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No. 7 — *The Nearctic Members of the Genus* ENTOMOBRYA (*Collembola*)[1]

By KENNETH CHRISTIANSEN

Grinnell College

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SYSTEMATIC DESCRIPTIONS

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[1] Most of the material contained in this work was submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Biology, Harvard University.

INTRODUCTION

Scope of Study

In 1758 Linnaeus fixed the name *Podura nivalis* for that form figured by Degeer in 1740 under the name of "Små grå insekter." Nicolet in 1841 recognized the separate generic identity of the group and he created the genus *Degeeria.* In 1848 Gistel found that this name was preoccupied and he renamed the genus *Mydonius;* but this was generally unknown and in 1861 Rondani again discovered the synonymy of *Degeeria* and created the name *Entomobrya,* which has been generally accepted by workers since that time. The name *Mydonius* was rediscovered independently by Salmon (1945) and Laing (1945). Upon petition by Hermann Gisin the International Commission recently validated the name *Entomobrya* under the Plenary Powers, (Opinion 440, January 8, 1957).

By the time the first revision of the European members of this group was made (Lubbock 1873), sixteen species were considered valid, with six synonyms. By the time of the only world revision of the group (Brook, 1883), this number had grown to twenty-four species with eight synonyms, which Brook reduced to eleven species with twenty-one synonyms. Until 1933 the work on the genus consisted of very local treatments of the group and descriptions of many new species. Most of the workers commented on the variable patterns within one species of the group, but many new species have been described on pattern alone. In 1933 Bonet put together a key to the species of the world, based on the descriptions which were sufficiently complete and on the specimens which he had examined. In this, he keys out over one hundred species, and lists twenty-seven names which he is unable to place in the key. Since then, Denis, Gisin and others have investigated particular questions regarding the classification of *Entomobrya,* but no general revision has, to my knowledge, been attempted.

The confusion in the group has been brought about largely by the lack of consideration of the nature and quantity of infraspecific variation concerned and by the almost exclusive utilization of the pattern criteria in distinguishing species. In the following paper I attempt to achieve a more stable classification, as far as the Nearctic fauna is concerned.

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Without the aid of Dr. Frank M. Carpenter, under whom this study was initiated, the author could never have hoped to make any progress with the problem. His complete cooperation and understanding, as well as his very valuable guidance, have been major forces in keeping this project alive, and the author is sincerely grateful to him.

Another great debt of gratitude is owed to Dr. Harlow B. Mills of the Illinois State Natural History Survey at Urbana. Dr. Mills has shown the greatest kindness to the author, and always found time to discuss the many troublesome questions which arose from time to time in this study.

A considerable number of helpful ideas have been received during the last six years from discussions concerning theoretical considerations and matters of procedure. Dr. J. C. Bequaert, University of Houston, Drs. P. J. Darlington and W. L. Brown of the Museum of Comparative Zoology, Dr. F. G. Werner of the University of Arizona, Drs. H. H. Ross and L. J. Stannard of Urbana, Illinois, Dr. M. Hammer of Bakkevej, Denmark, Dr. H. Gisin of Geneva, Switzerland, Dr. M. F. Bonet of Mexico City, Dr. Delamare-Deboutteville of Banyuls-sur-Mer, France, Dr. E. A. Maynard of the University of Rochester, New York, Dr. J. Paclt of Bratislava, Czechoslovakia, and Dr. C. L. Remington of Yale University have been particularly helpful in this respect. Dr. Bequaert has also been extremely cooperative in matters pertaining to the collections in the Museum of Comparative Zoology, and Dr. Delamare-Deboutteville was kind enough to loan the author his complete, extensive collection of European and African members of the genus *Entomobrya*. This loan made possible a considerable portion of the comparative studies.

In addition to this great aid, a large number of people have sent material of one kind or another, all of which was of use in the completion of this work. Space will permit only a listing, but the author wishes to express his gratitude to each of the following persons: Mr. Carl Cook of Crailhope, Kentucky; Mr. Elmer Gruenloh of Lamar, Colorado; Mr. David Malsed of Palouse, Washington; and Mr. Harry Thorne of Hayward, Wisconsin, who did Berlese funnel collecting for this study; Dr. J.

T. Salmon of Wellington, New Zealand; Dr. V. Roth of Corvallis, Oregon; Mr. H. E. Goto of London, England, who cooperated in exchanges with the author; Dr. N. A. Weber of Swarthmore College; Dr. S. W. Frost of Pennsylvania State College; Mr. A. Van Pelt of North Carolina Appalachian State College, who contributed considerable amounts of unworked material; and Dr. H. W. Levi of the Museum of Comparative Zoology; Mr. W. MacDonald of the University of California and Dr. Tuxen of the Copenhagen Museum in Denmark, who also contributed material.

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An extensive collecting trip was made possible in 1950 by a grant-in-aid from the Sigma Xi-RESA Research Fund. The material thus acquired was of great value in completing this study. A further grant from the same fund, in 1955, made possible the preparation of the manuscript for publication.

Methods and Materials

Studies of coloration, pattern, body form, and the larger body ratios were carried out with alcoholic material. For observation of finer structures, a compound microscope with oil immersion objectives and 20× oculars (or similar high-magnifying combination) was necessary. Of the various mounting media used, four were found to be good: glycerine jelly and lactic acid as temporary mountants, Faure's medium (Bonet, 1933), and Salmon's polyvinyl-lactophenol (Salmon, 1949) as permanent media. For examination of the more minute morphological characters it is best to mount the specimen dorsal side down, with the head and antennae stretched forward and the furcula pressed against the body. In this position most of the taxonomically important structures can be seen.

Certain structures are visible only if the animals are examined in a solution of KOH. Such specimens must be examined immediately, because they soon disintegrate.

Drawings of habitus and pattern were made from alcoholic specimens, using a squared disk and squared paper. Drawings of morphological details were made using a camera lucida. Descriptions were taken from typical specimens, but because some such specimens were not suitable for drawing under alcohol, habitus drawings are not always of the pattern form described.

Discussion of Characters

In this work I have come to the conclusion that morphological criteria must be used in the taxonomy of *Entomobrya.* Many of the characters discussed below have not hitherto been used in this group.

The color and pattern of the species of this group can be used taxonomically if a number of facts are kept in mind. Color and pattern vary more, and more visibly, than any of the morphological characters studied; unfortunately, much of this variation is infraspecific and has apparently little to do with geographical segregation. In most species completely pale specimens and very dark ones are found. Beyond this general type of increase-decrease variation, the same population may have several distinct patterns existing within it. The integrades between these may be common, rare, or, in a few cases, non-existent. Thus, in thinking of any pattern we must not consider a given specimen, but a given range of pattern forms. This frequently leads to a secondary resemblance of individual pattern forms among widely separated species. A good example of this occurs in the two-banded forms of *E. clitellaria, E. triangularis,* and *E. atrocincta,* all of which might be considered as the same species on a pattern basis; this pseudo-species is quite distinct from differently pigmented, corresponding forms of the actual species. The greatest value of the pattern lies in placing certain forms which are distinctly marked and which have no similarly marked relatives, and in separating two species where one always lacks a given type of mark or color and the other usually has it.

The *labral papillae* are four small setiferous knobs or cones, borne in a transverse row on the upper surface of the labrum, near its anterior edge. The shape of these papillae, and the number and types of setae which they bear, are of great taxonomic value (see figures).

The *labial appendages* are two small flaps of tissue, borne apically on the labium, one on either side of the median cleft, each bearing six large papillae, upon which there are a number of setae of different sizes. The most external of the papillae bears a differentiated seta, the shape, size, and position of which, relative to the apex of the papilla are of very great taxonomic importance. (See Figs. 1, 6.)

The members of the genera here studied, along with a few other genera of the subfamily Entomobryinae, are peculiar in the differentiated nature of the setae of the *male genital plate.* This peculiarity permits the use of these differing shapes in taxonomy, and this is by far the most useful character found in the course of this study. The form of these setae is with very few exceptions specifically distinct, and with fewer exceptions infraspecifically constant.

The literature gives evidence of considerable confusion concerning the structures of the *ungues* and the *empodial appendages.* These organs are described in detail in the generic description of the genus *Entomobrya,* and Figures 4 and 5 of Plate I show a diagrammatic representation of the typical structure. Many references to "six teeth along internal edge" or "three pairs of internal teeth" are due to the misconception that each of the apical two internal teeth is double. Salmon (1944) mistook the reinforced lateral teeth, present in large individuals of most species, for a single large external tooth. The true external tooth is never as large as that, and in all species so far examined it is always a part of a small and thin lamella, acting as an external keel on the unguis. If these facts are kept in mind, along with the growth differentiation of the structure and the relative positions, then the size and shape of the ungual teeth are of considerable taxonomic value and represent one of the few morphological characters which have been given any attention by previous authors.

The shape of the *mucro, antennal sense organs, setae, trochanteral organ,* and the *general body facies* are of occasional taxonomic value. There is a great amount of variation in body shape within a given species, due to diet, moisture content, and nearness to time of ecdysis; all of these must be kept in mind when considering general appearance as a taxonomic character.

Ratios have long been used as specific criteria in this genus, but after exhaustive statistical analysis of the variation in the ratios of 26 different body organs in 18 species, I concluded that the level of significance of the variations among populations of a given species was so high as to be indistinguishable from that occurring among the majority of species. For this reason the use of such ratios as specific criteria is at present invalid in this genus.

Growth and Differentiation

The failure to recognize the morphological changes occurring during the course of the life of a collembolan has led to a great number of difficulties in the taxonomic treatment of *Entomobrya*. These difficulties can be overcome in three ways: first, the morphological changes occurring throughout growth can be carefully mapped for each species; second, the types of morphological changes can be determined, and these kept in mind in all considerations; lastly, the comparison of specimens can be largely limited to specimens in approximately equivalent developmental stages. A combination of all three methods was used in this work. Descriptions were taken from sexually mature specimens of a given size range. Illustrations were taken from such specimens except as otherwise noted, and the major variations of peculiar importance for each species are mentioned in the discussion at the end of the description. A number of general trends in differentiation are discussed below; these should be kept in mind in working with any of the species, because larger or smaller specimens than those described will exhibit these modifications.

All morphological characters appear to become more differentiated with increasing age. This is in part a mechanical process, since most of the structures involved are exceedingly small, and in small specimens pass beyond the level of optical resolution. Beyond this phenomenon, there is a general increase in the numerical parts of many organs, and a change in shape or in the relationships of parts in others. These changes will be considered here, under the individual type of differentiation involved.

The labral papillae and the antennal sensory organs demonstrate no visible growth differentiation. The mucro usually fails to show any significant change, although in forms with long and unusually formed mucrones, such as *Entomobryoides dissimilis,* the peculiarity of the form becomes more striking in larger specimens.

The trochanteral organ and the dental spines of the genus *Homidia* show a striking increase in the number of parts with increasing size of specimens. The trochanteral organ usually starts out in the first instar as one or three setae, and then slowly increases the number involved until the mature form is reached. In postmaturity molts the number is further increased, but at a much slower rate, so that unusually large specimens have only a few more setae than small, sexually mature ones.

The teeth of the unguis increase in size with the size of the specimen, and in first and second instar specimens only the internal basal and median teeth are clearly visible. The external, lateral, and apical internal teeth appear at the third or fourth instar and then remain constant in number. The unguis itself is relatively shorter and broader in earlier stages, and consequently the various teeth are usually relatively nearer the apex of the unguis in smaller stages than they are later in life. Labial appendages remain constant, except that in older specimens the external differentiated seta is slightly longer in relation to the papilla which bears it.

The type of pattern is usually the same in young and old animals, but in young forms the pattern is less distinct, and almost all species have the first instar either uniformly pale or with extreme faint indications of the adult pattern. The colors are paler in smaller specimens, and tend to be somewhat brighter (or darker) just before molting.

SYSTEMATIC DESCRIPTIONS

Notes on the Tribe Entomobryini

The present constitution of this tribe represents an expansion and fragmention of the old genera *Lepidocyrtus* and *Entomobrya.*

If the tribe is divided into scaled and scaleless forms, it will be seen that the former are in a state of considerable confusion. Some genera such as *Lepidocyrtinus* represent strikingly polyphyletic groups, while others, such as *Lepidocyrtus*, are not at the present time clearly defined. Furthermore, it is not clear at present whether the scaled condition has been developed independently several times, or is an indication of common ancestry. Mr. Goto's forthcoming work upon the genus *Lepidocyrtus* should greatly clarify the situation, but until such time no clear idea of the relationships of these forms can be obtained. Most of the scaleless members of the tribe appear to form a more natural assemblage. Some are obviously closely linked, and most of the others, while obviously aberrant, show definite relationships to the group as a whole.

The genera which have been described as members of this group are *Entomobrya*, *Calistella* (Schött, 1894), *Homidia* (Borner, 1906), *Drepanura* (Schott, 1891), *Sinella* (Brook, 1882), *Metacoelura* (Salmon, 1951), *Parasinella* (Bonet, 1942), *Pseudentomobrya* (Salmon, 1941), *Mesentotoma* (Salmon, 1941), *Deuterosinella* (Salmon, 1941), *Isotobryoides* (Maynard, 1950). Of these the genus *Calistella* has been considered a member of the *lepidocyrtiform* group by most recent workers (Salmon, 1951), while the genus *Pseudentomobrya* (Salmon, 1941) cannot be accepted as valid upon present criteria (see discussion under genus *Entomobrya*). In the following work the subgenus *Entomobryoides* (Maynard, 1951) is raised to generic level, the genera *Mesentotoma* and *Drepanura* are redefined, and the new genus *Calx* is created.

Relationships

The phylogenetic position of *Mesentotoma* is entirely moot. The lack of a basal mucronal seta plus the peculiar antennae and empodial appendages, show wide separation from the other genera. The dental spines present upon one species are in no way homologous with those of *Homidia* and therefore cannot be considered as indicative of relatedness. The discontinuous range may be an indication of great antiquity, or of insufficient data, but in any case the genus is not closely related to any other member of the *Entomobryini*.

Considering the relationships among the remaining genera, we find that the putative ancestral form is not apparent; however, the genus *Calx* would appear to have the greatest possibilities. The relatively primitive condition of the male genital plate and the comparatively short fourth abdominal segment, combined with the simplicity of the body setae, indicate its possible proximity to the ancestral form. On the other hand, the lack of an anteapical tooth probably represents a specialization, thus indicating that *Calx* cannot be directly ancestral.

The remaining genera are clearly derivable from, or related to, the genus *Entomobrya*.

The work that follows the key is concerned exclusively with those Nearctic genera which are still considered by some workers to belong to the genus *Entomobrya*, viz. *Entomobrya*, *Drepanura*, *Mesentotoma*, *Homidia*, *Entomobryoides*, and the new genus *Calx*.

Key to the Scaleless Entomobryini

1.	Mucro without basal spine	2
	Mucro with basal spine	3
2.	Mucro with anteapical tooth	*Mesentotoma*
	Mucro lacking anteapical tooth	*Calx*
3.	Dens with spines	*Homidia*
	Dens without spines	4
4.	Second antennal segment longer than fourth, eye patches without color	*Isotobryoides*
	Second antennal segment shorter than or subequal to fourth	5
5.	Eyes 16	7
	Eyes fewer than 16	6
6.	Tibiotarsus with a number of smooth, unusually finely ciliate setae	*Sinella*
	Tibiotarsus lacking, or with only one such seta	*Parasinella*
7.	Mucro reaching head	*Coelura*
	Mucro not reaching head	8
8.	Tibiotarsus with double row of unusually finely ciliate or smooth setae	9
	Tibiotarsus with only one such seta	10
9.	Unguis with 3 internal teeth	*Deuterosinella*
	Unguis with 4 internal teeth	*Entomobryoides*
10.	Mucro with anteapical tooth	*Entomobrya*
	Mucro without anteapical tooth	*Drepanura*

Genus ENTOMOBRYA Rondani

Podura, 1758, Linné, Systema Naturae, ed. 10:609 (*ad partem*).
Choreutes, 1838, Burmeister, Handbuch der Entomologie, **2**(2):450.
Isotoma, 1839, Bourlet, Mém. Soc. Sci. Agric. Lille, **1**:448 (*ad partem*).
Degeeria, 1842, Nicolet, Nouv. Mém. Soc. Helvet. Sci. Nat., **6**:68.
Mydonius, 1848, Gistel, Naturgeschichte des Tierreichs, **16**:9.
Pseudentomobrya, 1941, Salmon, Trans. Roy. Soc. N.Z., **70**:282-431 (new synonymy).
Entomobrya, 1861, Rondani, Dipterologiae Italicae Prodromi, Pars (4):40.
Genotype: Entomobrya muscorum (Nicolet) *loc. cit.*

Color and Pattern. Pigmentation variable.

Antennae. Four segmented, fourth segment usually longest and first shortest (commonly 8-6-6-3). Fourth segment usually fusiform, basally blunted, in *E. bicolor* group subcylindrical and apically rounded. Remaining segments subcylindrical. Fourth segment rarely with signs of ringing or subsegmentation, apically a thin-walled retractile bulb in a pit (absent in one species); densely clothed with setae, as follows: short, smooth, truncate to clavate, straight setae located apically on all sides, and ventrally for apical nine-tenths of segment; numerous blunt, curved, smooth setae over whole segment, apically subequal in size to the short truncate setae, basally about twice as long; in intervening area a mixture, with longer setae more numerous; acuminate, heavily ciliate setae of various lengths occur over the entire surface. Two minute subapical sensory pegs, one below and slightly external of the other, on the dorsum of the segment.

Third segment clothed as basal portion of fourth segment, but ciliate setae longer. Apical sensory organ usually of two curved pegs, dorso-externally, in shallow folds. Basad of these a slender rod and apicad a conical to cylindrical peg, smaller than the median pair.

Apical sensory organ of second segment of one or two sensory pegs, usually much thinner than those of the third segment, and one to three additional narrow rods.

Clothing first and second segment similar to third segment, but short smooth setae tend to be concentrated on the ventral surface, covering this surface except for apical area of varying size and shape.

Head. Two labial appendages, each of six papillae, with eighteen to twenty smoothly tapered, slender setae, and apical one on each papilla slightly truncate, remainder acuminate. Typically, external papilla bears a differentiated seta, varying in shape, but usually blunt, not uniformly tapered, and basally about as thick as the largest acuminate setae. On labrum are four small, round, setiferous papillae in a transverse row. Eyes sixteen, situated on two heavily pigmented eyepatches. Eyes vary in size, but the inner posterior two usually somewhat smaller than remainder.

Body. Fusiform to elongate elliptical, usually more or less circular in cross-section, occasionally somewhat compressed. Antenna four-segmented, frequently with basal ring of cephalic integument, giving appearance of small basal segment. First thoracic segment reduced, soft and membranous. All other segments somewhat sclerotized. Second and third thoracic segments with sclerotized areas as distinct tergites covering dorsal and lateral areas, ending bluntly just above leg bases. First abdominal segment greatly narrowed ventrally, and here the tergite usually appears to come to a point. Second and third segments soft ventrally, but without distinct demarcation. Fourth segment with two longitudinal furrows marking off a lateral triangular area, and below this a triangular, blunted lobe (parafurcular lobe), one lobe on either side of the furcula when contracted against the body. The fifth abdominal segment completely sclerotized except for small ventral area, bearing genital plate. Sixth segment completely sclerotized.

The body segment lengths vary; however, the fourth abdominal segment is always at least twice as long as any other body segment. The second thoracic segment is next in size, being larger than the second, third, and fifth abdominal segments, which are variable but comparable. The first and sixth abdominal segments are the shortest segments.

Clothing. Body clothed with five types of setae. These vary, but the five categories are always present and recognizable. In the specific descriptions they will be referred to as categorized here.

Body setae, type one: ("Flexed" setae, Salmon, 1951). These heaviest setae are thick, straight or slightly curved, apically clavate or bent, basally contracted at point of articulation, and bearing uniform fine ciliations on all sides. Usually scattered sparsely over the entire dorsum, but more concentrated on the anterior half.

Body setae, type two: ("Pubescent" setae, *idem*). Length varying, uniformly tapered, finely and uniformly ciliate. Thickness varies from about as thick as type one setae to about half as thick. These are found all over the ventral and dorsal regions of the body, more numerous on the posterior half.

Body setae, type three (lasiotrichia): extremely long and thin, untapered except at distal end, uniform ciliations slightly larger than those previously discussed. These setae are very few in number, and constant in position (frequently knocked off in the course of preparation). The normal condition is four of these on each of abdominal tergites two, three, and four.

Body setae, type four: about half as large as type one, basally untapered and smooth for the basal half to fifth of their total length, apically tapered and ciliate. These are usually limited to fifth and sixth abdominal segments.

Body setae, type five: common setae of body, and are found on all parts. They form an under layer out of which the others arise. These vary, but never more than one-half the size of type four setae, coarsely ciliate, always acuminate, and usually smooth basally.

Legs. Prothoracic and mesothoracic legs subequal, much smaller than metathoracic legs. Leg of two precoxal short segments (not always visible as discrete), longer coxa, a short trochanter, a femur about as long as all the more basal segments, and a much longer tibiotarsus (rarely broken by a false joint two-thirds of the distance from base). Apically with unguis, small empodium, and empodial appendage opposed to unguis. Clavate tenent hair present on tibiotarsus, just basal of unguis. Empodial appendage quadrilamellate, with posterior edges of one or both posterior lamellae often finely ciliate. Unguis consists of four heavy lamellae, apically joined, each lamella gradually thickened toward the axis of the unguis so that lines of jointure between lamellae are not distinct. Internal lamellae with four teeth, usually small and subequal; two most basal form a pair, one on each lamella. Two lamellae join at middle tooth, and thus these apical teeth are unpaired, with basal one appearing double due to its split basal origin. Lateral lamellae present, each with one tooth. If large, this tooth is often reinforced with chitinous ribs, giving appearance of being discrete from rest of lamellae. One or two external teeth may occur, usually very thin and on thin external lamellae, not running the entire length of unguis.

Legs, manubrium, dens clothed with acuminate, finely and uniformly ciliate setae. Length varies, longest on legs at bases of the femora. All tibial setae with ciliations approximately equal in size. A single stiff, spinelike seta is apical on metathoracic legs.

Trochanteral organ consists of smooth straight acuminate setae. These typically arranged in a more or less triangular pattern, formed (see Pl. 1, fig. 7) by two ventral and two posterior lines of setae (ventral and posterior arms respectively), between which are a varying number of setae which may or may not be arranged in some definite pattern (internal setae), and a few other setae scattered over the same surface of the trochanter (external setae). The setae of the two arms tend to increase in size toward their own joining point, and these setae tend to be considerably larger than the others.

Furcula and genital plate. Male genital plate located at base of the dorsal side of manubrium, on fifth abdominal segment (see Pl. 1, fig. 2). It consists of a large setiferous papilla, round to reniform in ventral aspect. In lateral view the organ is of three parts; a domed open ring of integument, broken medioposteriorly, bearing distinct reticulations and having a ring of large smooth, usually thin-walled setae around its inner margin. These are highly specific in shape and differentiated from all other setae on the animal. Basal pair (or all) half as long as longest distance across integumentary ring. Internal of this ring is a truncately conical projection bearing a cylindrical lobe with apical genital aperture, slightly projected so as to form an acuminate tip. The terminal cylindrical structure bears four small, pointed, smooth setae. Although the actual aperture of the genital organ is very small and irregular in shape, the break in the first integumental ring, combined with the aperture and the form of the more internal parts, gives the appearance of a longitudinal slit. Whole organ surrounded by one or more rows of ciliate setae, like body setae type four.

Female genital apparatus simple, consisting of a transverse slit and integumentary lip on either side; each lip with two small smooth setae.

Dens longer than manubrium, dorsally crenulate, with a distinct uncrenulate area just before the mucro. Mucro two-toothed, with a basal spine. Furcula displaced posteriorly, so as to appear appended beneath the fifth abdominal segment. Anal aperture triangular, protected by integumentary flaps and posteriorly (sometimes slightly ventrally) directed.

Discussion

The members of this genus appear to break down in the Nearctic region into four distinct subgroups. I do not feel that it would be wise at the present time to raise these groups to generic stature, for as well as can be judged from the literature, the exotic species of the genus would in some cases erase the lines between these groups, and in other cases many species of a group are not at present available for study. For the purpose of clarifying the relationships, these groups are discussed here, with a taxonomic characterization of the species group. A number of species of doubtful relationships are not included.

The *Entomobrya nivalis* group includes (among others) *E. nivalis*, *E. atrocincta*, and *E. griscoolivata*. All these species are characterized by general facies, usually having multisetaceous labral pipillae, tending to have the apical mucronal tooth much longer than the anteapical, a bilobed or trilobed apical antennal bulb, and the tendency to have the basal seta of the male genital plate apically expanded. The *Entomobrya triangularis* group is characterized by the tendency for the mucronal teeth to be subequal, the presence of very long setae on the basal antennal segments, the general trend toward homogeneity among the setae of the male genital plate, and the tendency for the bilobed condition on the antennal apical bulb to be unclear but still present. This group includes (among others) these species: *E. triangularis*, *E. ligata*, and *E. washingtonia*.

The *Entomobrya bicolor* group is possibly the same as the group given the generic name *Calistella* by Schott in 1894. Since this group is not clearly demarcated from the remaining members of the genus, and the application of the name *Calistella* is still in doubt, I feel it better to leave this matter in abeyance until such a time as the world fauna can be studied. The members of this group are characterized by the elongate body, tending to be bilaterally compressed, extremely long appendages, simple elongate apical bulb on the antenna, and by the occasional occurrence on the antennal apex of a non-retractile accessory papilla. There is a tendency for the anteapical mucronal tooth to be longer than the apical. The species comprising this group are usually somewhat larger than those in the other groups; maximum normal size is about 3.5 mm., as compared with 2.8 mm. in other groups. In all other comparisons, the post-maturity molts cause the total size to be of little importance, but here the difference is so great that this objection is minimized. The following are some of the species included in this group: *E. bicolor, E. quadrilineata, E. decemfasciata, E. nigriceps,* and *E. gisini.*

The *Entomobrya comparata* group is quite closely linked to the last group by the aberrant form *E. kincaidi.* The group is characterized by the strong unisetaceous labral papillae, the usually sigmoidal, stoutly curved male genital setae, the occasional tendency for dorsoventral flattening, the salient basal external teeth on the unguis, and usually simple apical antennal bulb. This group includes the species *E. comparata* and *E. clitellaria.*

E. assuta is aberrant in many respects and does not appear to be closely allied to any of the above groups. Other aberrant forms will be dealt with in the specific descriptions.

I feel that when the world fauna of this group can be studied many of the above mentioned divisions will prove to be valid genera, but on the basis of presently available knowledge these relationships can only be indicated as probable.

Salmon's redefinition of the genus *Entomobrya* (Salmon, 1941) cannot be considered a valid one, because it is based upon a misconception concerning the nature of the unguis (see discussion of ungues). In the species of "*Pseudentomobrya*" which

I have examined I have not found any valid and constant differences between these species and typical members of the genus *Entomobrya*.

Four species of Nearctic *Entomobrya* are not included in the key and descriptions are not herein presented. *E. brunnecapella* Maynard may not be a member of this group of genera. In view of this I feel it unwise to include this species until a few specimens can be examined. Bueker's *duolineata* and Harvey's *pygmaea* are both unusual patterns for the genus, but have not been recovered since their original records. In both cases the types are unavailable and the descriptions are not sufficient to determine whether they are poor descriptions of common species, or of unrecovered rare forms. In view of this, I am leaving the matter in abeyance and reprinting the original figures here. *E. lateropicta* Hammer may be a synonym of the subalpine form of *E. comparata* but further series are required to settle this point (see footnote with *E. comparata*).

Key to the Nearctic Species of the Genus ENTOMOBRYA

1. With retractile bulb near apex of antenna 2
   Without apical retracile bulb . . . . . *E. sinelloides* n. sp.
2. Body setae of type five medially expanded, flattened and leaf-shaped on dorsum of abdominal segment four . . . . . *E. kincaidi*
   Body setae of type five otherwise formed 3
3. Head strikingly longer than broad 4
   Head at most only slightly longer than broad 8
4. External seta of labial appendage not extending beyond the apex of same papilla 20
   External seta of labial appendage extending beyond apex of same papilla for at least one-fourth of its length 5
5. Mesonotum strikingly produced so as to force the head into a hypognathous position . . . . . *E. bicolor*
   Mesonotum not so produced 6
6. Dark areas of head much greater than pale areas . . . . . *E. nigriceps*
   Dark areas of head much less than pale areas 7
7. External labial seta extending beyond apex of same papilla for less than half its length, dorsum of second abdominal segment (in well pigmented specimens) with two solid or broken diagonal lines . . . . . *E. decemfasciata*
   External labial seta extending beyond apex of same papilla for more than half its length, second abdominal segment (in well pigmented specimens) with four longitudinal bands . . . . . *E. quadrilineata*

8\. Apical sense organ of third antennal segment with four sensory knobs, Cavernicolous *E. troglodytes* **n. sp.**

Apical sense organ of third antennal segment with two or three sensory knobs 9

9\. Most of setae of male genital plate sickle-shaped 10

At most only one or two of setae of male genital plate sickle-shaped 12

10\. Body slightly dorsoventrally flattened, pigment in broad bands *E. clitellaria*

Body not flattened, pigment in irregular bands, spots and stripes 11

11\. External differentiated seta of labial appendage attaining apex of same papilla, apical bulb of antennae usually not lobed (sometimes apically indented or bilobed) *E. comparata*

External differentiated seta not attaining apex of same papilla, apical bulb bilobed or trilobed *E. ligata*

12\. Body dorsoventrally compressed, male genital plate with two lateral setae on either side strikingly larger than remainder *E. assuta*

Body not dorsoventrally compressed, male genital plate not as above 13

13\. Labral papillae multisetaceous 14

Labral papillae unisetaceous 16

14\. Body without distinct pattern, basal seta of male genital plate with contracted basal part about as long as expanded apical part *E. griseoolivata*

Body (in well pigmented forms) with a definite pattern, basal seta of male genital plate with contracted basal portion much longer than expanded apical part 15

15\. Fifth and sixth abdominal segments unpigmented *E. atrocincta*

Fifth and sixth abdominal segments with some pigment *E. nivalis*

16\. Basal seta of male genital plate with apex expanded, well pigmented specimens with mid-dorsal line on all segments *E. unostrigata*

Basal seta of male genital plate not apically expanded, well pigmented specimens without mid-dorsal line on most segments 17

17\. Male genital plate with all setae acuminate 18

Male genital plate with at least one pair of setae blunt 19

18\. Body with definite pattern, basal setae of genital plate different from others *E. suzannae*

Body uniformly pigmented, basal setae of genital plate similar to other setae *E. confusa* **n. sp.**

19\. Fourth abdominal segment with definite longitudinal bar or stripe, male genital plate with one pair of blunted setae *E. washingtonia*

Fourth abdominal segment without definite longitudinal bar or stripe, male genital plate with two pairs of blunted setae *E. triangularis*

20\. Antennae definitely longer than trunk *E. arnaudi*

Antennae shorter than trunk *E. gisini* **n. sp.**

ENTOMOBRYA NIVALIS (Linné)[1]

Plate 2, figs. 1-18

Podura nivalis, 1758 (et subs. ed.), Linné, Systema Naturae, ed. **10**:609; 1776, Muller, Zoologiae Danicae prodromus, Havniae:183; 1778, Degeer, d. Ins., Stockholm **7**:15; 1781, Schrank, Ennumeratio Insectorum Austriae, Augustae Vindelicorum:498; 1781, Fabricius, Species Insectorum Hamburgi et Kolonii:383; 1788, Gmelin in Linnaeus, Systema Naturae, ed. 13, Lipsiae; 1788, Wulfen, Schrift. Berl. Ges. naturf. Fr., **8**:83; 1827, Brebisson, Mém. Soc. Linn. Normandie, **3**:254-274; 1835, Boisduval and Lacordiare, Fauna entomologique des environs de Paris: 114; 1838, Burmeister, Handbuch der Entomologie, **2**(2):443-458; 1842, Lucas, Histoire Naturelle des Crustaces Arachnides et des Myriapodes, **2**:565.

Podura annulata, 1775, Fabricius, Systema Entomologica, **2**:450.

Podura nigromaculata, 1835, Templeton, Trans. Ent. Soc. London, **1**(2):94.

Choreutes nivalis, 1838, Burmeister, Handbuch der Entomologie **2**(2):450.

Degeeria minuta, 1838, Burmeister, Handbuch der Entomologie, **2**(2):449.

Podura variegata, 1838, Guerin, Genera des Insectes:57.

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Entomobrya nivalis, var. *lateralis*, 1922, Stach, Magyar Tud. Akad. Balk.-kut. Tudo, ered. Kot., **1**:115.

Entomobrya nivalis, var. *abrupta*, 1922, Stach, *idem.*

Entomobrya nivalis, var. *transiens*, 1934, Bonet, Eos, **9**:147.

Entomobrya nivalis, var. *maculata*, 1896, Schaeffer, Jahrb. Hamb. Wiss. Anstalten, **13**:149.

Entomobrya nivalis, var. *immaculata*, 1896, Schaeffer, *idem.*

Entomobrya multifasciata, ab. *cincta*, 1903, Agren, Stett. Ent. Zeit., **64**: 155, 156.

Entomobrya muscorum, var. *pallida*, 1872, Tullberg, Svenska. Vet.-Akad. Handl., **10**(10):64.

Entomobrya muscorum, var. *obscura*, 1872, Tullberg, *idem.*

Entomobrya muscorum, var. *obscurior*, 1872, Tullberg, *idem.*

Color and pattern. Background yellow to white to pale blue. Pigment purple to blue. Pigment as follows: Antennae lightly pigmented, apical two segments darker. Blue-black ring on base and a connecting band. Dorsum of head, thin V-shaped mark, base at median ocellus, arms approaching lateral internal sides of eyepatches. Light pigment runs posteroventrally from ventral posterior angles of eyepatch to ventral margin of head. Prothorax, spotty pigment on leg bases. Mesothorax and metathorax with irregular black lateral margin, thicker on metathorax, running onto anterior border on mesothorax. Mesothorax through abdominal segment three with dorsal dark band along posterior margins not connected with lateral dark markings on two. Abdominal one a narrow band of more or less uniform width; on other segments bands produced forward at right angles at lateral ends, larger on abdominal two and three. Abdominal one and two with lateroventral areas darkened. Abdominal three with large ventro-anterior spot in contact with ventral dark color on second segment. Abdominal four with two elongate, roughly triangular, longitudinal dark stripes, extending for basal two-thirds of dorsum, connected basally by a short stripe along the posterior segmental border. Posterior margin with dark spot at contact with parafurcular lobe. Space between lateral suture and parafurcular lobe dark for posterior half, anteriorly with roughly triangular spot in contact with lateral suture and broadly joined at apex with posterior dark color. Posterior half of fifth and dorsum of sixth segment dark. Coxae spotted basally, meso- and metathoracic femora ringed apically with dark pigment (metathoracic darker). Remainder of body pale.

Antennae. Segments one and four subequal in diameter, thicker than others. Retractile apical bulb distinctly tri- or bilobed, in a deep apical pit. Apical organ of third segment normal. Apical sensory organ or second antennal segment with two minute oval pegs, in individual shallow folds. Clothing of antennae typical, longest setae less than one and one-half times as long as the diameter of the corresponding segment.

Head broadly oval, 1.15 times as long as broad. Labral papillae broadly truncate, erect, with three to eight minute setae per papilla, rising directly from surface of papilla. Labial appendages normal, with external differentiated seta very long and slender, tapered only at apex; about as thick as largest normal seta on some papillae. Eyepatches black, subrectangular. Two anterior eyes three times as great in diameter as inner posterior two. These about one-half diameter remaining eyes.

Clothing of head and body of typical five kinds of setae. Setae of type one moderately long (longest about twice as long as longest antennal setae). Setae of type five relatively long, slender, gradually tapered from insertion to apex, coarsely multilaterally ciliate. Body fusiform to elongate, elliptical in shape, round in cross-sectional view.

Legs. Clothing typical. Tibiotarsus with double row of stout, basally expanded, ciliate setae, about three times as thick as smallest setae of segment at same level. Trochanteral organ typical, internal setae few, usually not present in apical half of space between arms. Unguis tapering uniformly, with usual seven teeth. Basal internal teeth opposite, slightly apical of the mid-level of the internal edge. Internal teeth small and subequal in size. Lateral teeth large and salient. Laterals slightly below level of internal basal teeth, external tooth about two-thirds of distance from base of claw to laterals. Empodial appendage not ciliate, acuminate, more abruptly tapered at extreme apex.

Furcula and genital plate. Mucro with apical tooth, slightly longer than anteapical, curved at extreme apex. Anteapical tooth slightly curved, basal spine attaining apex of anteapical tooth. Genital plate with twelve to fourteen setae on low blunt papillae. Two basal setae flattened, wide, apically expanded and truncate. Remaining setae slender, suddenly constricted halfway from base to apex and filamentous beyond this point.

Discussion

The species is extremely variable in pattern, but only slightly variable in morphological characters. A complete exposition of all the various stages in pigmentation would fill a separate volume. It is sufficient to say that every variation exists, from the pattern described to that of an animal with almost the entire body black to an animal with only a few dark spots on the head and on posterior regions of the body (see figures). The commonness of the species in Europe and North America and the huge variation in patterns, combined with the spotty occurrence of some of the forms, has led, as many investigators have pointed out, to large synonymy in the group, but there has been no general agreement as to its exact nature. Species which have been synonymized by some authors with *E. nivalis* and/or *E. multifasciata* include *E. arborea, E. marginata, E. pulchella, E. orchesellides* (*E. muscorum, sensu* Schaeffer), *E. spectabilis,* and *E. corticalis.* The tendency on the part of modern authors has been to consider all the members of this group as indistinguishable except on a basis of color pattern. Denis (1933) broke away from this by insisting that ratios alone showed a difference between *E. lanuginosa* and *E. nivalis,* but I found no such differences between any of the patterns which were seen from North America. Denis' differences may have been due to allometric growth.

Gisin (1947) gathered together all the major works on the group, and with personal research concluded that *E. nivalis, E. multifasciata* and *E. lanuginosa* were sympatric and ecologically separated. Feeling that the term subspecies should be reserved for geographical entities, he separates these as distinct species. In Switzerland he has not observed intermediates among these groups.

After examining a large number of European specimens, I have been unable to find any significant difference between the Nearctic and Palearctic populations. In all I have found samples containing every conceivable intermediate between *multifasciata* and *nivalis* (see figures). I am in agreement with Gisin concerning the ecological separation of the forms here involved, but I disagree on the matter of taxonomic treatment. I feel that some of the numerous, named species and varieties represent ecologically adaptive genotypes, but that these can have no taxonomic standing. Completely patternless forms have not been seen in Nearctic material.

The morphological variation in Nearctic material is small. The usual growth variations occur (trochanteral organ, etc.), and there is a basal shift of the external and lateral teeth of the unguis, with increasing size. The labial appendage may have the external differentiated setae exceeding the apex of the same papilla. The mucro may have the two teeth subequal in size, and the apical tooth may project directly posterior.

Distribution

Maine: Boothbay Harbor, Bailey's Island, Orono, Brunswick; *Massachusetts:* many localities; *Vermont:* Burlington; *New Hampshire:* Mount Washington (at the base), Kingston, Peterborough; *Connecticut:* New Haven, Hartford, Middlefield; *New York:* many localities; *New Jersey:* Ramsey, Princeton; *Pennsylvania:* State College, Bear Meadow, Lockhaven; *Virginia:*

Roanoke; *North Carolina:* Raleigh, Chapel Hill; *Kentucky:* Crailhope; *Tennessee:* Knoxville; *Minnesota:* localities unknown; *Iowa:* Ames; *Illinois:* many localities, mostly Cook County; *Montana:* Butte, Bozeman; *California:* San Francisco, Laguna Beach, Claremont, San Dumas Canyon, Santa Barbara, Sycamore Hill; *Oregon:* Corvallis; *Washington:* Tampico, Yakima; *Utah:* Kanosh, Uinta Mountains; *Colorado:* Lamar, Cotapaxi; *Arizona:* Globe; *Ontario:* Alamonte, Arnprior, Prescott.

Type locality: Europe.

ENTOMOBRYA ATROCINCTA Schött

Plate 3, figs. 1-12

Entomobrya atrocincta, 1896, Schött, Proc. Calif. Acad. Sci., **6**(2):181.

Entomobrya flava, 1933, James, Trans. Can. Inst., Toronto, **19**:77-116.

Entomobrya nigrocincta, 1923, Denis, Bull. Soc. Ent. France, **92**:54, 1924, Denis, Arch. Zool. Exp. Gen. Paris, **62**:282; 1930, Stach, Ann. Hist. Nat. Mus. Hung., Budapest, **26**:271; 1934, Bonet, Eos, **9**:164; 1937, Drenowski, Eigene Ausgabe, **16**:3; 1938, Kseneman, Bull. Inst. Nat. Agron. Brno, **26**:19.

Entomobrya pseudoperpulchra, 1931, Mills, Amer. Mus. Novitates, **464**:6, 7.

Entomobrya clitellaria, ssp. *australiasiae*, 1941, Salmon, Trans. Roy. Soc. New Zealand, **70**(4):356.

Entomobrya atrocincta, ssp. *nigrocincta*, 1944, Salmon, Rec. Domin. Mus. Wellington, **1**(2):154, 155.

Entomobrya atrocincta, ssp. *citrina*, 1944, Salmon, *Idem.* (new synonymy).

Entomobrya pseudoperpulchra, 1950, Wray, Bull. Brooklyn Ent. Soc., **45**(2):63.

The following varieties are considered as syonyms of *Entomobrya atrocincta* (only the original reference is given in each case):

Entomobrya atrocincta, var. *citrina*, 1934, Bonet, Eos, **9**:149.

Entomobrya atrocincta, var. *aurata*, 1947, Delamare-Deboutteville, Rev. Franc. D'Ent., **14**(2):138.

Entomobrya atrocincta, var. *lineata*, 1947, Delamare-Deboutteville, *idem.*

Color and pattern. Background bright yellow to orange, pigment blue-black. Antennal segments three and four lightly pigmented. First two antennal segments apically ringed with dark pigment. Antennal bases with narrow connecting band, and a wide dark band running laterally from posterior border of eyepatch. All leg bases darkened. Mesothorax, narrow lateral margin dark. Remainder of body pale.

Antennae. Apical retractile bulb of fourth segment trilobed, in a deep apical pit. Clothing of antennae normal, longest setae of second segment about one and one-half times as long as diameter of segment.

Head about one and one-half times as long as broad. Labral papilla low, truncately conical, multisetaceous, setae minute, and on micro-papillae. Eyepatches subrectangular, medio-internally indented. Four inner median eyes on either side much smaller than others. External differentiated seta of labial appendage long, narrow, tapered at extreme apex, slightly wider than normal setae of same papilla and exceeding apex of papilla for at least one-eighth of total length.

Body elliptical in shape, circular in cross-section.

Clothing of five typical varieties of setae. Setae of type five slender, coarsely unilaterally ciliate for apical two-thirds to four-fifths of length.

Legs. Clothing normal. Trochanteral organ lacking internal setae (or at most, two setae present). Internally on tibiotarsus one or two rows of large setae. Unguis sharply tapered for apical half of length, possessing normal seven teeth. Internal teeth moderate in size, distinctly larger than lateral and external teeth, median larger than others, basals slightly apical of middle of internal edge. Lateral teeth basad of basal internals, and external tooth basad of these.

Furcula and genital plate. Dorsal crenulations of dens end gradually. Mucro elongate, apical tooth distinctly longer than anteapical and slightly curved. Basal spine exceeds apex of anteapical tooth. Male genital plate twelve to fourteen setae. Basal setae apically expanded and flattened, truncate. Remaining setae basally somewhat expanded, sharply constricted above median level, filiform for apical one-third of length. Apical two setae on either side slightly shorter than other setae.

Discussion

Several different patterns occur in this species. Pure yellow specimens occur, as well as specimens with the described pigment plus the metathorax and first abdominal segment dark.

Since all these patterns occur in the same population, with no morphological separation, and since any large population will have most, if not all, patterns present, I cannot consider them as being other than parts of the normal specific variation.

This species is morphologically extremely close to *E. nivalis,* but may be separated from that species on the basis of the setae of the tibiotarsus. In *atrocincta* the largest setae at the middle of the segment are about twice the diameter of the smallest, while in *nivalis* the largest are about three times the smallest. The mucro of the former tends to have the anteapical tooth more equilateral in shape than in the latter, and the external tooth of the unguis is more apical in position in the former. The simplest criterion for separating the two species is the type of color pattern, which consists of segmental transverse bands in the former and irregular jagged marks in the latter. Almost all Nearctic specimens of *E. nivalis* have traces of pigment on the terminal abdominal segments, whereas *E. atrocincta* lacks these in even the darkest specimens. The pigmentation of *E. atrocincta* bears in some patterns a secondary resemblance to *E. clitellaria,* but the morphological distinctions between these species are striking and obvious (see description). I have examined a number of the European specimens originally assigned by Denis to *E. nigrocincta,* and I find no significant differences between them and the Nearctic populations of *E. atrocincta.*

Distribution

Oregon: Baker; *California:* Claremont, Hanford, San Francisco, Chino, Tuba City, Gasquet; *Utah:* Logan; *Tennessee:* Knoxville; *Texas:* College Station.

Type locality: California.

ENTOMOBRYA GRISEOOLIVATA (Packard)

Plate 4, figs. 1-15

Degeeria griseo-olivata, 1873, Packard, Rep. Peabody Acad., **5**:39.

Entomobrya griseo-olivata, 1884, Brook, Journ. Linn. Soc. London, **17**:281, 282.

Entomobrya marginata, 1934, Mills, Monog. Collembola Iowa, :67, 68 (*partim, nec Degeeria marginata,* 1871, Tullberg); 1951, Maynard, Collembola New York State :143-145.

Entomobrya griseo-olivacea, 1944, Gisin, Verh. Naturf. Ges. Basel, 55:73.

Color and pattern. Background color pale blue to white. Pigmentation purplish blue, uniform on body, except darker at extreme posterior borders of segments. Head irregularly pigmented over lateral, ventral and anterior surfaces, darker patch running ventrally and posteriorly from the ventroposterior angle of the eyepatch, expanded below. Antennae uniformly darkened, antennal bases and connecting band being dark blue. A similarly colored longitudinal stripe between the eyes originates at the median ocellus and runs forward to join the interantennal band, slightly expanded anteriorly.

Antennae. Fourth segment slightly thicker than third. Apical retractile bulb of the fourth segment trilobed (sometimes bilobed). Third antennal apical organ normal. Antennal setae normal. Longest setae on second antennal segment about one and one-half times as long as diameter of segment. Smooth short setae absent from the apical one-third to one-fourth of ventral surface of segment one.

Head. Dorsal view roughly circular. Labral papillae truncately conical, multisetaceous, with two to five minute setae on each papilla, arising from small micro-papillae. Labial appendages with usual number of papillae. External differentiated seta elongate, slender, slightly curved, about as thick as the normal setae of same papilla, tapered from base, but more suddenly tapered at extreme apex. Seta not attaining, or barely attaining, apex of same papilla. Eyepatches black, subrectangular, with lateroventral margin medially indented. Internal posterior two eyes on either side about one-half as great in diameter as remainder.

Body fusiform, circular in cross-sectional view.

Clothing. Usual five kinds of setae present on body and head. Setae of type five slender, gradually tapered, coarsely unilaterally ciliate for apical one-half to two-thirds of length.

Legs. Tibiotarsi internally a double row of stout setae, ciliate for apical two-thirds, about twice as thick as remaining setae of segment. Trochanteral organ typical, internal setae lacking, or at most three in number and very small. Unguis slender, tapered from base. Usual seven teeth small, external and lateral teeth slightly larger than internal. Basal internals slightly apical of midlevel of internal edge. Lateral teeth distinctly basad of basal internals. External tooth acute, about two-thirds distance from laterals to unguis base. Empodial appendage acuminate, not ciliate.

Furcula and genital plate. Dorsal crenulations of dentes shallow, broad, ending gradually. Mucro with apical tooth strikingly longer than anteapical tooth (two to three times as long). Male genital plate with twelve to fourteen setae. Basal pair short, broad, apical half suddenly expanded and flattened, spoon-shaped, with apical expanded portion twice as thick as, and subequal in length to, contracted basal portion. Remaining setae acuminate, subequal in size and about twice as long as basal pair.

Discussion

The general color may be gray-green (as in Packard's original description) to gray-blue to blue to purple to brown. Background colors may be white, blue, bright yellow, or (rarely) orange-red. The posterior borders of the trunk segments may be dark or pale. The markings on the head may be absent, faint, or, in dark specimens, with a V-shaped mark in addition to the interocular longitudinal line (see figures). Position of external and lateral teeth of unguis is more apical in smaller specimens. Empodial appendage sometimes finely ciliate on internal border. Mucro and basal setae of the genital plate vary somewhat, as shown in figures.

This species bears a striking resemblance in pattern, body shape, and almost all other morphological characters to *E. marginata* from Europe. The only differences which could be discovered by the author were in the male genital plate and in the mucro. In the genital plate, *marginata* has the expanded apical portion of the basal setae about one-half as long as, and three times as wide as, the contracted basal portion, whereas in *griseoolivata* the apical part is only twice as wide as, and subequal in length to, the basal part. The mucro in *griseoolivata*, as mentioned, has the apical tooth at least twice as long as the anteapical, whereas the forms of *marginata* which I have seen or which have been described have the apical tooth at most one and one-half times as large as the anteapical one.

This species also resembles *E. confusa.* It can readily be separated on the basis of the head markings (see Pl. 4, figs. 2-5), and morphological details. It also resembles the darkly colored form of *E. triangularis*, but they can be separated on similar morphological grounds.

There has been a large amount of confusion surrounding these species. In collections the name *griseoolivata* has been limited to green forms of that species, and the name *E. marginata* applied to *E. confusa* and all non-green forms of *E. griseoolivata* (the green form makes up about ten to twenty per cent of most populations of this species), as well as dark specimens of *E. triangularis.* Folsom's table for separating "*E. marginata*" from *E. griseoolivata* (Mills, 1934) is completely useless.

I have not seen any Nearctic specimens conspecific with the European specimens of *E. marginata.*

Distribution

Maine: Boothbay Harbor, Bailey's Island, Saco; *Massachusetts:* many localities; *New York:* Ithaca, New York City, Macedon, Long Island, West Point, Rochester; *Pennsylvania:* State College; *Iowa:* Ames, Iowa City, Malvern; *Tennessee:* Knoxville; *Washington:* Puyallup, Yakima.

Type locality: Salem, Massachusetts.

ENTOMOBRYA UNOSTRIGATA Stach

Plate 5, figs. 1-13

Entomobrya unostrigata, 1930, Stach, Abhand. Senckenberg. Naturf. Ges., **42**(1):63, 64.

Drepanura kanaba, 1953, Wray, Nature Notes, No. **1**:4.

Color and pattern. Background white to orange-yellow to pale green. Pigment purple, blue or blue-black, as follows: Antennae purplish, darker toward segmental apices, forming distinct ring on first segment. Antennal bases dark, with connecting band. Dorsum of head with more or less complete Y-shaped mark, arms of Y connecting with posterior internal angles of eyepatches, and base at posterior margin of head. Prothorax with irregular dense pigment dorsally and laterally. Remainder of thorax and abdominal segments one through four with an irregularly expanded dorsal median longitudinal stripe (expanded to definite large spot on segment three), and faint lateral blotches of pigment. Leg bases dorsally rimmed with dark pigment, and segments ventrally with scattered very dark patches. Abdominal segments two and three with posterior borders edged with irregular dark stripes. Abdominal segment four, two posterior short lines lateral and parallel to midline, parafurcular lobes and ventral surfaces more or less regularly and moderately darkened; coxae with irregular dark patches. Remainder pale.

Antennae. Apical bulb unilobed or bilobed. Apical sensory organ of third segment with sensory pegs distinctly bent in indistinct sockets. Clothing normal, acuminate ciliate setae of fourth segment only slightly longer basally. Second segment with several very long ciliate setae (more than twice as long as the diameter of segment at that point). First segment with large apical ventral bare area.

Head. Slightly longer than broad. Labial papillae with typical number of setae, external differentiated seta very long, sharply curved, about as wide as the other setae of the same papilla. Labral papillae unisetaceous.

Clothing of body normal, setae of type five short to long, narrow, uniformly tapered, coarsely multi- and unilaterally ciliate, and bare for basal half to fourth of length.

Legs clothed typically, except for irregular rows of large, heavy, finely ciliate setae internally on tibiotarsus. These are smooth basally and bare or very sparsely ciliate at extreme apex. Unguis with typical seven teeth, the single external very salient and midway between level of internal basals and base of claw. Unguiculus usually short, acuminate and finely ciliate internally. Trochanteral organ typical, with ventral arm shorter than posterior (usually), and with a few small internal setae.

Furcula and genital plate. Mucro atypical, having large apical tooth, much smaller anteapical (less than one-fifth as large), and minute to moderately large basal spine, very close to anteapical tooth. Apices of basal setae of genital plate abruptly expanded, expansion extending somewhat posteriorly. Remainder of setae acuminate, rather abruptly tapered at mid-level. Apical setae slightly smaller than remainder.

Variation

The usual variation is present in setae, etc. Unguis with external and lateral teeth more apical in position in smaller specimens. Larger specimens with external tooth more basal. Cilia not visible on many empodial appendages. Color varies considerably. In almost all specimens the ventral region is somewhat pigmented, usually quite irregularly. The entire body may be washed in the blue or purple pigment, or only certain parts. The dark patterns are frequently outlined (rather broadly) by paler pigment of the same color. Irregular scabrous patches of pale pigment may occur anywhere on the dorsum or lateral parts. The fifth and sixth segments are usually unpigmented, but may be faintly washed with light pigment. The Y-shaped mark between the eyes is often reduced to an irregular spot. Rare unmarked specimens may be observed. This is an introduced species, first described from collections made in Spain during 1918. It has also been found in North Africa since 1933.

Distribution

California: San Diego; *Colorado:* Fort Collins; *Utah:* Kanab.

Type locality: "Flix" Prov. Tarragona, Spain, 1916, under bark of fallen tree, Haas Coll.

ENTOMOBRYA ASSUTA Folsom

Plate 6, figs. 1-13

Entomobrya assuta, 1934, Folsom, Amer. Mus. Novitates, **108**:6.

Entomobrya maizii, 1948, Wray, Bull. Brooklyn Ent. Soc., **43**(2):50-52 (new synonymy).

Color and pattern. Background color off-white to dull waxy yellow. Pigment variable blue, distributed as follows: apical two antennal segments and apices of basal two antennal segments lightly pigmented. Antennal bases narrowly blue, connected by a wide dark band, produced posteromedially. Dorsum of head with two dark blue triangles, bases near inner median edges of eyepatches, apically joined at median ocellus. A light blue rectangular patch running ventrally and posteriorly from the posteroventral angles of eyepatch. Prothorax pale except for upper margin of leg base. Mesothorax with irregular dark patches laterally on anterior margin. Lateral margins of thorax with narrow uniform dark border. Metathorax lightly pigmented except for narrow anterior and a broader lateral unpigmented band. Posterior margin narrowly black, not joined to lateral margin.

First abdominal segment with irregular pigment running jaggedly rearward from anterior margin. Posterior margin of second segment narrowly lined with black, laterally and dorsally, with this line having a short broad lateral anterior projection on either side. Third abdominal segment with sides and posterior two-thirds of dorsum spottily marked with dark pigment. Fourth segment with dark anterior spot just below lateral suture, and four irregular longitudinal bands covering the posterior two-thirds of the segment. The dorsal bands are divided by a thin, mid-dorsal, pale line. The two thinner lateral bands are separated from the two dorsal ones by a wider pale band, these bands (lateral and dorsal) being medially excavated on opposing surfaces and joined at posterior margin of segment., Fifth segment black except for wide mid-dorsal stripe and two laterodorsal semicircular pale spots on anterior margin. Sixth segment dark blue with apical pale ring, metathoracic femora apically dark. Remainder of body pale.

Antenna. Apical bulb of fourth antennal segment distinctly bi- or trilobed, located in a deep apical pit. Apical sensory organ of third segment with sensory rods, slightly thinner than usual. Clothing of antennae typical, fourth segment without any very long setae, all being less in length than the greatest diameter of the segment. Second antennal segment with several setae longer than twice the diameter of that segment. Smooth short setae on ventral surface of the first antennal segment, lacking from apical one-fourth of segment.

Head circular, sides slightly flattened; labral papillae subrectangular, multisetaceous, with setae minute and situated on micro-papillae. Number of micro-papillae per papilla varies from two to five. Labial appendage with usual number of papillae; external differentiated seta only slightly curved, tapered at extreme apex, slightly thicker than normal setae of same papilla, and attaining, but not exceeding apex of same papilla. Eyepatches very dark, truncately triangular in shape. Inner posterior two eyes on each side about one-half as great in diameter as remaining eyes, which are subequal.

Clothing of head and body of typical five kinds of setae. Setae of type one are long, greatly expanded for basal one-fourth of length. Setae of type five of two kinds, the larger being uniformly tapered, and coarsely, multilaterally ciliate for apical nine-tenths of length; the smaller ones are about one-half as long and sparsely ciliate for apical one-third to one-half of length.

Body broadly fusiform in shape, somewhat dorsoventrally flattened, giving an oval cross-sectional shape.

Legs clothed typically, setae of tibiotarsus subequal in diameter. Trochanteral organ typical, except internal setae lacking, or at most two or three. Unguis with internal edge straight except at extreme apex. Basal teeth unequal, opposite, distad of middle of internal edge of unguis, subequal to median tooth, and about twice as large as apical tooth. Lateral teeth distinct, situated about two-thirds of the distance from base of unguis to basal internal teeth. External tooth small, halfway between laterals and base of unguis. Empodial appendage sharply acuminate, ciliate on apical two-thirds of internal edge.

Furcula and genital plate. Dorsal crenulations on dentes comparatively shallow. Mucro with anteapical tooth erect, subequal to apical, which is strongly curved. Basal spine just attaining apex of anteapical tooth. Genital plate with papillae being very long and erect, so as to hide most of the setae, leaving only the extreme tips visible above the tops of the papillae. With proper clearing, setae seen as follows: sixteen to seventeen in number, basal setae large, moderately thick, slightly curved, and tapered for apical half of length; parabasals similar and slightly smaller in size. Lateral two on either side heavy, shorter than basals, sharply tapered for apical one-fourth of length. Remainder slender, slightly shorter than parabasals, erect, and gradually tapered from base.

Discussion

This species is readily distinguishable on the basis of the labral papillae, the flattened body shape, the male genital plate, and the type of pattern. There is much variation in pattern. However, the huge majority of specimens have something fairly near the form described. The usual darkening can take place, but the dorsum of the mesothorax is usually pale. Mills (1934) has mentioned taking a dark form in Texas, but typical forms and possible intergrades were found in that population. Uniformly pigmented individuals have been found in Utah, Louisiana and North Carolina. In this last area they were described by Wray as a separate species; however, the occurrence of the form as a part of typical population (in Utah), combined with the lack of morphological differentiation between the species and the great variation in pattern throughout all, points to the synonymy of the two species.

There is a little variation in the structure of the claw, on some specimens the internal teeth being subequal in size, and on some the median being distinctly larger than the basal teeth. The lateral teeth may change in relative position, but are always basad of internal basals. The mucro may have the apical tooth larger than the subapical. The basal part of the mucro is not always swollen.

Distribution

Louisiana: Harahan; *Maine:* Boothbay Harbor; *Vermont:* Clarendon; *Massachusetts:* Cambridge, Dedham, Lexington, Waban, Neponset; *New York:* Geneva, Macedon, Ithaca; *Illinois:* many localities; *Iowa:* many localities; *North Carolina:* Raleigh, Chapel Hill, Bern, Fayetteville; *South Carolina:* Georgetown; *Mississippi:* Washington; *Texas:* Bryan; *Utah:* Kanosh, Smithfield; *Ontario:* Rondeau Park.

Type locality: Geneva, N. Y., June 18, 1917. Glasgow, Coll.

ENTOMOBRYA ARNAUDI Wray

Plate 18, figs. 11-15

Entomobrya arnaudi, 1953, Wray, Nature Notes, No. 1:4.

Color and pattern. Background color yellow, pigment purple as follows: Antennae with basal ring and connecting band. Paler pigmented band from outer ventral corner of eyepatch to margin of head. Thoracic meso- and metatergites and first abdominal tergite narrowly edged with dark pigment. Irregular longitudinal bands on mid-lateral regions from middle of second thoracic to posterior margin of third abdominal segment. Each band consists of series of segmental, roughly triangular structures, apices anterior, bases posterior. Faint pigment traces on mid-dorsum of abdominal segments two and three. Fourth abdominal segment with pair of irregular mid-lateral longitudinal stripes. Fifth abdominal segment with a pair of dorsolateral spots. Sixth segment with a trace of pigment.

Antennae distinctly longer than trunk of animal. All segments subcylindrical, fourth segment slightly longer than second, first and third segments slightly shorter than these. Apical bulb distinctly bilobed.

Head elongate, oval. Labral papillae unusual, bisetaceous to unisetaceous, papillae low, setae small and unclear. Labial appendage with external seta about as thick as neighboring large setae, barely reaching apex of same papilla. Eyepatches black, subrectangular.

Clothing typical, setae of type one with bent apex unusually long. Setae of type five coarsely unilaterally ciliate.

Legs. Unguis normal. Internal median and apical teeth unusually long.

Furcula and genital plate. Mucro with apical tooth distinctly longer than anteapical. Genital plate with basal seta flattened, broad and crenulate. Lateral setae broad, flattened, with apical half strikingly acuminate, basal half somewhat expanded. Apical four setae slender, acuminate.

Discussion

Because only a single specimen was seen, no consideration of the variations can be made. The pattern could be confused with that of several species (*decemlineata*, *suzannae*), but the unusual genital plate and antennae make it quite probable that it is not conspecific with any known Nearctic species. More specimens must be seen before this can be absolutely determined.

Distribution

Washington: Fort Lewis (type locality), Feb. 1946. P. H. Arnaud, collector. *New Mexico:* Grant Co.

ENTOMOBRYA COMPARATA Folsom[1]

Plate 7, figs. 1-18

Entomobrya comparata, 1919, Folsom, Rep. Canad. Arctic Expdn. 1913-1918, **3**:13, 14.

Entomobrya frontalis, 1935, Mills, Bull. Brooklyn Ent. Soc. **30**(4):136 (new synonymy).

Color and pattern. This varies with the locality and shows no universal characteristics (see discussion under variation).

Antennae. Fourth segment subequal to second and third. First slightly wider. Apical retractile bulb with apical indentation but not clearly lobed, situated in a deep pit at true apex of segment four. Apical sensory organ of third segment normal. Clothing of antennae normal. Longest setae on second and third segments about twice diameter of corresponding segment.

Head. Slightly longer than broad. Labral papillae roundly conical with setae small but distinct. Labial appendage with external differentiated seta short, strongly curved, and about one and three-fourths times as thick as the largest normal setae of the same papilla, gradually and uniformly tapered with apex just attaining level of apex of same papilla. Eyepatches very dark, subrectangular, slightly indented along middle of ventral edge.

Body. Fusiform to elliptical in shape and circular in cross-sectional view.

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[1] I have recently examined the types of *E. lateropicta* Hammer. These specimens agree in every morphological respect with *E. comparata*. All of the specimens (3) are immature and since they represent a pattern not previously seen in *comparata*, the final determination of the status of these specimens must await further series.

Clothing. Body and cephalic setae of typical five kinds. Type one very narrow at point of insertion, expanded for basal one-seventh to one-fifth of length. At widest part about two and one-half times as wide as point of insertion. Slightly bent for apical one-fifth to one-tenth. Setae of type five acuminate, uniformly tapered, or lightly expanded medially, multilaterally, moderately, coarsely ciliate.

Legs. Clothing normal. Tibiotarsus with a single staggered row of very stout, finely and uniformly ciliate setae, more than twice as thick as remaining setae of segment. Unguis narrow, only slightly tapered from base to apex, apex curved slightly, possessing usual seven teeth. Basal and median internal teeth subequal in size, about twice as large as apical tooth. Internal basal teeth opposite and distad of mid-level of internal edge of unguis. Lateral and external teeth small, laterals slightly basad of internal basals, and external tooth distinctly basad of laterals. Empodial appendage acuminate, smooth, or with internal border sparsely and coarsely ciliate. Trochanteral organ typical, with very few small internal setae.

Furcula and genital plate. Dentes with crenulate dorsal part gradually reduced . Uncrenulate dens unusually long. Mucro moderately long, distinctly wider basally. Apical tooth slightly longer than, or subequal to, anteapical tooth. Male genital plate with fourteen heavy acuminate setae. Basal and parabasal setae smaller than remainder. Basals simply curved, remaining setae sigmoidally curved. Papillae low and small.

Variation

The members of this species vary strikingly in pattern. The species is limited to boreo-alpine and taiga zones in mountain areas, and the corresponding areas in the Arctic. Specimens found in the tundra or alpine regions are always very lightly pigmented. Except for a dark inter-antennal band, and the dorsum of the fifth and sixth segments, the whole body is pale yellow to light green in color.

Specimens captured in the forested zones have a striking and definite pattern, which is constant in any locality but varies geographically. This pattern consists of a series of longitudinal and transverse bands. Although most populations showed little or no variation in the form of this pattern, in several cases habitats were in some way intermediate between the typical treeless tundra region and a taiga forest. In such localities all intermediates existed between the tundra and the taiga patterns. (See Pl. 7, figs. 5-7). In a few areas the taiga form invades other peculiar habitats. In such cases the pattern is more variable than normal.

The species is quite uniform morphologically, having only small variations. In the largest specimens the claw is somewhat elongate, but as the size decreases, the width becomes relatively greater. The smallest specimens have the claw somewhat dilated at the base. The teething of the claw is fairly uniform throughout all the forms of the species. In the largest specimens the internal teeth start above the middle of the claw; in the smaller specimens, however, they start at about the mid-level or slightly below. A salient basal external tooth is never present. In the smaller specimens the external tooth may be missing, or so small as to be seen only with great difficulty.

The trochanteral organ varies greatly, but only in occasional specimens. In the largest individuals the addition of a number of external setae gives a striking double row arrangement to these.

Discussion

This species poses one of the most interesting problems in the whole of collembolan taxonomy. Obviously two types of pattern variation exist here, one associated with ecological differences and a second associated with geographical variation. It is possible that we are dealing with a pair of eco-species, but the close and almost universal co-existence of the two forms makes this unlikely. The exact genetic nature of the separation of the various forms will await more detailed work.

Distribution

Entomobrya comparata (tundra pattern): *New Hampshire:* Mount Washington — 6200 feet and 5800 feet; *Colorado:* Mount Evans — 13,500 feet and 14,000 feet; Monarch Pass — 12,000 feet; *Wyoming:* Snowy Range Pass — 10,800 feet; *Washington:*

Lake Tipsoe — 5,400 feet; *Northwest Territories:* Bernard Harbor, Perry River; *Alaska:* Demareation Point, Umiat.

Entomobrya comparata (taiga pattern): *New Hampshire:* Mount Washington — 2,300 feet; *Idaho:* 45 mi. N. E. Moscow — 5,500 feet, Palouse River Divide — 4,500 feet; *Montana:* vic. Nimrod — 4,200 feet, West Yellowstone — approx. 6,000 feet; *Wyoming:* Snowy Range Mountains — 9,000 feet, Teton Pass — 8,400 feet, 16 mi. W. Dayton — 8,000 feet; *Colorado:* vic. Winter Park — 9,800 feet, Long Lake Boulder — 10,500 feet, Cochetopa Pass — 10,000 feet, Mount Evans — 10,500 feet and 12,000 feet; *New Mexico:* Santa Fe.

Intermediate populations: *Montana:* Grinnell Glacier — 8,000 feet; *Colorado:* Monarch Pass — 11,500 feet.

Type locality: Bernard Harbor, N.W. Terr. Canada, May, 1915, F. Johansen Collection.

ENTOMOBRYA CLITELLARIA Guthrie

Plate 8, figs. 1-14

Entomobrya clitellaria, 1903, Guthrie, Rep. Geol. Nat. Hist. Surv. Minnesota, Zool. Ser., (4):75.

Entomobrya albicollis, 1905, Franklin, Ent. News, **16**:77 (new synonymy).

Entomobrya cyanica, 1942, Schött, Pan Pac. Ent., San Francisco, **18**:177-86 (new synonymy).

Entomobrya ontariensis, 1933, James, Trans. Canad. Inst. Toronto, **19**:76 (new synonymy); 1944, Gisin, Verh. Naturf. Ges. Basel, **55**:72.

Entomobrya atrocincta, var. *clitellaria*, 1942, Bonet, Ciencia, **3**(2):56, 57; 1947, Delamare-Deboutteville, Rev. Franc. d'Ent., **14**(2):136; 1951, Maynard, Collembola of New York State: 152.

Entomobrya atrocincta, ssp. *clitellaria*, 1944, Salmon, Rec. Domin. Mus. Wellington, **1**(2):155.

Entomobrya atrocincta, var. *millsi*, 1951, Maynard, *op. cit.* :152.

Entomobrya atrocincta, var. *albicollis*, 1951, Maynard, *op. cit.* :153.

Entomobrya atrocincta, var. *ontariensis*, 1951, Maynard, *op. cit.* :151.

Color and pattern. Background pale yellow to bright yellow-orange. Pigment blue-black where dark, with paler pigment violet, blue, or brown. Antennae lightly pigmented with brown, bluish on distal two segments, first segment apex yellow ventrally. Third segment slightly darkened, basally and apically. Fourth segment slightly darker on apical half. Antennal bases and head between eyepatches and before median ocellus darkened irregularly, purplish to blue in color; the posterior margin of this region more heavily pigmented, forming a roughly U-shaped mark, with the arms of the U expanded anteriorly. A faint, irregular blue patch running posteriorly from hind ventral angles of either eyepatch. Ventral surface of head speckled irregularly with blue pigment. Prothorax lightly pigmented laterally and on leg bases. Mesothorax with broad irregular dark blue band along anterior border. Leg bases anteriorly darkened. Metatergite completely blue-black. First three abdominal segments dorsally blue-black, laterally and ventrally pale, with dorsal dark area decreasing in size posteriorly. Fifth abdominal segment with scattered specks of brown. Remainder of body yellow.

Antennae. Fourth segment slightly thicker than third with simple retractile bulb in distinct pit, which is slightly displaced from exact apex of segment. No non-retractile protecting papilla. Apical sensory organ of third segment normal. Clothing of antennae typical, with the longest ciliate setae of the fourth segment about as long as the segment is wide, and those on the other segments less than one and one-half times as long.

Head about as wide as long, distinctly narrower than second thoracic segment. Labral papillae high, blunt, rounded, and distinctly unisetaceous. External differentiated seta of labium distinctly curved, subequal in diameter to large normal setae, tapered gradually for apical one-third of length and attaining, or slightly exceeding, apex of same papilla. Anterior two eyes on either side very large, being at least twice as large as the others.

Body broadly fusiform in shape, usually somewhat dorsoventrally compressed, so as to give an elliptical cross-sectional appearance.

Clothing of head and trunk typical. Setae of type one large, brown in color. Setae of type four smooth for basal one-fourth of length. Setae of type five smooth for basal one-third to one-half of length, remainder coarsely, mostly multilaterally, ciliate, tapering for apical half, some slightly and gradually expanded from base to middle of seta.

Legs. Setae typical. Tibiotarsus without unusually stout setae. Trochanteral organ typical. Internal setae few in number, about half as long as setae in either arm, and concentrated near apical seta. Unguis with basal internal tooth at about the middle of the inner edge. External tooth salient, midway between lateral teeth and the base of the unguis. Lateral teeth small. Empodial appendage acuminate, with apical fourth of internal edge faintly ciliate.

Furcula and genital plate. Mucro with teeth short, sturdy, and subequal. Apical tooth strongly upcurved. Basal spine stout, barely reaching apex of anteapical tooth. Genital plate with basal setae small, acuminate, slightly curved. Remaining setae large, acuminate, and sickle-shaped.

Discussion

This species is readily distinguished on morphological grounds. The compressed body, small round head, salient external tooth of the unguis, single apical antennal bulb, and the genital plate are all peculiar. This last structure resembles that of *E. comparata*, but differs in the shape of the basal setae.

This species varies primarily in color and pattern. Three of the pattern types have been considered as distinct and valid species. Guthrie described *E. clitellaria* from specimens having only the anterior border of the mesothorax, the dorsum of the metathorax, and abdominal segments one, two and three dark. Franklin in 1905 described as *E. albicollis* specimens having abdominal segments four and five also dark, and James in 1933 described as *E. ontariensis* specimens having the first and second abdominal segments pale. In material which I have studied, all intermediates among these patterns occurred, although good intermediates between *ontariensis* and the other forms are rare. In all the morphological characters noted, these three forms are similar. It is of interest that the occurrence of the three types of pattern is not completely haphazard. *E. ontariensis* has been taken from Ontario, northern New York, and Washington. The typical pattern has been found in Minnesota, Ontario, Iowa, Illinois, New York, Massachusetts, and North Carolina. The *albicollis* form has been found in New York, Massachusetts, Illinois, and Louisiana. The series in most cases are very small.

The specimens from the midwest (Iowa, Illinois, and Louisiana) tend to have the pigment on the fourth segment appear or disappear spottily, while those in the eastern part of the range have the pigment on this segment increased or decreased more or less uniformly over the entire segment.

There is some variation in the position of the external and lateral teeth of the unguis, these being relatively more basal in older specimens.

The peculiar dorsoventral flattening is not uniform, but is clearly present in at least a few specimens of every series. In this character it resembles *E. assuta* Folsom, but the other morphological structures link this species with *E. comparata.*

Distribution

California: Los Angeles; *Massachusetts:* Arlington, Winchester, Amherst; *New York:* Ithaca, Macedon; *Illinois:* Homer, Oak Park; *Iowa:* Ames, Ledges State Park; *North Carolina:* Raleigh; *Louisiana:* Tallulah; *Washington:* Yakima; *Ontario:* Pottageville, Arnprior, Mattawa.

Type locality: Minnesota: "northern part of the state."

ENTOMOBRYA KINCAIDI Folsom

Plate 9, figs. 1-8

Entomobrya kincaidi, 1902, Folsom, Proc. Washington Acad. Sci., **4**:96, 97.
Entomobrya erratica (synonym?),[1] 1932, Brown, Ann. Mag. Nat. Hist., (10)**10**:336-338.

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[1] It is difficult to place Brown's species (described from Hudson Strait in Canada) on the basis of the description. That this author had some difficulty in placing the species is evidenced by the following quotation from his description (*op. cit.,* pp. 136-137): "Measurements made on a number of individuals indicate considerable variation in the relative lengths of the antennal and abdominal segments, characters commonly made use of in discriminating species, while the uniform structure of the claws, empodial appendage, and spring in members of the genus make specific determinations based on colour more imperative." Then nine lines below this, "*E. kincaidi* Fols., taken by the Harriman Alaskan Expedition . . ., is rather similar to the present species in general body-colour though differing in detail, but is easily distinguished by structural features. . . ." Since he fails to describe or figure either the structural differences or the "detail" in color differences, I can only consider it as a probable synonym of this species. The usual antennal ratios, as well as the color body form, and "bothriotrichae on the abdomen very prominent" would seem to make it this species. I have not received any answer to communications with Mr. Brown, and final determination of this species must necessarily await a time when further information is available.

Color and pattern. General body color yellow-green to dark olive green, with darker specimens possessing oval to round pale spots and a slightly darker color suffusing posterior lateral regions of abdomen. Dark pigment blue-black, limited to antennal bases and (sometimes) small band between them. Antennae suffused with purplish blue, darker toward segmental apices.

Antennae. Basal two segments distinctly wider than apical two. Apical retractile bulb of fourth segment trilobed (or bilobed), located in a distinct apical depression. Apical sense organ of third segment and clothing of antennae normal. Short smooth setae of first segment covering ventral surface, except for a flatly arcuate apical area, at greatest depth about one-third the length of segment.

Head slightly longer than wide. Labral papillae low, blunt, unisetaceous, setae distinct. Labial appendage normal with external differentiated seta basally about one and three-fourths times as wide as largest typical seta on the same papilla, gradually tapered from base and barely reaching apex of papilla.

Clothing of head and trunk typical. Setae of type one distinctly clavate, not expanded near base, and with apex slightly bent and reduced. Setae of type four smooth on basal half and gradually expanded apically. Setae of type five are usually flattened and gradually but greatly expanded medially, and apically pointed, rarely cylindrical, apically tapered, always multilaterally finely ciliate.

Legs. Clothing typical, tibiotarsus with a double row of stout ciliate setae, about twice as large as neighboring setae. Trochanteral organ with apical and near-apical setae of the arms extremely long and basally expanded. External tooth of unguis large, salient, and usually located on a level with, or near, the smaller lateral teeth. Apex of unguis internally slightly excavated on apical half. Empodium unusually high, causing apex of empodial appendage to be more nearly on a level with apex of unguis than usual.

Furcula and genital plate. Mucro with apical tooth curved and subequal to anteapical tooth. Basal spine exceeds apex of anteapical tooth. Male genital plate with seventeen acuminate setae. Basal setae much larger than, and parabasal setae smaller than, remaining setae, which are slightly flattened and subequal.

Discussion

The lack of pattern (except inter-antennal band) is constant in all specimens seen to date. The claw and mucro vary in shape, the latter sometimes with the anteapical tooth distinctly larger than the apical, or with basal spine not attaining apex of anteapical tooth. The peculiar short clothing setae of the body and head are enough to separate this species quite readily. These setae are almost scale-like, but, because they are ciliate, very flexible, and evidently more in the nature of collapsed cuticular hairs, there is no question as to their true identity. The empodial appendage may be sparsely ciliate on posterior edge, or smooth.

The only types existing have almost all the setae removed, but since I have found what appear to be two characteristic scale-like setae on one specimen, and because the male genital plate is visible on one specimen, I feel certain of this species identity. The species appears to be related to the *clitellaria* group, but is in a specialized branch of this.

Distribution

Alaska: Muir Glacier, Point Barrow, Anaktuvuk Pass; *Quebec:* Hudson Strait (Akpatok Island).

Type locality: Muir Glacier, Alaska, June 11, 1899.

ENTOMOBRYA TROGLODYTES n. sp.

Plate 9, figs. 9-16

Color and pattern. Completely white except for black eye-patches, pale blue antennal bases and connecting band, and very light gray-blue uniform coloring on antennae.

Antennae. First segment slightly, and fourth definitely thicker than third. Apical retractile bulb of fourth segment large, subspherical, simple, in a deep apical pit, and with a small dorsal non-retractile guard papilla. Apical sensory organ of third antennal segment normal except that the central rods are larger than in other species. Sensory organ of second antennal segment of two rods similar in shape and two-thirds as large as those of third segment. Clothing of antennae normal except for the first antennal segment, which has several small setae similar to the body setae of type one. Short smooth setae on ventral surface of first segment, absent from a large apical semicircular space.

Head roughly circular in shape with sides straightened. Labral papillae low, rounded, unisetaceous, with unusually large, basally expanded setae. Labial appendages typical, with external differentiated seta tapering during apical half, slightly thicker than the largest normal seta of the same papilla, and not attaining apex of same papilla. Two inner posterior eyes about one-third as large in diameter as remaining eyes, which are subequal.

Clothing of body and head normal. Setae of type one unusually short, largest about one and one-half times as long as longest antennal setae; type one setae expanded abruptly above point of insertion, slightly bent just before apex, and slightly expanded at extreme apex. Setae of type five slender, uniformly tapered, and coarsely, multilaterally ciliate for apical half of length.

Legs. Clothing typical, none of the setae on tibiotarsus strikingly thicker. Trochanteral organ atypical, with numerous setae in the arms, but these comparatively short and not graduated regularly in size. Many internal setae present, not regular in disposition, mostly of two sizes, one subequal to the setae in the arms and the other about half as long. Unguis long and narrow, slightly tapered; outer edge strikingly and inner edge moderately curved at apex. Basal internals between one-half and two-thirds the distance from base of internal edge to apex. All internal teeth thin and salient, median one twice as large as the others, which are subequal. Lateral and external teeth small, all slightly below basal internals. Empodial appendage acuminate, coarsely and heavily ciliate for apical three-fourths of internal edge.

Furcula and genital plate. Dentes with dorsal crenulations very deep. Mucro long and deep, with apical tooth distinctly longer and wider than the short anteapical one. Basal seta stout, attaining or barely exceeding apex of anteapical tooth. Genital plate with fourteen to sixteen similar setae, basal setae somewhat smaller. The setae are blunted, expanded (usually unilaterally) for basal half of length and then smoothly tapered. Papillae low and rounded.

Discussion

The entire series seen of this species came from a single cave. The specimens were found at all levels, from the twilight zone to the deepest recesses, but there is no significant variation (other than the usual growth ones) in all the 150 specimens examined. This is not entirely surprising when we consider the uniformity of habitat and the probable small ancestral stock. There is some variation in the trochanteral organ (some specimens having only a few internal setae) and a slight variation in the mucronal teeth. The apical tooth is always larger than the anteapical tooth. On some specimens the median internal tooth of the unguis is only slightly larger than the others, and in a few the basal internals are distinctly larger than the apical ones.

On the basis of the body ratios, apical antennal bulb, type of unguis and labral structure, I hold this species to be a specialized branch of the *E. comparata* group. It is peculiar in many characters (i.e., short fourth antennal segment, genital plate, long unguis, sensory organs of third and second antennal segments), but I do not feel that there is any basis for assuming that these are modifications for a cavernicolous existence.

Distribution

Known only from type locality: unnamed cave on property ot Sturgis Water Company, Sturgis, South Dakota, August 10, 1950.

ENTOMOBRYA TRIANGULARIS Schött

Plate 10, figs. 1-17

Entomobrya triangularis, 1896, Schött, Proc. California Acad. Sci., **6**(2): 182, 183.

Entomobrya tampicensis, 1935, Mills, Bull. Brooklyn Ent. Soc., **30**(4):137 (new synonymy); 1944, Gisin, Verh. Naturf. Ges. Basel, **55**:72.

Color and pattern. Body fusiform to cylindrical, background orange-yellow to off white; markings blue-black to purplish blue. Dark color typically distributed as follows: Antennae with apices of first three segments ringed, limits of ring abrupt on first segment, but on second and third gradually darkening from basal third of segment. Fourth antennal segment uniformly darkened. Antennal bases dark and with irregular broad black connecting band. Eyespots subrectangular, black. On either side a truncately triangular dark patch runs posteriorly and ventrally from posterior, ventral angle of eyepatch to ventral edge of the head, widest part along this edge. Prothoracic leg bases irregularly spotted externally. Dorsum of mesothorax laterally and anteriorly edged narrowly with pigment; connected to this at either anterior corner is a small elongated spot. Third thoracic tergum laterally with irregularly dark borders, posterior edge with transverse dark band not connected with lateral dark areas.

Dorsum of abdominal segment one with lateral borders darkened. Dorsum of abdominal segment two with a large latero-anterior spot and an abrupt narrow band along the posterior margin. Dorsum of abdominal segment three dark, lateral areas dark except for extreme margins. Fourth segment with a median transverse dark band, starting slightly below the lateral suture, where it is about one-third as wide as the fourth segment is long, decreasing in width irregularly until at a mid-dorsal point it is only a thin line, forming two apically joined triangles. Fifth segment completely darkened except for a regular, antero-lateral, semicircular pale spot on either side. All dark markings of the body contain numerous irregular small, round to oval, pale spots. Metathoracic legs with a dark band along the internal edge of the femur, and a somewhat more pale area on the middle of the tibiotarsus. Remainder of body pale.

Antennae. Fourth segment thicker than remainder. Apical antennal bulb bilobed or trilobed. Clothing of antennae typical, longest ciliate setae at the base of the fourth antennal segment, one and one-half times as long as antennal diameter. Apical organ segment three normal. Apical sensory organ of second antennal segment with two short rods half as long as, and one-third as wide as, those on the third segment. Longest setae of this segment are about half as long as segment. First antennal segment with short, smooth, ventral setae, lacking on only a very small apical semicircular area.

Head oval in shape. Labial appendages typical. External differentiated seta long and stout, one and one-half times as wide as, and about two-thirds as long as, the longest normal seta on the same papilla, and tapered for apical fourth of length, attaining or exceeding apex of same papilla. Labral papillae large, distinct, unisetaceous. Eyes with internal pair on each side about one-third size of anterior pair.

Clothing of head and trunk typical. Type five setae coarsely multilaterally ciliate for apical half to four-fifths, and while uniformly tapered, sometimes appear to be very slightly expanded, due to the large ciliations.

Legs. All setae uniformly ciliate, tapered. Apical half of each tibia with an irregular double row of short, stout, uniformly ciliate setae, about twice as thick as the remaining setae of this segment. Unguis normal. Four internal teeth small and subequal, basal pair slightly more than half-way to apex of claw. External and lateral teeth distinct and not acute, laterals definitely basad of basal internals and with external tooth about half-way beween laterals and base of claw. Empodial appendage acuminate, posterior border indistinctly ciliate. Trochanteral organ typical, internal setae tending to form a line bisecting angle of arms. External setae also tending to be lined up perpendicular to line of internal row.

Furcula and genital plate. Mucro with teeth subequal; apical tooth distinctly curved, and basal spine exceeding apex of anteapical tooth. Male genital plate with twelve to fifteen setae; all are non-angulate. Basal setae acuminate, somewhat smaller than remainder. Next two setae on either side with rounded apices, somewhat larger than remaining setae, which are acuminate, erect, subequal, and slightly expanded above insertion.

Discussion

Schött described this species from a single individual from San Francisco. The type has been destroyed, but the color form which he described and figured is one which is not possessed by any other species in this area, so that the species can be fairly certainly determined.

There is a great deal of variation in the body color, many specimens being more or less uniformly dark, and every gradation seen between this and specimens with only scattered dark patches (see Plate 10; figs. 2-8). The apical antennal bulb may have the lobes indistinct, but in such cases the unusually wide shape of the bulb separates it from the truly simple condition. The mucro and trochanteral organ exhibit the usual individual and growth variations. In the former the apical tooth may be smaller than the anteapical. In the latter case the variation of the internal setae is striking in that on one specimen they may be lineate and regular on one side, while being irregularly scattered on the other side. The growth variation of the claw shows a striking basal drift of the external and lateral teeth, with increasing size, so that on a small specimen these teeth are all on about a level with the basal internal teeth, while large specimens have the condition given in the description.

This last variation, plus the (until then unrecognized) pattern variation caused Mills to separate *E. tampicensis* from *E. triangularis*, the latter species being larger and having lateral and external teeth more basal, and the former being smaller with varying color pattern. He also found a body shape difference, but this was of the artificial secondary type previously discussed.

This species is closely related to *E. confusa* and *E. ligata*, but can be separated from the former on the basis of the genital plate and the markings on the head and body regions (see figures) and segmental ratios, and from the latter by the longer differentiated labial seta.

Distribution

Oregon: Charleston, Corvallis; *Washington:* Tampico, Puyallup, Bellingham, Yakima; *California:* Clarence, San Francisco; *Texas:* College Station. *British Columbia:* Chilliwack, Chase.

Type locality: San Francisco, California. Eisen Coll.

ENTOMOBRYA LIGATA Folsom

Plate 11, figs. 1-7

Entomobrya ligata, 1924, Folsom, Amer. Mus. Novitates, **108**:3, 5.

Entomobrya corticalis, 1934, Bonet, Eos, **9**:169 (*partim*); 1944, Gisin, Verh. Naturf. Ges. Basel, **55**:78 (*partim*); 1951, Maynard, Collembola New York state :158-159.

Color and pattern. Background color yellow to tan to buff. Pigment blue-black to purple, distributed as follows: Antennae with dark apical ring on first and second segments, all segments with uniform light pigmentation, darker on apical two. Antennal bases and connecting band dark. Moderately dark, roughly triangular patch running posteriorly from beneath hind angle of eyepatch. Prothorax pale, meso- and metathorax with lateral and posterior margins bordered with irregular wide dark band, this band extending onto the anterior margin of the mesothorax. First and second abdominal segments with continuations of the darkened thoracic lateral borders, irregular and spotty on second segment. Third segment dark laterally and dorsally, save for small anterior dorsal band and ventrolateral posterior spot. Segment four with transverse band, expanded laterally forming a broad H-shaped mark. Space between lateral suture and parafurcular lobe with triangular spot, widest at anterior segmental margin. Fifth segment dark except for anterior lateral pale spot. Sixth segment dark. Hind femora apically and tibiotarsus medially lined with dark.

Antennae. Fourth segment distinctly thicker than third. Fourth segment retractile bulb distinctly bi- or trilobed, in a deep apical pit. Apical sensory organ of third segment typical. Clothing of antennae normal, second segment having a number of setae approximately twice as long as the diameter of segment. Smooth setae absent from apical one-fourth to one-half of ventral surface of first segment.

Head broadly oval, 1.2 times as long as wide. Labral papillae conical, unisetaceous, with minute setae. Labial appendages typical. External differentiated seta short, slightly thicker than largest normal seta, tapered for apical half, and slightly curved. Differentiated setae reaching only halfway to apex of same papilla. Three median eyes on each side much smaller than remainder.

Body fusiform, round in cross-sectional view.

Clothing typical. Body setae of type one long and heavy, expanded sharply for basal one-tenth of length, curved apically. Setae of type four comparatively long and slender, tapered at extreme apex only, uniformly and sparsely covered with fine ciliations, except for short smooth basal portions. Setae of type five slender, tapered from base, coarsely unilaterally ciliate on apical one-half to three-fourths.

Legs. Clothing normal, tibiotarsus with a double row of setae, about one and one-half times as thick as the remaining setae on segment. Trochanteral organ typical, internal setae sparse and not occurring in apical portion of the space between the arms. Unguis typical, strongly curved at apex. Internal teeth small, basal pair slightly above mid-level of internal edge of unguis. Lateral and external teeth large, external tooth unusually salient. Laterals about half-way between basal internals and external tooth. Empodial appendage acuminate, more strikingly tapered at extreme apex, sparsely ciliate for median two-thirds of internal edge.

Furcula and genital plate. Dentes with dorsal crenulations shallow, irregular, and ending gradually. Mucro with teeth subequal and distinctly curved, basal spine attaining apex of anteapical tooth. Male genital plate with basal seta small, straight and acuminate. Parabasal larger, acuminate for apical half. Remaining setae apically acuminate, narrow and recurved.

Discussion

This species has long been confused with the European *E. corticalis*. It may readily be separated from this on the basis of: (1) *corticalis* tends to have the body somewhat flattened, *ligata* does not; (2) the pattern of the fourth abdominal segment differs; (3) the male genital plate of *corticalis* has the basal setae untapered, very thin, and longer than the remainder, which are short and not strikingly recurved. Although specimens were seen from a large number of localities, there were in all cases only a few specimens in one lot. Occurrence in small numbers has also apparently been found in the European species, as an examination of these records shows only one or two specimens from most localities. The mucro varies, the teeth may both be straight or one or the other may be slightly larger. The labial papillae vary slightly, but in all cases the external differentiated seta does not attain the apex of the same papilla. The pattern seems to be exceedingly constant on this species. It is most closely related to *E. triangularis* but may be readily separated from this on the basis of the genital plate.

Distribution

Massachusetts: Tisbury, Lincoln, Neponset, Cambridge; *New York:* Ithaca, Karner, Voorheesville, Leon, Long Island (Mineola), Garden City, West Point; *Connecticut:* New Haven, Ansonia; *Pennsylvania:* Black Hawk Gap, State College; *Tennessee:* Carter Co., Dupont Mt., Sevier Co.; *Virginia:* Hightown; *North Carolina:* Linnville, McDowell County.

Type locality: Ithaca, New York, Aug. 5, 1891. MacGillavray Coll.

ENTOMOBRYA WASHINGTONIA Mills

Plate 11, figs. 8-16

Entomobrya washingtonia, 1935, Mills, Bull. Brooklyn Ent. Soc., **30**(4):135, 136.

Color and pattern. Background color yellow to dull white. Pigment dark blue to black, with many small circular pale areas. Dark pigment as follows: antennal segments two, three and four moderately dark, with pale bases. First antennal segment with lateral dark stripes and apical dark ring. Antennal bases and connecting band dark. A dark patch runs posteroventrally from hind ventral angle of eye to margin of head. A thin irregular line runs ventrally from middle of lower edge of eye-patch. Prothorax unpigmented. Meso- and metathorax and first abdominal segment each with a posterior dark band (especially dark on posterior margin), broken narrowly on mid-dorsal line and widely separated from dark lateral borders. Second abdominal segment with narrow black posterior border and a large spot laterally. Third segment completely dark, except for an anterior irregular pale spot located on either side, just below the mid-dorsal line. Fourth segment with three irregular longitudinal bands: one on either side, on and above the first lateral suture, and the third located mid-dorsally and stretching from just below the anterior margin two-thirds of the distance toward the posterior margin. Posterior border of segment narrowly ringed with black. Fifth segment laterally dark, dorsally pale. Sixth segment dark. Central half of tibiae of all legs darkened, apices of femora darkened (those of metathorax more so than the others), remainder of animal pale.

Antennae. Fourth segment thicker than third. Apical bulb apparently bilobed (seen on only a few specimens). Clothing of antennae typical.

Head broadly elliptical, being slightly longer than broad. Labial papilla typical, with external differentiated seta being strongly curved (see figure) and uniform in width for most of its length. Labral papilla distinctly unisetaceous, with large setae.

Clothing of body typical. Setae of type five moderately thick, uniformly tapered, mostly multilaterally ciliate, and often smooth for basal half of length.

Legs. Clothing typical, with tibiotarsal setae subequal in diameter. Unguis normal, teeth small, internal teeth subequal; basal internal teeth about two-thirds of distance from base of internal edge to apex; external tooth about half-way between basal teeth and base of unguis. Empodial appendage smooth. Trochanteral organ (large specimens not seen) lacking internal setae and with anterior portion of ventral arm curved (see figure).

Furcula and genital plate. Genital plate with parabasal setae blunt, remainder acuminate, non-angulate, with the most anterior setae on either side slightly truncate. Mucro with apical tooth only slightly upturned and usually smaller than erect subapical tooth.

Discussion

This species appears to be quite rare; only three records are known. The series examined was small and did not show much variation except in structure of the mucro (see figure), where the apical tooth varied considerably in size, sometimes being distinctly larger than the subapical tooth. One specimen appeared to have two small internal setae on the trochanteral organ.

Pattern varies considerably: dark median stripe on fourth abdominal segment varies greatly in size and shape; dark pigment on any segment may be reduced: a median ocellar dark patch sometimes appears on the head.

Distribution

Washington: Yakima, Tampico and *British Columbia:* Vancouver Island. Also recorded by T. A. Scott (1942) as being taken in *California:* San Antonio Canyon, and *Oregon:* Portland.

Localities of cotypes: Yakima, Washington, September 26, 1931 (under leaves), A. Rolfs collector; Tampico, Washington, April 15, 1932 (under log), A. Rolfs collector; Tampico, Washington, May 30, 1932 (under log), A. Rolfs collector.

ENTOMOBRYA CONFUSA n. sp.

Plate 12, figs. 1-14

Entomobrya marginata, 1934, Mills, Monogr. Collembola Iowa: 67, 68 (*partim,* nec *Degeeria marginata,* 1871, Tullberg).

Color and pattern. Background color pale yellow, pigment purplish brown. Uniformly pigmented except for the following: apical two segments; posterior margins of the body segments, which are slightly darker; dorsum of head, which is pale with a dark V-shaped mark, developed to a greater or lesser extent; and legs and furcula, which are pale except for extreme bases.

Antennae. Apical segment about one and one-half times as thick as subapical. Retractile bulb of fourth segment bi- or trilobed, in a moderately deep, exactly apical pit. Clothing of antennae normal, with longest setae of the second segment about twice as long as diameter of that segment. Short smooth setae absent from large apical area on ventral surface of first antennal segment.

Head seen from above broadly oval in shape, slightly longer than broad. Labral papillae low, conical, unisetaceous, with small indistinct setae. Labial appendages with typical number of papillae and setae. External differentiated seta stout, smoothly tapered from base to apex, about one and one-half times as thick as largest normal setae on same papilla, weakly curved, and attaining, or slightly exceeding, apex of same papilla. Eyepatches dark blue, subrectangular in shape.

Clothing. Body clothing typical. Setae of type one expanded gradually for basal one-tenth of length and very slightly expanded at apex; setae gradually bent for apical one-fifth of length or at extreme apex only. Setae of type five stout, acuminate, very slightly expanded medially, coarsely multilaterally ciliate for apical three-fourths to one-half of length.

Legs. Clothing typical; internal face of tibiotarsus with thickest setae about one and one-half times as thick as others, and ciliate from just above point of insertion to apex, with ciliations slightly smaller basally. Unguis tapered from base, with typical seven teeth, all being small and subequal in size, except for apical internal tooth, which is about one-half as long as others. Internal basal teeth slightly apicad of the mid-level of internal edge. Lateral teeth approximately on a level with basal internals, and external tooth about one-third of way from base of unguis to lateral teeth. Empodial appendage acuminate, not ciliate. Trochanteral organ typical, with internal setae few in number and dorsal in position, being absent from apical two-thirds of space between the arms.

Furcula and genital plate. Mucro with anteapical tooth subequal to slightly smaller than apical tooth, and basal spine exceeding apex of anteapical tooth. Dens with fourteen to sixteen setae, all slender, acuminate, and subequal in size. Genital plate with fourteen subequal acuminate setae.

Discussion

There is a good deal of variation in the position of the lateral and external teeth of the unguis; in small specimens the lateral teeth are on a level with, and the external tooth slightly basad of, the basal internal tooth. The empodial appendage may be finely ciliate on internal edge. The trochanteral organ shows the usual growth variation. The mucronal teeth vary in their relative sizes, but in no case is the apical tooth more than one and one-half times as long as the anteapical.

The color gives some of the most striking variations, from pale bluish purple to dark purple-brown, with the background color varying from white to orange-red. The darkening of the posterior margin may be distinct, indistinct, or wanting, and the pattern on the dorsum of the head shows a great deal of variation (see figures), with rare specimens lacking dark pigment except on ocellar spot, and others entirely dark except for a pale V-shaped area.

This species is a common inhabitant of the leaf-mold in the western and mid-western areas. It has frequently been identified as *E. marginata*, but may be readily distinguished on morphological grounds.

Distribution

Colorado: Mount Evans — 12,000 feet, Winter Park; ***Wyoming:*** Dayton, Teton Pass; ***Montana:*** Nimrod, Babb, Armington, Neihart, Riceville, West Yellowstone, Butte; ***Idaho:*** Victor, Fernwood, Pierce; ***South Dakota:*** Deadwood, Sioux Falls; ***Iowa:*** Ames. ***British Columbia:*** Boston Bar, Revelstoke; ***Alberta:*** Banff.

Type locality: Mount Evans, Colorado, 12,000 feet, July 10, 1950.

ENTOMOBRYA SUZANNAE Schött

Plate 13, figs. 1-12

Entomobrya suzannae, 1937, Schött, Pan-Pac. Ent., San Francisco, **13**:132.

Color and pattern. Background color amber, pigment dark blue, distributed as follows: Terminal two antennal segments pigmented, ventral surface of apex of second segment dark. Internal half of antennal bases and connecting band dark. Dorsum of head sometimes with small V-shaped mark at median ocellus and an elongate triangular patch running posteriorly from apex at hind margin of either eyepatch. Prothorax with slight dark color on leg bases.

Body extremely irregularly pigmented. On the dorsum of thoracic segments two and three, the markings are usually in the form of two large separate patches bordering the posterior margin of each segment. On the rest of the body the pattern consists of a variety of spots, stripes and jagged markings. The sixth segment is without pigment. Meso- and metathoracic coxae lightly pigmented. Metathoracic femora apically ringed with dark pigment. All tibiotarsi medially dark.

Antennae. Segments one and four definitely thicker than remaining segments. Apical retractile bulb of fourth segment unlobed. Apical organs of the other segments typical. Clothing of antennae normal, with the longest setae of the second and third segments about twice as great in length as the diameter of those segments.

Head definitely longer than wide. Labral papillae unisetaceous. Labial appendage with external differentiated seta long, not reaching apex of same papilla, narrow, gradually tapered from base, and slightly curved.

Clothing of body typical. Setae of type five coarsely, unilaterally ciliate for apical half of length, slender and uniformly tapered.

Legs. Clothing normal, largest setae on tibiotarsus about one and one-half times as thick as remainder. Trochanteral organ typical, but with all setae large, those on the posterior arm about twice as long as the others (i.e. those on internal and ventral arm), which are subequal in size. Unguis unusually long, but distinctly and gradually tapered from base to apex. Teeth large, acute, and salient, being subequal in size except for apical internal tooth, which is about half as large as others. Basal internal teeth at about mid-level of internal edge of unguis. Lateral teeth distinctly basad of internal basals, and external tooth slightly basad of laterals. Empodial appendage unusually long and slender, tapered for apical one-third of length, acuminate, and not ciliate.

Furcula and genital plate. Dorsal crenulations of dens large, but ending gradually. Mucro elongate, anteapical tooth erect and straight, slightly smaller than the weakly curved apical tooth. Basal spine just attaining apex of anteapical tooth. Male genital plate of twelve short flattened setae, abruptly acuminate apically. Basal pair smaller and more gradually acuminate.

Discussion

This species shows immense variation in pattern, and as a rule the pattern is so irregular that exact description becomes unrewarding. In general we can say that each segment from thoracic segment two to abdominal segment five bears some marking. The first abdominal segment is the least heavily marked and may be almost lacking pigment. Some specimens of this species bear a striking resemblance to *E. triangularis* and *E. washingtonia* but the three species may be readily distinguished on morphological criteria.

Distribution

California: Santa Cruz Mts., Topanga Canyon, Salinas Valley.
Type locality: Alpine Creek, Santa Cruz Mts., California. Schött collection.

ENTOMOBRYA SINELLOIDES n. sp.

Plate 17, figs. 1-7

Color and pattern. Background color white, pigment dark blue and more or less pale violet. Pigment as follows: First antennal segment pale with moderately dark lateral lines and apical ring. Remainder of antennae violet. Antennal bases dark and with two lightly pigmented connecting bands. Head with median ocellar spot and lateral patches running ventrally from posterior ventral angles of eyepatches, these pale violet dorsally, and darker near ventral edge. Region anterior to patches with scattered dark spots. Mesotergum bordered by a dark blue band, wider laterally and medioposteriorly. Metathorax anteriorly pale, otherwise similarly marked. First three abdominal segments with medial dark blue bands along posterior edges, tending to be irregular laterally. Fourth segment with posterior four-fifths slightly pigmented, and a broken, wide, dark band along posterior edge. Fifth segment with dark band along entire posterior edge; remainder of body pale.

Antennae. Basal segment distinctly wider than apical three. Apex lacking retractile bulb. Clothing of antennae typical, longest ciliate setae of base of fourth segment twice as long as those on apex. Longest setae on first and second segments less than half as long as the segments bearing those setae, most less than one-third as long. Apical sensory organ of third antennal segment normal. Apical sensory organ of second segment with two small rods. The first, more apical one, is oval and about half as large as the second, which is cylindrical, blunt, and abruptly bent. Smooth short setae of first segment absent ventrally from external apex and from a roughly triangular area covering apical half of external, ventral edge.

Head oval, slightly longer than broad. Labral papillae unisetaceous, setae distinct. Labial appendage typical, external differentiated seta very large, gradually and uniformly tapered, about one and one-half times the width of the normal setae and protruding beyond the apex of same papilla.

Clothing of body normal. Setae of type one uncommon, seen only on thorax and head, not as clavate in appearance as usual, tip not bent or prolonged. Setae of type five moderately long, coarsely and unilaterally ciliate.

Legs. Setae normal. Trochanteral organ with internal setae, usually arranged in a line parallel to posterior arm. Setae of arms not greatly increasing in size toward apex. Apical seta about twice as long as internal ones. Unguis typical, the basal internal teeth at about the middle of the internal edge. Basal and median internals subequal in size and about twice as long as apical internal tooth. Lateral teeth small, external tooth small to minute, all of these being positioned slightly below level of basal internals. Empodial appendage acuminate, external edge coarsely ciliate for median half.

Furcula and genital plate. Mucro with a large heavy basal spine (exceeding anteapical tooth) and two teeth. Ventral edge of mucro with shallow indentation below anteapical tooth. Apical tooth distinctly larger than anteapical and more or less distinctly curved. Male genital plate with basal setae straight, apically rounded. Remainder of setae acuminate, slightly and gradually expanded medially, with the more basal ones tending to be somewhat truncate for apical third of length.

Discussion

The small series available does not show great variation. The amount of pale violet pigment present varies considerably, some having none except on antennae, and others (see figures of specimens from Sioux Falls, South Dakota, Pl. 17, fig. 2) with almost the entire body strikingly suffused with violet. In darker specimens a narrow V-shaped mark may appear on the dorsum of the head, running from the mediant ocellar spot to the antennal bases. The trochanteral organ may have the internal setae irregular (lacking in some specimens). The median internal tooth of the unguis may be noticeably longer than either the basal pair or the apical one. On small specimens the lateral and external teeth are not visible.

This species is very easily separated from all other known species of the genus *Entomobrya* (*sensu stricto*) by the lack of an apical bulb on the fourth antennal segment. This would make it appear to be a link between *Entomobrya* and *Entomobryoides*. I feel, however, that this is probably a secondary resemblance, since on the basis of the other characters (i.e. genital plate, ratios, claw and head appendages) this species is closely allied to the *E. triangularis* group.

Distribution

Known only from Sioux Falls, South Dakota, and type locality.

Type locality: Lamar, Colorado, July 30, 1950.

ENTOMOBRYA BICOLOR Guthrie

Plate 14, figs. 1-8

Entomobrya bicolor, 1903, Guthrie, Rep. Geol. Nat. Hist. Surv. Minnesota, Zool. Ser., (4):72, 73.

Color and pattern. Pale color dull waxy yellow, dark pigmentation purple-brown to chocolate-brown. Head, thoracic segments two, three, and abdominal segment four dark; remainder of trunk pale. Elliptical areas along anterior border of fourth abdominal segment pale. Femora with incomplete dark rings subapically. Antennal segments two and three apically ringed.

Antennae. Fourth segment with simple retractile bulb, and an integumentary papilla, of thicker integument, not sunken in pit, and non-retractile (see Plate 14, fig. 6). Setae of antennae typical, longest setae no more than one and one-half times as long as width of segment at that point.

Head from above oval, narrower toward posterior margin. Labral papillae low, conical, unisetaceous, with setae minute and not clearly visible. Labial appendage with external differentiated seta very heavy, tapered from base, exceeding apex of same papilla by one-fourth to one-third of its total length. Mesothorax enlarged, forcing the head into a hypognathous position when at rest.

Body slightly compressed bilaterally, so as to have a broadly elliptical cross-section. Abdominal segment four strikingly elongate.

Clothing of body of typical five varieties of setae. Setae of type one (see Plate 14, fig. 5) unusual, with apical or clavate portion often longer or wider than usual. Setae of type five uniformly tapered and finely ciliate, smooth for only a short basal distance.

Legs clothed with ciliate setae; many setae internally on tibiotarsus are thicker than the remaining setae, and distinctly swollen above point of insertion. Unguis normal. The median internal tooth sometimes greatly enlarged (as in *Entomobryoides guthriei*). External tooth well-developed, located basad of lateral teeth, which are slightly below the level of the basal internals. Empodial appendages finely ciliate and acuminate. Trochanteral organ without differentiated ventral arm, possessing only posterior arm and many irregularly arranged small setae anterior to this.

Furcula and genital plate. Mucro short, with stubby subequal teeth and unusually stout basal spine, shorter than anteapical tooth. Genital plate setae weakly recurved; large, with anterior pair somewhat smaller in size.

Discussion

In color the variation is simple, dark colors sometimes increasing to include abdominal segments one, three, five and part of six. On paler specimens the pale color will include the anterior one-fifth of the dorsum of the fourth segment. This species fades greatly when preserved in alcohol, so that some old specimens appear dirty yellow in color. Few fresh specimens were seen, but Folsom's unpublished notes give the fresh color as frequently orange.

There is considerable variation in the position of the ungual teeth in relation to the size of specimens. On smaller specimens the external tooth is more basad of the laterals, and these are nearer, and level with, the basal internals. There is some variation in the structure of the apical bulb of the fourth antennal segment. Both the bulb and the non-retractile papilla may rarely be double.

Distribution

Pennsylvania: State College, The Barrens; *New Jersey:* Ramsay; *Virginia:* Alberta; *North Carolina:* Madison, Raleigh; *Minnesota:* Minneapolis; *Iowa:* Sioux City, Ames; *Kansas:* Wellington.

Type locality: Minneapolis, Minnesota.

ENTOMOBRYA GISINI n. sp.

Plate 14, figs. 9-16

Color and pattern. Background pale greenish yellow, dark pigment, gray to black. Pigment as follows: Antennal segment one apically ringed with dark; antennal segment four and apical half of three purplish; antennal bases and connecting band black. Irregular band of gray running posteriorly from eyes, widening posteriorly and ending irregularly before posterior margin of head. Thin, irregular V-shaped mark dorsally on head, with base at median ocellus and arms ending just before eyepatches. Coxae black. Two irregular mediolateral longitudinal black bands running from anterior border of mesothorax to posterior border of fourth abdominal segment, wider at posterior edge of segments and reduced on mesothorax to a series of irregular spots. Fourth segment with a pair of lighter lateral longitudinal bands, on and bordering the lateral suture. Parafurcular lobes darkened posteriorly. Fifth abdominal segment with posterior half black, finely divided with pale green mid-dorsally. Remainder pale.

Antennae unusually long, basal segment slightly wider than remainder. Fourth segment rounded apically, showing definite signs of ringing or subsegmentation. Apical bulb of fourth antennal segment simple, in a distinct large pit, completely apical in position. Protecting papillae absent. Apical sensory organ of third segment normal except for accessory peg, which is more elongate than usual. Second antennal segment with small, poorly demarcated basal sub-segment. Short smooth setae on ventral surface of first segment, absent only from narrow apical ring. Clothing typical, with longest setae less than one and one-half times as long as the corresponding segment at that level.

Head elliptical, longer than broad. Labral papillae roundly conical, unisetaceous, with setae heavy and distinct. Labial appendages typical. External differentiated seta small, narrower than largest normal setae on same papilla, acuminate, slightly curved and not attaining apex of same papilla. Three inner posterior eyes on either side, about one-half as large as the remaining ones.

Body elongate, elliptical seen from above.

Clothing of head and trunk of typical five types of setae. Setae of type one greatly expanded just above insertion and uniformly wide distal of this point, apically bent. Setae of type five unusual, finely and multilaterally ciliate and fulsiform in shape.

Legs. Clothing typical. Tibiotarsus with a single irregular row of very stout ciliate setae, more than twice the size of neighboring setae. Unguis broader than usual. Internal teeth small and subequal in size, the basal pair slightly distal of the middle of the internal edge. Lateral teeth extremely salient, with reinforcing ridges. External tooth small, positioned four-fifths of distance from internal basals to base of unguis. Lateral teeth about halfway between basals and base of unguis. Empodial appendage acuminate and smooth. Trochanteral organ without clearly demarcated ventral arm, possessing a posterior arm and an irregular mass of anterior, shorter setae.

Furcula and genital plate. Dorsal dental crenulations, ending comparatively abruptly. Mucro with anteapical tooth erect, much larger than weakly upcurved apical tooth. Basal spine short, broad, not attaining apex of anteapical tooth. Male genital plate with basal setae small and acuminate, remainder thick, inner surface flattened, outwardly rounded, slightly recurved and bluntly pointed, tapering for apical fifth of length.

Discussion

This species is one of the *E. bicolor* group, but has several characters which place it in an intermediate position between this group and the *E. comparata* group. The single bulb is found in both groups (more typical in the former), but the lack of protecting papillae is like *comparata*. The shapes of the body, claw, labial and labral appendages, eyepatch, and fourth antennal segment, and the body ratios all link this species with the first group, showing the species' true affinities.

The specimens seen consisted of the type series and a single specimen from Banff, Alberta. The type series is quite uniform, but the Banff specimen is darker in color, all the dark areas having expanded and solidified. A longitudinal interocular line and a pale color present on the unpatterned parts of metathorax through abdominal segment three, absent only from narrow mid-dorsal line. The legs and furcula and antennae are similarly pale blue in color. In the smallest specimens examined, the lateral teeth lose their striking prominence, and the external tooth is slightly more apical in position.

The presence of a weak basal subsegment (not visible in about half of the specimens) on the second antennal segment would, according to certain arbitrary classifications, place this species in the genus *Orchesella,* but the presence of a retractile apical bulb, the great comparative length of the fourth abdominal segment, the type of mucro, genital plate, body setae, claws, and, in short, every other morphological character, show that this species is in no way related to this genus, and points up the artificiality of splitting off this whole tribe (*Orchesellini*) on the basis of the number of antennal segments alone.

Distribution

North Carolina: Busick. *Alberta:* Banff.

Type locality: Busick, Yancy County, North Carolina, June 1950.

ENTOMOBRYA NIGRICEPS Mills

Plate 15, figs. 1-9

Entomobrya nigriceps, 1932, Mills, Iowa State Coll. Journ. Sci., **6**(3):268, 269.

Color and pattern. Background pale yellow, pigment blue-black as follows: Antennae with basal third dark. Head completely dark except for a narrow broken ring around the mouth-parts, and scattered minute spots, more concentrated on the ventral surfaces. Prothorax heavily and irregularly pigmented dorsally and laterally. Mesothorax through abdominal segment three with four longitudinal bands, median pair broken on anterior border of third abdominal segment, and lateral pair along the lateral edges of thoracic tergites and ending on anterior margin of second abdominal segment. These stripes are represented on third abdominal segment by faintly pigmented spots. Fourth segment with lateral suture lined with dark on both sides, and a median, weakly pigmented indication of a transverse band, broken into several longitudinal short lines, lacking on mid-dorsum. Parafurcular lobes with median, wide, dark band. Fifth segment with lateral areas dark, narrowing anteriorly. Metathoracic femora with external dark line, and dark apical ring, mesofemora with apical dark spot. All heavily pigmented areas with numerous small, round to irregular pale areas.

Antennae. Fourth segment blunt-tipped. Apical bulb of fourth segment simple, elongate, lacking accessory papilla. Second and third antennal segments each with one or two long setae, about one-half as long as corresponding segment. Clothing otherwise normal.

Head longer than broad, oval in shape. Labral papillae bluntly conical, uni- or bisetaceous. Labial appendage with external differentiated seta slightly narrower than the largest normal seta of the same papilla.

Clothing typical. Setae of type one somewhat longer and more strikingly clavate apically than usual. Those on abdominal segments two and three are definitely greater in length than these segments. Setae of type five are tapered only at extreme apex, unilaterally ciliate for most of their length, and appressed.

Legs with normal acuminate ciliate setae of various sizes. Both femora and tibiotarsi have numerous long setae, more than twice as long as the diameter of the leg at corresponding locus. Tibiotarsus internally with setae of two diameters, thicker ones very slightly more finely ciliate than the more slender ones. Unguis typical. Basal internal teeth slightly below mid-level of internal edge. Lateral teeth normal and slightly basad of basal internals; external tooth large, salient, and slightly basad of laterals. Empodial appendage acuminate and smooth. Trochanteral organ not clearly observed, apparently similar to condition found in *E. gisini.*

Furcula and genital plate. Dental crenulations deep and heavy. Mucro short and heavy, anteapical and apical teeth short and subequal. Basal spine short and heavy. Genital plate of male with all setae thin, cylindrical, weakly recurved or straight, and acuminate.

Discussion

Only the type series was seen, but even in these specimens there was a considerable variation in the pattern (see figures). The dorsum of the head sometimes has one to several large pale spots. The basal mucronal spine is not complete in many specimens, but there is always a large basal stump left. The lateral teeth of the unguis may be more apical in position than those described.

This species is closely related to *E. decemfasciata* and *E. quadrilineata*, but can be readily distinguished from both by the head pigmentation and the genital plate structure of the male, as well as the structure of the unguis. The only capture of the species was in Texas, and it may occur somewhat farther south in greater numbers.

Distribution

Texas: College Station. (Type locality.)

ENTOMOBRYA QUADRILINEATA Bueker

Plate 15, figs. 10-15; Plate 16, figs. 1-4

Entomobrya quadrilineata, 1939, Bueker, Trans. Acad. Sci. St. Louis, **30**(1):15.

Entomobrya anthema, 1952, Wray, Bull. Brooklyn Ent. Soc., **47**:95-106 (new synonymy).

Color and pattern. Background white to pale yellow. Pigment dark blue to violet, as follows: Third and fourth antennal segments slightly darkened, prothorax with lateral spot and dorsal part of leg bases dark. Four longitudinal black bands run from anterior border of mesothorax to posterior border of second abdominal segment, the more lateral pair bordering the tergal edges of the thoracic segments; on abdominal segments one and two these marks maintain the same level and direction, joining a transversely elongate spot on the posterior margin of the second segment. Dorsal bands end on posterior border of the second abdominal segment, and on this segment curve slightly toward each other. Third abdominal segment with mid-dorsal, roughly rectangular spot and two lateral diagonal bands, combined with a thin line along median part of this segment's posterior border to form a roughly W-shaped mark, with the ends of the mark in contact with lateral dark bands of the previous segment. Fourth abdominal segment with large V-shaped dark band, basally widely broken on mid-dorsal line, apices of mark in contact with posteroventral margin of third segment. Fourth segment with mid-dorsally broken posterior transverse band, just before posterior margin. Fifth abdominal segment with two posteroventral dark spots. Coxae with few lightly pigmented spots; prothoracic femora slightly darkened medially, and meso- and metathoracic femora darkened apically. All tibiotarsi slightly darkened except at bases. Posterior sides of base of furcula slightly darkened, remainder pale.

Antennae. Fourth segment roundly tapered, and with simple retractile apical bulb, located in a deep pit, slightly displaced ventrally from true apex. Apical sensory organ of third segment normal. Apical sensory organ of second segment of two small oval (almost round) sensory pegs, about one-fifth as large as those on third segment, with one (possibly two) minute accessory peg. Clothing of antennae normal, many comparatively long ciliate setae on fourth segment; the longest about one and one-third times as long as diameter of segment. These long setae densely cover basal one-half to two-thirds of the segment. Longest setae on remaining segments about twice as great in length as diameter of corresponding segment. First antennal segment with three or four setae similar to type one. These are smaller and less bent apically than those on body. Smooth setae absent from narrow apical band on ventral surface of first segment.

Head about one and one-half times as long as broad, elliptical in shape with sides of head (seen from above) distinctly convergent from antennal bases to the posterior rounded margin. Labral papillae low, rounded, unisetaceous, with small but distinct setae. Labial appendages normal, external differentiated seta extremely long, apical half exceeding apex of papilla. Seta weakly curved, tapered from base, more sharply so for apical fourth, a little thicker than the largest normal setae of same papilla. Two anterior eyes on each side, four times as large as the inner posterior two, which in turn are half as large as remainder.

Body elongate and elliptical, seen from above; circular in cross-section.

Clothing of body typical. Setae of type one large, heavy, abruptly expanded above point of insertion, slightly expanded and strongly bent apically. Bent part sometimes very long (one-tenth of total length). Setae of type five slender, gradually tapered from base to apex, coarsely unilaterally ciliate for apical five-sixths of length.

Legs clothed normally. Tibiotarsus with no setae unusually thick. Unguis triangular in lateral view, expanded basally. Median internal tooth slightly larger than, or subequal in size to, basal teeth. Apical tooth much smaller. External tooth salient, distinct, located about midway between basal internals and base of unguis. Lateral teeth small, positioned two-thirds of distance from basal internals to external. Unguiculus acuminate, not ciliate. Trochanteral organ typical, with setae very numerous, those in the arms and the internal setae all uniformly small. Arm setae only slightly larger toward apex.

Furcula and genital plate. Dentes with dorsal crenulations ending abruptly. Mucro short and deep, apical tooth extending directly posteriorly, or only slightly upcurved. Anteapical tooth short, stout, and erect. Basal spine stout, attaining or exceeding apex of anteapical tooth. Male genital plate with all large setae except basals being uniform, recurved, and acuminate; basals slightly smaller, curved, and acuminate.

Discussion

The pigmentation varies greatly, as is usual, some specimens entirely pale except for a faint indication of the transverse bands on abdominal segments three and four, and the broken posterior marginal band on fourth segment. The unguis often has the lateral and external teeth nearly on a level, in which case the laterals are more basal in position than usual. The median internal tooth is usually subequal to the basals, occasionally much larger. The mucro may have the apical tooth slightly upcurved, and while the teeth are usually subequal, one or the other may be slightly larger. The apical bulb of the antenna sometimes shows an indentation, perhaps a forerunner of the lobed condition.

Bueker described this species from St. Louis, Missouri; in personal communication I have been told by him that the types designated in this paper were lost and "probably destroyed." Since this species is quite well marked, and in several cases specimens have been found which closely match his figures and dscription, there can be little doubt as to its identity.

This species is one of the *E. bicolor* group, and although it bears a striking superficial resemblance to *E. decemfasciata*, a close examination of the genital plate, trochanteral organ, setae of body, and the antennae shows that it is also closely related to *E. bicolor*. From this species it is easily separated by the structure of the unguis (very long internal median tooth in *bicolor*), details of genital plate structure, type of pattern, and body ratios. It may be separated from *E. decemfasciata* by the lack of large setae internally on the tibiotarsus, by the longer and more apical external seta on the labial appendages, by the genital plate and unguis structure, by the type of pigmentation on the second abdominal segment, and the convergent side margins of the head.

Distribution

Virginia: Blue Ridge Mountains; *Kentucky:* Crailhope; *Tennessee:* Knoxville; *Illinois:* Bell Smith Springs, Dixon Springs, Fountain Bluff; *Arkansas:* Mount Mayozion, Logan County.

ENTOMOBRYA DECEMFASCIATA (Packard)

Plate 16, figs. 5-16

Degeeria decemfasciata, 1873, Packard, Rep. Peabody Acad., **5**:40.

Entomobrya intonsa, 1931, Mills, Iowa State Coll. Journ. Sci., **6**(3):265-268 (new synonymy); 1934, Bonet, Eos, **9**:169; 1944, Gisin, Verh. Naturf. Ges. Basel, **55**:78.

Entomobrya stachi, 1957, Wray, Acta Zool. Cracoviensia, **6**(5):114-116 (new synonymy).

Color and pattern. Background dull yellow (in old collections), dark pigment blue-black, as follows: Antennae with slight darkening of apex on third segment and on apical two-thirds of fourth segment; antennal bases and connecting band dark. Dorsum of head with V-shaped mark, its base at median ocellus and arms touching inner posterior corners of eyes. Faint darkened area running posteriorly and slightly downward from hind edge of eyepatch. Prothorax pale, remaining thoracic and first abdominal segments with wide lateral dark borders on tergum, with numerous small, pale areas. Mesothorax with dorsal dark spots, forming irregular band across posterior half of segment. Metathorax and first abdominal segment each with a pair of large spots on the posterior margins, roughly triangular on the thorax and rectangular on the abdomen. Second abdominal segment with similar spots, somewhat enlarged, laterally connecting with darkened tergal margin of first segment. Third abdominal segment with two broad dark bands, parallel to the spots of second segment and running thus diagonally from anterior to posterior borders of the segment. Fourth segment with a median, roughly V-shaped band parallel to those on the third segment, mid-dorsally divided, continued below the lateral suture, but slightly displaced rearward. The fourth segment possesses two large medio-lateral spots anterior to V-shaped mark, and has the posterior margin ringed with black, mid-dorsally divided and medio-laterally produced. Fifth and sixth segments posteriorly black. External sides of coxae spotted with black; apices of femora ringed with black (rings larger posteriorly). Remainder of body pale.

Antennae. First segment slightly thicker than remainder. Apical bulb of fourth segment simple, in a deep pit, displaced slightly from extreme apex, with accessory swollen, non-retractile papilla attached to side of pit. Apical sensory organ of third antennal segment normal. Clothing of antennae typical. Longest setae of fourth segment about as long as diameter of that segment. Longest on other segment less than one and one-half times as long as diameter of corresponding segment. Short smooth setae on ventral surface of first segment, absent only from thin arcuate apical area. First antennal segment with several small setae, similar to body setae of type on.

Head roughly elliptical in shape, strikingly longer than wide with sides of head (seen from above) parallel from eyepatch to posterior rounding. Inner posterior two eyes on either side about half as wide as remaining eyes, which are subequal in size. Labral papillae rounded, unisetaceous, with setae small but distinct. Labial appendages normal. External differentiated seta distinctly wider at base than normal setae of same papilla, and greatly exceeding apex of same papilla.

Clothing. Setae of type one expanded gradually and slightly for basal one-fifth of length, not expanded apically, and either slightly bent at extreme apex or, occasionally, slightly bent for apical one-eighth of length. Setae of type five long, uniformly tapered, and uniformly ciliate for apical three-fifths to four-fifths of their total length. Body elongate, elliptical in shape seen from above, some specimens slightly compressed bilaterally, especially in abdominal regions.

Legs. Clothing normal, tibiotarsus internally with a staggered single row of very heavy, ciliate setae, swollen above insertion, and more than twice as thick as remaining setae of segment. Unguis stout, tapered only on apical half. Median internal tooth often larger than basals and three times as large as apical tooth. External and lateral teeth small, about on a level with each other, and slightly basad of the basal internals. Empodial appendage acuminate, smooth, on an unusually high empodium, distad of basal internal ungual teeth. Trochanteral organ typical, ventral arm straight, but posterior arm irregular. Internal setae scattered, but absent from large area behind anterior arm. All setae large and subequal. Dens with dorsal crenulations ending very abruptly. Mucro short and stout. Anteapical tooth larger than apical. Apical tooth weakly upcurved. Basal spine attaining, or barely exceeding, apex of anteapical tooth. Genital plate observed on one specimen, but not clearly; apparently with lateral and apical setae short, acuminate, flattened, and medially irregularly expanded. Basal and parabasal setae acuminate, thin, somewhat longer, and gradually tapered.

Discussion

There has long been a considerable amount of confusion surrounding this species. Packard described it from a number of specimens from three localities: Salem, Massachusetts; Knoxville, Tennessee; and Waco, Texas. I have not been able to find the Salem specimens. The Knoxville specimens are in the Mills collection and are unrecognizable, due to drying damage. The series from Waco, Texas, bearing the type label and type number, is at the Museum of Comparative Zoology, Cambridge; it consists of two species: the one later described by Mills as *Drepanura sabulicola* and the species described in the same paper by Mills as *Entomobrya intonsa.* Packard's description is so vague that it is difficult to determine exactly what he was looking at, and in all likelihood the description itself is partly composite; however, "third joint [of furcula] with two hooks as usual" would seem to eliminate *sabulicola*, and "first dorsal abdominal band narrow and faint, two succeeding heavier, and at each end produced anteriorly" makes *intonsa* of Mills the logical choice.

This species has long been considered a synonym of *E. multifasciata* (= *nivalis*). This has been due largely to a figure published by Harvey in 1895, labelled *Degeeria decemfasciata.* In the text he states that Packard refused to give him a definite opinion as to whether or not this was actually *decemfasciata.* Since this figure was obviously a specimen of *E. nivalis* (=*multifasciata*), workers since that time have erroneously considered Packard's species a synonym.

Another point involves Packard's species *Degeeria flavocincta* (=*flavopicta*). There is a figure in Packard's *Entomology* in the 1872 edition, labelled *Degeeria flavopicta*, and in subsequent editions, *D. flavocincta.* In his Essex County paper, Packard synonymized this species (never described, only figured) with *E. decemfasciata.* A series of types was, however, deposited in the Museum of Comparative Zoology and labelled *D. flavocincta* Packard, without locality or collector. Of these, only one specimen remains that could possibly be the species in question.

This was mounted as a lectotype by Bonet in 1948. I am certain that this is not *E. decemfasciata*. It is either the two-striped form of *E. clitellaria* or a pale specimen of *E. triangularis*. Because the figure is so poor and the specimen is in such bad condition that a definite determination is unlikely, I feel that the name should be considered a *nomen dubium*.

A final matter concerns Handschin's supposed rediscovery (1928, Handschin) of *E. decemfasciata* from Mexico. His species is evidently closely allied to, if not synonymous with, *E. nivalis*, and thus far removed from the true *decemfasciata*. This further led to Womersley's recording a specimen (probably a new species) from Africa, as *decemfasciata* (1934, Womersley).

To summarize this taxonomic jungle, *E. decemfasciata* Packard is synonymous with *E. intonsa* Mills. Determinations of *decemfasciata* as a synonym of *E. nivalis* (=*E. multifasciata*) given by Bonet 1933, Mills 1934, Gisin 1944, Maynard 1951, and most other modern authors are in error. The identity of the species identified by Handschin 1928, and Womersley 1934 as *E. decemfasciata* cannot be presently determined; however, they are certainly not synonyms of the true *decemfasciata*. *Degeeria flavopicta* of Packard which he later synonymized with *decemfasciata* is not a synonym of that species. Since the description and remaining species of *flavopicta* are entirely inadequate for a determination I recommend that this be considered a *nomen dubium*.

Variation

There is considerable variation in the relative lengths of the teeth of the mucro, the apical sometimes being as long as, or even slightly longer than, the anteapical. In all cases, the mucro is still very short, and both teeth are broad and stout. The only specimens seen were the types of *decemfasciata* and *intonsa*. All these were very old specimens, and the colors had probably changed. Both authors (Mills and Packard) give original background color as greenish yellow. The pattern varies a good deal, some specimens having only scattered pigmented spots anterior to the third abdominal segments. In some specimens the anterior part of the body is covered with irregular pigment which may be broken into separate patches. This species is one of the *E. bicolor* group; in this group it is most closely related to *E. quadrilineata.* It can be easily distinguished from this species by the pigment on the second abdominal segment; in the present species the pigment on this segment when present always runs diagonally down and forward from the dorsal posterior spots, whereas in *quadrilineata* the pigment on this segment is in four straight longitudinal bands, the lateral pair in line with the anterior tergal borders. A better method of separation than this uses the external differentiated seta of the labium (see Plate 16, fig. 15).

Distribution

Tennessee: Dupon Mt.-Sevier Co., London Co.; *Texas:* College Station, Waco.

Lectotype: (new designation) Waco, Texas, Belfrage collection, present location Museum of Comparative Zoology.

Genus DREPANURA Schött

Drepanura, 1891, Schött, Bih. K. Svenska Vet. Akad. Handl., (17)**4**(8):1-25.
Genotype: Drepanura californica, 1891, Schött, *op. cit.* :19.

Similar to *Entomobrya.* Antennae similar except that the apical bulb is always single and slightly displaced from true apex. The labral papillae are poorly developed, and the external differentiated seta of the labium is about as thick as the remaining setae. The mucro has no anteapical tooth but has a basal spine.

Claw, genital plate and other characteristics as in *Entomobrya.*

Discussion

This genus is probably polyphletic in its present constitution; however, a clear understanding of this phenomenon must await a world revision. Until such a time I feel it best to maintain its separate identity on the basis of the readily identified sickle-shaped mucro and presence of a basal spine.

There are two Nearctic species, *D. californica* and *D. perpulchra.*

DREPANURA CALIFORNICA Schött

Plate 18, figs. 1-10

Drepanura californica, 1891, Schött, Bih. K. Svenska Vet. Akad. Handl., (17)**4**(8):19.

Entomobrya (Drepanura) californica, 1934, Bonet, Eos, **9**:157; 1944, Gisin, Verh. Naturf. Ges. Basel, **55**:71.

Drepanura rolfsi, 1935, Mills, Bull. Brooklyn Ent. Soc., **30**(4):134, 135 (new synonymy).

Entomobrya (Drepanura) rolfsi, 1944, Gisin, Verh. Naturf. Ges. Basel, **55**:71.

Color and pattern. Background pale yellow. Blue pigment as follows: antennae pale blue, darker at apices, and with a dark apical ring on first segment; head with antennal bases and connecting band dark, dorsally with a dark V-shaped mark opening forward, irregular small dark patches near posterior margin of head. Prothorax with scattered blue spots. Mesotergum outlined with blue band, thicker at mid-dorsal regions. Metathorax and abdominal segment one similar along lateral and posterior borders. Abdominal segments two through four with posterior margins irregularly, and narrowly darkened. All dark areas with numerous small round pale spots. Remainder of animal pale.

Antennae. Apical bulb slightly displaced from apex, and with strongly granulate surface. Longest setae of antennae slightly longer than width of segment at same level.

Head. Labial papillae with external seta about as wide as neighboring setae, and smoothly tapered.

Clothing as in *Entomobrya.* Setae of type one are long and slender, only slightly contracted at point of insertion. Setae of type four tapered only at apex.

Legs. Tibiotarsus with a double row of setae twice as thick as remainder. Apical internal tooth of unguis rarely absent.

Furcula and genital plate. Mucro with small basal spine. Crenulate dentes ending abruptly. Genital plate of male with small claw-shaped setae (8 to 10), the basal four more strikingly recurved than the remainder.

Discussion

Even though few specimens were seen, the variation in pattern is striking. The second thoracic segment may have two or four curved lateral longitudinal lines, the dorsal and lateral regions of the third abdominal segment may be entirely dark, while the darkened areas on the posterior borders of the various segments may be reduced or absent. In addition completely pale specimens have been seen.

The external labial seta frequently exceeds the apex of the same papilla.

The species was first described from an unknown locality in California. The pattern originally described evidently represents one extreme of the pattern variation. In spite of numerous supposed captures this is a very rare species, and is apparently limited to the Pacific coast area.

Distribution

California: San Diego, and unknown locality; *Washington:* Yakima.

Type locality: California.

DREPANURA PERPULCHRA (Packard)

Plate 17, figs. 8-12

Degeeria perpulchra, 1873, Packard, Rep. Peabody Acad., **5**:38, 39.

Entomobrya perpulchra, 1884, Brook, Journ. Linn. Soc. London, **17**:281.

Entomobrya (Drepanura) perpulchra, 1931, Mills, Amer. Mus. Novitates, **464**:7; 1934, Bonet, Eos, **9**:156; 1944, Gisin, Verh. Naturf. Ges. Basel, **55**:71.

Color and pattern. Background color not clear in observed material (only specimens seen were the ten types, all in poor condition). Packard says that the background color is purplish on head, thorax and antennae, and honey yellow on abdomen and base of furcula. Pigment black to gray as follows: Ring on antennal bases and connecting band, and a dark gray band posterior of eyepatch. Head with dorsal V-shaped mark opening forward. Mesothorax anteriorly and laterally margined with gray, metathorax entirely black. Third and fourth abdominal segments with scattered gray areas. Remainder pale.

Antennae. Apical segment thicker than others. Retractile bulb of fourth segment simple, in a shallow pit, slightly displaced from true apex. Apical sense organ of third segment without accessory pegs. Smooth setae on ventral surface of first segment absent from a small arcuate apical area.

Head. Broadly oval, one and one-third times as long as broad. Labral papillae conical, unisetaceous with small setae. External differentiated seta of labial appendage long, about as thick as neighboring setae, and just attaining apex of same papilla.

Clothing. Setae of type five unusually slender, uniform in width for basal half of length, then acuminate, coarsely unilaterally ciliate for apical two-thirds to half of length.

Legs. Setae of tibiotarsus subequal in size, slender. Unguis not strongly tapered. Empodial appendage acuminate, internal edge ciliate for median half of length.

Furcula and genital plate. Crenulations on dorsal part of dentes deep and ending abruptly. Mucro with very large basal spine. Genital plate not seen.

Discussion

The known material is too meager and too poorly preserved for an adequate discussion of variation. The size of the median tooth of the unguis may be greater than the remainder of the teeth.

This species has never been taken since the original capture, and may very well represent a neotropical stray.

Distribution

Texas: Waco; Belfrage Coll. (Type locality.)

Genus ENTOMOBRYOIDES Maynard

Degeeria, 1873, Packard, Rep. Peabody Acad., **5**:39, 40.

Entomobrya, 1884, Brook, Journ. Linn. Soc. London, **17**:282 (ad partim).

Entomobryoides (subgenus), 1951, Maynard, Collembola New York State: 161.

Genotype: Degeeria purpurascens, 1873, Packard, Rep. Peabody Acad., **5**:39, 40.

Similar to *Entomobrya.* Antennae similar except that the apical retractile bulb is always completely lacking (sometimes with a non-retractile papilla). The body always more or less circular in cross section, never dorsoventrally compressed. Labial appendage with the external spine-like differentiated seta always about twice as thick at its base as the base of the largest normal seta on the same papilla. Eyes always sixteen in number. The clothing of the body as in *Entomobrya* but smallest under setae always unilaterally ciliate. The legs similar, except that the tibiotarsus has a double row of setae, bearing exceedingly fine ciliations, definitely differentiated from normal heavily ciliate tibiotarsal setae. Under all but the highest magnifications these setae look entirely smooth.

The claws of this genus have the same lamellae as in *Entomobrya*, but internal teeth tend to have one or more members greatly enlarged. The coloration is less variable than that of *Entomobrya.* Mucro always bidentate, with basal seta, and usually with apical tooth considerably longer than the subapical one.

Discussion

This genus is closely allied to *Entomobrya* and *Sinella.* It can readily be distinguished from the former by the finely ciliate setae of the tibiotarsus, the lack of an apical antennal bulb, and the heavy, short external setae on the labial appendages. It can be distinguished from the latter by the presence of sixteen eyes, by the clavate tenant hair, the large trochanteral organ, and the untoothed empodial appendage. The New Zealand *Deuterosinella* is also closely related but can be easily distinguished by the short tenant hair and lack of an apical internal ungual tooth.

The genus is almost exclusively Nearctic, having only one indigenous Palearctic species. The genus displays an unusual amount of geographical variation, showing the best subspecific divisions of the whole group. There are four Nearctic species: *E. purpurascens, E. mineola, E. guthriei,* and *E. dissimilis. E. myrmecophila* is the single Palearctic species.

Key to the Nearctic Species of the Genus ENTOMOBRYOIDES

1. Setae of male genital plate straight or slightly curved, never angulate; internal median tooth of unguis often much longer than basal tooth; color uniform . . . . *E. guthriei*

   Most setae of male genital plate angulate (see Plate 19, fig. 2); median tooth of unguis never strikingly larger than basal tooth 2

2. Pattern on thorax and first three abdominal segments in a series of large dorsal spots . . . . *E. mineola*

   Pattern uniform, or in irregular bands, never in a series of spots . . . 3

3. Mucro with apical tooth unusually long, and sharply upturned at apex (see Plate 20, fig. 13) . . . . *E. dissimilis*

   Mucro with apical tooth only slightly longer than anteapical, not sharply upturned at apex (see Plate 19, fig. 12) . *E. purpurascens*

ENTOMOBRYOIDES PURPURASCENS (Packard)

Plate 19, figs. 1-15

Degeeria purpurascens, 1873, Packard, Rep. Peabody Acad., **5**:39, 40.

Entomobrya purpurascens, 1884, Brook, Journ. Linn. Soc. London, **17**:282; 1903, Guthrie, Rep. Geol. Nat. Hist. Surv. Minnesota, Zool. Ser., (4):76, 77;1928, Folsom, Cornell Univ. Agric. Exp. Sta. Mem., **101**:15; 1934, Bonet, Eos, **9**:152; 1934, Mills, Monog. Collembola Iowa :67; 1944, Gisin, Verh. Naturf. Ges. Basel, **55**:72, 73.

Entomobrya subpurpurascens, 1934, Denis, Rev. Franc. d'Ent., **1**:212 (new synonymy).

ENTOMOBRYOIDES PURPURASCENS (Northern form-A)

Color and pattern. Background color white, pigment bluish purple. Pigment slightly darker on posterior segments. Pale, double, V-shaped mark on dorsum of head, two thin dark lines running ventrally from median ventral margin of eyepatch to venter of head. Antennae slightly darkened. Furcula and base pale, remainder of body uniformly and moderately pigmented.

Antenna. Shape of antennae typical. Third segment with normal paired rods. No accessory pegs were observed. Apical sensory organ of second segment with three minute rods, largest similar in shape and half as large as those of third segment, the smallest about one-third as large as the largest. Smooth setae of first antennal segment absent from apical one-fifth of segment. First antennal segment with numerous short clavate setae, similar to body setae of type one, but about half as large.

Head. Slightly longer than broad. Labral papillae conical, unisetaceous or bisetaceous, with setae small but distinct. Labial appendages with typical number of papillae; external differentiated seta broad, tapered from base, more strikingly so at extreme apex, slightly curved, exceeding apex of same papilla for from one-fifth to one-third of its length. Eyepatches black, trapezoidal, with inner posterior angle acute, about as wide as antennal diameter. Two anterior eyes on either side slightly larger than the two inner posterior ones, which are slightly smaller than the remaining four.

Clothing. Setae of type one normal, slightly curved for entire length, those on anterior body segments sharply bent at expanded apical portion, numerous on all segments save abdominal six. Setae of type two scarce, small in size, never as long as longest setae of type one. Setae of type five slender, gradually tapered from base, coarsely unilaterally ciliate for apical one-half to two-thirds of length.

Legs. Clothing typical, finely ciliated setae on tibiotarsus slightly larger than normal setae of same segment. Trochanteral organ typical, with many setae, those in arms extremely long, strikingly graduated toward apical seta. Internal setae usually about one-third as long as apical seta. Unguis normal, with usual seven teeth moderate in size, apical internal tooth about half as large as others, which are subequal. Basal internals slightly above mid-level of internal edge, laterals on a level with basal internals, and external tooth. Empodial appendage acuminate, heavily ciliate along internal edge.

Furcula and genital plate. Anteapical tooth of mucro subequal to apical. Apical strongly curved, anteapical erect. Basal spine exceeding apex of anteapical tooth. Genital plate with sixteen acuminate setae; basal pair gradually tapered and slightly curved, slightly larger than remaining setae which are strongly angulate.

Found in northeastern United States and southeastern Canada; rare on Pacific Coast.

ENTOMOBRYOIDES PURPURASCENS (Southern form-B)

Entomobrya purpurascens, 1939, Bueker, Trans. Acad. Sci. St. Louis, **30**(1): 12.

Similar to form A, except as follows: a definite but irregular pattern on trunk. Commonly dark on lateral and posterior edges of meso- and metathorax. Dark median dorsal area of the mesothorax somewhat expanded. First abdominal segment with a posterior line, thickened so as to cover whole of imbricate area at extreme lateral edges, and with an anterior projection mediolaterally. Second abdominal segment with ventral half of lateral area dark, plus a posterior line and median anterior projection, as on first segment. Third segment dark except for a small medioanterior area. Fourth segment with extreme lateral areas dark and median lateral longitudinal dark area running from base of fifth segment to near the anterior border. Fifth and sixth segments entirely black.

Unguis with external tooth no more apical than three-fourths of distance from base of unguis to basal internal teeth.

Found in southern and mid-western United States.

Discussion

The two forms of *E. purpurascens* vary considerably in color and pattern. The southern form may have the fourth abdominal segment dark except for an anterior transverse pale band; the amount of dark on the remaining segments may be increased or decreased. The pigment in these patterns gets gradually lighter as we go northward in the western part of this form's range. The two forms intergrade rather widely in northern Illinois, Michigan, and Iowa (and probably elsewhere, but no records are available), and in these regions the dark coloration on form B is as pale as the normal pigment on form A.

Form A has a lot of color variation, but never has a distinct dark pattern, as does form B except in the region of intergrade. The most common and typical coloration is uniform and pale blue (more rarely violet or yellow-brown), often with scattered white, round to oval to elliptical areas, usually most concentrated on the anterior border of the fourth abdominal segment. The actual pigment is usually in the form of granules whose scattered nature is shown most clearly in a rare color form, where the pigment granules are black and scattered, giving the specimens a gray color. The general pigment may be darker (some deep blue or violet), or almost lacking, giving the specimens a very pale cast of gray, blue or violet.

In addition to these variations, there is considerable variation in the distribution of the color upon the animals. A common variation has very dark lines on the posterior borders of the segments, frequently combined with a pale area on the mid-dorsal region of the thoracic segments. The darker lines may be clearest on the thorax, but in many they are clear on all segments. In such cases the last two abdominal segments, as well as the extreme lateral parts of the fourth segment, are usually dark, but both features can occur independently.

The coloration of the head furnishes many interesting variations, but as far as I can see, they have no correlation with geography. In the first place, there is usually a patch of very dark (usually black) pigment between the antennal bases of the larger specimens. This is most commonly in the form of a band running directly between the antennal bases and sometimes around and behind them. Commonly, particularly on the larger forms, there is a posterior short band projecting from the middle of the transverse dark area. A more universal marking is the pale V-shaped area which opens forward and approaches the eyespots about thee-fourths of the distance back from their anterior margins. Commonly this area has a dark posterior margin, giving the effect of a dark V, and sometimes the anterior margin is also darkened. Rarely, only the anterior margin is darkened. A second common body mark is a dark mark laterally below the middle of the eyespot; this mark has many forms, the most typical being a dark line flanked by pale areas on either side. The dark line is usually slightly thicker at the center and near both extremities, and in some cases has been reduced to three dots located at these three points. The line runs from just below the middle of the eyepatch down to near the ventral edge of the cheek area. Frequently, especially in the pale, uniformly colored specimens and in young specimens, the dark line has disappeared completely, but usually in such cases one or both of the flanking pale areas remains to mark its position. Rarely a band of darker pigment extends from the posterior pale area to the vertex.

The teeth on the unguis vary somewhat. As pointed out in the description, the position of the external tooth usually serves to separate the two forms. There is some variation within each form, but a true approach is found commonly only in the area of color intergradation. The labral papillae are more variable than is usual, each bearing from one to three setae. There is some variation in the structure of the external differentiated seta of the labial appendage (see Pl. 19, figs. 10, 11), but the normal situation (found in 80% of the specimens) is for it to exceed the papilla for one-third to one-fourth of its total length. The mucro may have the apical tooth longer than the anteapical and only slightly curved.

Distribution

Entomobryoides purpurascens form A: *Maine:* Boothbay Harbor, Bailey's Island, Brunswick, Saco, Portland; *New Hampshire:* Pine Mountain, Mount Washington (base); *Vermont:* Brattleboro; *Massachusetts:* many localities; *New York:* many localities; *Pennsylvania:* State College, Bunnel Hill; *West Virginia:* Ridgeville; *Wisconsin:* Hayward; *Minnesota:* Minneapolis; *Washington:* Tampico. *Ontario:* Mattawa, Iron Bridge, Arnprior. Recorded in Europe from *France*,[1] living in houses.

Entomobryoides purpurascens form B: *Florida:* Gainesville, Monticello; *Louisiana:* Tallulah, Norco, Ponchatoula, Harahan; *Missouri:* Ranken; *Texas:* Wheeler County, College Station.

Type locality: Brunswick, Maine, Sept. 10.

ENTOMOBRYOIDES MINEOLA (Folsom)

Plate 20, figs. 1-6

Entomobrya mineola, 1924, Folsom, Amer. Mus. Novitates, **108**:5; 1928, Folsom, Cornell Univ. Agric. Exp. Sta. Mem., **101**:15; 1934, Bonet, Eos, **9**:170; 1944, Gisin, Verh. Naturf. Ges. Basel, **55**:78; 1951, May-

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[1] I have examined cotypes of Denis' species (*subpurpurascens*) and find no differences between it and *E. purpurascens* form A. Since this species has been recorded only from a house and a sewer (unpublished record), and it frequently occurs in houses in this area, it probably has been introduced there.

nard, Collembola New York State :156.
Entomobrya purpurascens, 1951, Wray, Insects of North Carolina, suppl. 2:7, *nec Degeeria purpurascens,* 1873, Packard.

Color and pattern. Background color yellow, sometimes suffused with blue or brown. Pattern purple to black. Dark as follows: Mesothorax through abdominal segment three each with two large irregular mediolateral dark spots, those on the first abdominal segment small and indistinct, and those on third segment triangular, with bases against posterior border of segment. Lateral borders of meso- and metatergites with wide dark border, wider anteriorly. First abdominal segment with medioventral spot, second and third segments each with a pair of ventroposterior elongate spots. Lateral suture bordered with dark. Fourth abdominal segment with a wide irregular dark posterior border; projecting anteriorly from this is a pair of small lateral, longitudinal stripes, reaching halfway to anterior border of segment and anteriorly expanded and then contracted, with a small spot just above expansion. Parafurcular lobe with posteroventral half dark. Fifth segment dark.

Antennae. Normal in shape. Normal with paired rods slightly expanded near base. Clothing of antennae normal, with the longest setae on the second segment less than twice as great in length as the diameter of that segment.

Head very slightly longer than broad. Labral papillae conical, unisetaceous. Labial appendage with external differentiated seta stout, slightly curved, and either barely attaining, or slightly exceeding, apex of same papilla. Eyespots dark, rectangular, shorter than usual, ventroanterior eye on either side somewhat longer than others, which are subequal in size.

Clothing. Body setae as in *E. purpurascens.*

Legs. Unguis with external tooth one-third of distance from base to the level of the internal basal teeth. Remainder of unguis and clothing of legs as in *E. purpurascens.*

Furcula and genital plate as in *E. purpurascens.*

Discussion

This species is extremely close to *E. purpurascens.* The variation is such that only three characters are of any use in separating the two species: the external differentiated seta of the labial appendage, the external tooth of the unguis, and the pattern. The external seta in *mineola* usually barely attains, or does not quite attain, the apex of the same papilla, while in *purpurascens* it usually exceeds the apex for as much as one-fourth of its total length. The external tooth of the unguis is always more basal in *mineola* than in *purpurascens* form A, but intergrades in relative position with the condition found in *purpurascens* form B. The pattern is similarly distinct from the northern form of *purpurascens*, but has a possible series of intergrades with the southern form. The background pigment in *mineola* is frequently washed with darker pigment. This darker pigment can become so dense as to blend in with the pattern, giving very dark, uniformly colored specimens. Such dark specimens would be very similar to the darkest forms of *E. purpurascens* form B. That such forms do occur is shown by specimens from North and South Carolina; these appeared uniformly darkened in alcohol, with only anterior segmental borders pale, but upon clearing, the typical *E. mineola* pattern showed through the dark pigment. Thus in both the claw structure and color pattern, *mineola* seems to blend in with the southern form of *purpurascens* at the southern edge of the former's range. The labial appendage does not give the same picture, because here, while there is some overlap in structure, it is geographically random and very rare in occurrence.

The apparent pattern approach of the two forms may be secondary, because many species show a tendency for increasing dark color with decreasing latitude. If *E. mineola* were a subspecies of *E. purpurascens*, we would be confronted with two subspecies remaining distinct while sympatric, since most of the range of *E. mineola* lies within the range of *E. purpurascens* form A. There are very few specimens of *E. mineola*, for although a large number of collections were seen, each (including the author's) consisted of only a few specimens. Considering all the above facts, I feel that this form should be maintained as a separate species until such a time as sufficient data are available, from statistics or breeding, to prove that such is not the case.

Distribution

Massachusetts: Natick, Dedham, Neponset, Plymouth; *New York:* Long Island (Mineola), Ithaca, Macedon, West Point;

North Carolina: Chapel Hill, Raleigh; *South Carolina:* Georgetown.

Type locality: Mineola, L. I., New York, July 8, 1923. A. Wolf Collection.

ENTOMOBRYOIDES DISSIMILIS (Moniez)

Plate 20, figs. 7-13

Entomobrya dissimilis, 1894, Moniez, Rev. Biol. Nord France, **6**:207; 1923, Denis, Ann. Soc. Ent. France, **92**:228-230; 1934, Bonet, Eos, **9**:162.

Entomobrya purpurascens, 1944, Gisin, Verh. Naturf. Ges. Basel, **55**:72 (*ad partim, nec Degeeria purpurascens*, 1873, Packard).

Color and pattern. Background color white, pigment brown to purple. Antennae purple, darker than body, with apical half of fourth segment pale. Slightly darkened band connects antennal bases. Head pale dorsoposteriorly, with two pale V-shaped marks as in *purpurascens.* Head with numerous oval to round to elongate pale spots. Body with pigment scattered more or less uniformly over all imbricate regions. Pigment slightly denser on posterior margins forming thin dark lines. Numerous pale spots, mostly oval or elliptical, especially concentrated on the dorsum of the mesothorax and the anterior margin of the fourth abdominal segment. Coxae with scattered pigment, femora darkened irregularly on anterior and posterior sides, tibiae, medially darkened. Remainder pale.

Antennae. Normal in shape except that fourth segment is about as thick as third segment. Apical sensory apparatus of third antennal segment typical. Apical sensory organ of second antennal segment atypical, with three very small rods of the internodorsal side; these situated in a diagonal row, decreasing in size outward, with internal one slightly basad of the others: largest rod about one-half as long as third segment rod. In addition to these there are two extremely minute pegs on the externodorsal side. Clothing of antennae normal, except that the first segment has a number of medially slightly swollen, stout, ciliate setae, as well as a few clavate setae similar to, and about one-half as large as, the type one body setae.

Head. About one and one-tenth times as long as broad. Labral papillae conical, low, uni- or bisetaceous, with small setae.

Labial appendage with the external differentiated seta extremely stout, straight or only slightly curved, tapered from base but more strikingly so for apical one-third and exceeding the apex of the same papilla for more than half of the seta's total length. Eyepatches blue-black, rectangular, somewhat elongate and about half as wide as the diameter of antennal base. Anterior ventral eye much larger than others.

Body seen from above elliptical in shape, round in cross-sectional view, some specimens slightly bilaterally compressed (possibly artifact).

Clothing of head and body of usual five types of setae. Setae of type one unusually long and slender, expanded gradually for basal one-fourth of length, slightly and uniformly curved, or sharply bent for apical one-eighth to one-twentieth of length, usually slightly expanded at extreme apex. Setae of type four unusual, ciliate from base, slightly swollen medially, tapering for apical one-third of length. Setae of type five acuminate, coarsely unilaterally ciliate for apical one-half to three-fourths of length.

Legs. Clothing typical, with very finely ciliate setae of tibiotarsus subequal in diameter to largest coarsely ciliate setae of same segment. Trochanteral organ typical, with numerous internal setae, the median three of these being strikingly longer than remainder and about one-half as long as the apical seta of the arms. Unguis with basal internal teeth unusually large and not opposite in position. One basal tooth is unusually much larger than the other and twice as great as the median internal tooth, which in turn is about twice as large as the small apical tooth. Most basal tooth at, or slightly above, level of external tooth, which is basad of lateral teeth. Lateral teeth about four-fifths of the way from base of unguis to most basal internal tooth. Empodial appendage acuminate, ciliate along internal edge.

Furcula and genital plate. Mucro unusually long, apical tooth much greater than anteapical, projecting posteriorly for considerable length beyond anteapical, then curved upward sharply and abruptly. Genital plate of from fourteen to sixteen setae, basal setae acuminate, slightly curved, distinctly longer than remaining setae, which are angulate, almost straight, and subequal in size.

Discussion

This species was originally described from a set of specimens taken from ant nests in Washington, D. C., by Pergande. Although I have not seen the type specimens of this species, the complete redescription and figures published by Denis (1923) permit a good identification. I have rarely found this species outside of ant nests, and this distribution plus the peculiar nature of the unguis and leg structure lead me to the belief that the species may be synonymous with the European *Entomobryoides myrmecophila* (*Sinella* or *Entomobrya*, Auct.). This species has been described as lacking an apical internal tooth on the unguis and with unciliated empodial appendage; no mention has been made of a peculiarly-shaped mucro. For these reasons I feel it wise to maintain this species as separated from *E. dissimilis* until a comparison is possible.

E. dissimilis is closely related to *E. guthriei*, but can usually be distinguished by the expanded basal tooth of the unguis or the abruptly upcurved apical mucronal tooth. The adult males can always be distinguished on a basis of the genital plates.

The color may be blue (common in young specimens), gray, purple, or, (as described) brown. There is never any distinct pattern on the body, although the dorsum of the second segment occasionally has a distinct pale median area. The unguis varies greatly, especially in the size and positions of the basal teeth, every condition being present between specimens with the basal teeth greatly unequal in size and one positioned far above the other, to specimens with the teeth of equivalent size and opposite in position. The mucro varies slightly, tending to lose the angulate upbending of the apical tooth in smaller specimens. The external differentiated seta of the labial appendage can exceed the apex of the same papilla for as much as four-fifths of its length, always for at least one-half of its length, and can be distinguished readily from *E. purpurascens* on the basis of this character alone. The genital plate of the male is very similar to that found on *E. purpurascens*, differing only in having the lateral and apical setae slightly straighter.

Distribution

Washington, D. C. (in nests of *Aphaenogaster fulva* and *Crematogaster lineolata*); *West Virginia:* Ridgeville (in ant nest — species unidentified); *Virginia:* Hightown (under bark); *Pennsylvania:* Cooperstown (in nest of *Formica* sp.), Bunnel Hill (in ant nest — species unidentified); *Massachusetts:* Medford (in nest of *Tetramorium caespitum*).

Type locality: Washington, D. C. Pergande Collection.

ENTOMOBRYOIDES GUTHRIEI (Mills)

Plate 21, figs. 1-13

Entomobrya guthriei, 1931, Mills, Amer. Mus. Novitates, **464**: 4, 5; 1934, Bonet, Eos, **9**:165; 1944, Gisin, Verh. Naturf. Ges. Basel, **55**:75.

Color and pattern. Background color white or pale yellow, with pigment of black to blue color, scattered in fine granules over body surface, leaving numerous small, pale, oval to round areas. Antennae slightly darker than body, interantennal band somewhat darker than rest of body. Pale double V-shaped mark present on head, as in *E. dissimilis.*

Antennae. Typical, fourth segment elongate, about as thick as third segment. Apical organ of third segment typical. Second antennal segment apical sensory organ of three internodorsal rods, and two externodorsal pegs. Clothing of antennae normal, first segment with many setae similar to, but smaller than, the type one body setae. Second segment with several unusually short, stout, acuminate setae, tapered for apical half of length.

Head. About one and one-fifth times as long as broad. Labral papillae basally hemispherical, apically conical, uni- or bisetaceous, with small unclear setae. Labial appendage typical, external differentiated seta stout, curved, and exceeding apex of same papilla for from one-third to one-half of length. Eyespots small, black, elongate, about as wide as base of antenna. Eyes small in size, scattered, anterior pair on either side slightly larger than others.

Clothing of head and body of the usual five kinds of setae. Setae of type one are long, slender, sharply expanded just above point of insertion. Setae of type four ciliate for all but basal one-tenth to one-eighth of length and tapered for apical half. Setae of type five uniformly tapered and coarsely, mostly unilaterally, ciliate for apical one-half to two-thirds.

Legs. Clothing typical, with the finely ciliate "smooth" setae on the internal surface of the tibiotarsus distinctly thicker than the coarsely ciliate setae of same segment. Trochanteral organ with many internal setae, most of them less than one-third as long as apical seta of arms. Unguis tapered from base, with typical number of teeth, unusual in that the median internal tooth is often strikingly larger than the others. The unguis has the apical internal tooth much smaller than the basal internals. Empodial appendage acuminate, ciliate along internal edge.

Furcula and genital plate. Mucro with apical tooth usually somewhat longer than anteapical. Genital plate with all setae straight or slightly bent. Basal setae, or basal and parabasal setae, may be much thicker than remainder.

Variation

Unlike most Entomobryini, much of the variation in this species is geographic. It is not congruent for the different characteristics concerned and therefore does not readily lend itself to subspecific interpretation.

Color: from a blue to gray to almost white. The gray forms largely limited to the northern and central Rockies (Montana, Wyoming and Colorado), and darkest blue forms are found in the eastern extensions of the range. Pacific coast specimens tend to be paler (palest forms here), although occasional dark forms are also found.

Genital Plate: Here the differences are more discrete and in fact follow a clear-cut subspecific distribution. There are three forms: (1) with two thickened basal setae on each side, (2) with one such, and (3) without thickened setae (Pl. 21, figs. 1, 2 and 3 respectively). Type (1) occurs only in the Pacific Northwest and adjacent western areas — i.e., Oregon, Washington, British Columbia, northern Idaho and northwestern Montana. Type (2) is the most widespread, covering most of the western mountain states and California, at least as far north as San Francisco. The third form has only been taken from a few areas in Colorado, and one in Louisiana. Where forms (1) and (2) meet in Montana extensive integradation occurs, but no collections have as yet been seen from areas where form (3) meets other forms.

Mucro: The variation of this organ is considerably more complex. In the first place the apical tooth is largest (in comparison to anteapical) in forms from the eastern central part of the species range (Colorado), and going southwest and northwest from this there is a striking but irregular reduction in the tooth until in southern California and British Columbia forms frequently occur which have the teeth subequal in size. Superimposed upon this is a considerable change in the degree of upturning of the apical tooth, with the forms from the northeastern part of the range tending to have apical teeth more strikingly upturned than the other areas. All of the above mentioned phenomena represent tendencies only, and a few members of any of the described variations may be found in almost any region.

Unguis: This represents the most complex picture of all, because here there are two sets of apparently independent variables. The first of these is the internal teeth, which may be normal in size or have the median tooth variously elongate (see Pl. 21, figs. 4-7). In addition to this the external tooth may vary in position from basad of the level of the basal internal to well distad of the same. The occurrence of normal internals (Pl. 21, fig. 7) is apparently at random and rare. The largest median teeth occur in the northeastern part of the animal's range, but long teeth occur occasionally elsewhere. The external tooth level varies in all parts of the range but in the northwestern region the distal condition is almost exclusive, while in California the basal condition is very frequent. In all other regions both conditions occur with the distal being more common.

Labium: The external differentiated seta of this organ varies from having its tip as in *E. purpurascens* barely exceeding the apex of the same papilla, to conditions where it exceeds this for more than half of its entire length. The former condition is dominant and extreme only in southern California. Intermediate stages (Pl. 21, fig. 13) occur in most of the species range and the opposite extreme (Pl. 21, fig. 12) is most common in the extreme northwestern part of the range.

In addition to these geographical variations, the species has the normal growth variations in ratio and structure of the trochanteral organ, etc. The shape of the eyepatch also varies a great deal, but apparently at random within a given population.

The species was first described from a termite nest in California, but has not since been taken with termites, although it is occasionally found in ant nests. This wide-ranging western species replaces *E. purpurascens,* but does not intergrade with this species in Washington or Louisiana where both species occur commonly.

Distribution

Alberta: Banff; *Arizona:* Mount Graham; *British Columbia:* Chase; *California:* Gasquet, Berkeley, San Francisco, Los Angeles, San Luis Obispo, Santa Monica Mts., Westwood; *Colorado:* Monarch Pass, Cochetopa, Ward; *Idaho:* Moscow; *Louisiana:* Clarence; *Montana:* Philipsburg, Butte, Riceville, Harlowtown, Babb, Essex, West Yellowstone; *Oregon:* Corvallis; *South Dakota:* Deadwood, Wall, Rapid City, 40 mi. W. Rapid City; *Utah:* Bear River, Uinta Mountains, Butterfly Lake; *Washington:* Puyallup, Winton; *Wyoming:* Snowy Range Pass, Jackson Hole.

Type locality: Berkeley, California, from captive termite nest.

CALX new genus

Genotype: Entomobrya (Drepanura) sabulicola, 1931, Mills, Amer. Mus. Novitates, **464**:7-9.

General body form as in *Entomobrya.* Antenna with distal bulb double for whole length and distinctly subapical in position. Second and third antennal segments with a single line of small pegs, oval in shape and two to three times as long as broad.

Labral papillae with outer pair low, rounded and nonsetaceous. Labial appendages lacking any clearly differentiated seta.

Clothing of body and legs as in *Entomobrya.* Trochanteral organ lacking a ventral arm and with the posterior arm irregular in form.

Unguis with basal internal teeth three-fourths of distance from base to apex of claw. Internal edge of claw and of empodial appendage, finely ciliate.

Furcula with deep crenulations ending abruptly. Mucro without basal spine or anteapical tooth. Male genital plate with fourteen short, acuminate setae, subequal and similar.

Discussion

This genus is so strikingly distinct from all other Entomobryini as to be of doubtful relationship. Many of the peculiar characteristics (e.g., simple male genital plate) indicate a primitive condition, and it is possible that the genus is the closest existing form to the ancestral Entomobryini. There are no clearly related forms, but the *E. bicolor* group of the genus *Entomobrya*, the genus *Drepanura*, and the genus *Mesentotoma* all have some peculiar structures in common with this group.

There is one Nearctic species — *Calx sabulicola.*

CALX SABULICOLA (Mills)

Plate 22, figs. 1-13

Entomobrya (Drepanura) sabulicola, 1931, Mills, Amer. Mus. Novitates, **464**:7-9; 1934, Bonet, Eos, **9**:157; 1944, Gisin, Verh. Naturf. Ges. Basel, **55**:71.

Color and pattern. Background gray to dull yellow. Pigment dark blue or purple as follows: antennae moderately and uniformly dark, bases and connecting band blue black. An irregular band below eyepatches to posterior margin, continued forward as an irregular series of dots. Prothoracic leg bases and lateral edges of meso- and metatergites darkened. Metathorax with an irregular pair of mid-dorsal dark spots. First abdominal segment with lateral specks, and area above ventral tube darkened. Second and third segments each with large spot near anterior borders below lateral suture, and each has a mid-dorsally broken irregular median transverse band. Fourth segment with a posterior transverse band along the posterior margin of the segment, and a pair of spots below this projecting forward. Fifth segment with a posterior transverse band. Coxae of legs with pigmented blotches, remainder slightly darkened.

Antennae. Basal three antennal segments subcylindrical in shape and subequal in diameter, third segment slightly expanded apically. Apical bulb double, distinctly subapical. Apical sense organ of third segment of two small rods, less than half as thick as neighboring large ciliate setae, in deep individual fossae located in a large shallow depression. Second and third segments with a single line of oval pegs along ventrointernal margin, about as thick as neighboring ciliate setae, and three times as long as broad.

Head. Oval, about one and one-half times as long as broad. Outer labral papillae low, rounded and unsetaceous. Labial appendages lacking any clearly differentiated external seta.

Clothing. Normal five types of setae present. Type one very broad, sharply expanded basally, slightly so at apex. Setae of type five acuminate for apical two-thirds of length, slightly expanded medially. Coarsely multilaterally ciliate for apical one-half to two-thirds of length.

Legs. Trochanteral organ irregular, with a few scattered large setae. Basal internal teeth of unguis three-fourths of distance from base to apex, and internal edge of unguis ciliate to this point. Empodial appendage acuminate, ciliate along internal edge.

Furcula and genital plate. Furcula with extremely deep dental crenulations ending abruptly. Mucro with tooth heavy and short. Genital plate of male with fourteen short setae of similar shape. All are acuminate.

Discussion

The pattern shows great variation, but this is apparently of a population rather than a geographic nature. The types are difficult to describe (see figures), but in general there is a wide variety of irregular lighter or darker spots, which rarely have any degree of regularity.

This species is of great ecological interest in that it occurs in the driest habitats of any known Entomobryini, having been taken in the middle of desert regions in spots of very slight moisture. An investigation of the water requirements of the species might be most rewarding.

Distribution

Texas: College Station, Waco; *Arizona:* Benson, Globe; *Colorado:* Campo; *Wyoming:* Sandy Hat; *Oregon:* "Southern Oregon."

Type locality: Bryan, Texas, November 1930.

Genus MESENTOTOMA Salmon

Entomobrya, 1913, Bacon, Journ. Ent. Zool. Claremont, Calif., **5**:202-204.
Mesentotoma, 1942, Salmon, Rec. Domin. Mus., Wellington, **1**(1):55-60.
Genotype: Mesentotoma exalga, 1942, Salmon, *loc. cit.*

General body facies as in *Entomobrya.*

Antennae with apical retractile bulb, fourth (and sometimes third) antennal segments with definite signs of subsegmentation or ringing. All setae of third and fourth segments shorter than diameter of segment. First and second antennal segments with long clavate setae, similar to, but shorter than, those of the body.

Large clavate setae of body comparatively greatly expanded apically, unilaterally produced to a narrow acuminate tip.

Unguis without external teeth, with a pair of small to large lateral teeth, a pair of large basal internal teeth, and with or without a small median single internal tooth. Empodial appendage strikingly and uniformly expanded for basal half, acuminate for distal half, with internal face strongly concave.

Mucro lacking basal spine, bidentate, with apical tooth strikingly longer than anteapical. Habitat littoral.

Discussion

Many of the peculiar characteristics of this genus are modifications for littoral life. For example, in the case of the form of the empodial appendages and ungues, for we find almost exact duplicates of this condition in the littoral genera *Actaletes* and *Archisotoma*. In the case of the other peculiar common structures, i.e., clavate hairs, lack of basal mucronal spine, shape of mucro, lack of antennal bulb, general body facies, and long type one setae on first and second antennal segments, the resemblance appears to indicate true relatedness.

There is one Nearctic species, *M. laguna* (Bacon).

MESENTOTOMA LAGUNA (Bacon)

Plate 23, figs. 8-12

Entomobrya laguna, 1913, Bacon, Journ. Ent. Zool. Claremont, Calif., **5**:202-204; 1934, Bonet, Eos, **9**:157; 1942, Essig, College Entomology :83; 1944, Gisin, Verh. Naturf. Ges. Basel, **55**:71.

Color and pattern. Pigment gray-brown to gray-blue except for appendages which are always blue. Pigment generally distributed over body except for mid-region of venter. Many small pale spots scattered over body. Head with a double V-shaped pale mark running from the posterior corner of each eye to the mid-posterior head region. Irregular pale areas occur on the dorsum of the fourth segment and all intersegmental membranes are pale.

Antennae. Apex of fourth segment with four or five flat knobs. Largest setae of antennae similar to but shorter than type one setae of body. Second antennal segment with a distinct subsegment, or a partial suture.

Head. Labial appendage with external differentiated seta slightly expanded subapically.

Clothing. Setae of type one unusually long (longest longer than antennae). Setae of type two few, situated only on ventral and lateral regions of abdomen. Setae of type four slightly expanded apically.

Discussion

Only a few specimens have been examined. The most striking variation concerns the color. The subsegment of the second antennal segment may be indistinct or incomplete. The knobs on the apex of the antennae may be very small or indistinct. Bacon illustrates an external tooth on the empodial appendage, but this was not visible on any specimen I examined.

Distribution

California: Palos Verdes (under submerged rocks), Laguna Beach (lower tide zone, under rocks).

Type locality: Laguna Beach, California, under stones, July-August, 1912, Bacon Collection.

Genus HOMIDIA Börner

Homidia, 1909, Börner, Sitz. Ges. Naturf. Freunde, (2):101-103.
Genotype: Homidia sauteri, 1909, Börner, *loc. cit.*

Similar to *Entomobrya* in facies, ratios of body, and structure of the setae. Heaviest setae are more strongly clavate than is typical for that genus. Antennae usually (always?) with two small, closely packed apical bulbs on each fourth antennal segment, located in a single deep apical pit. Subapically on the dorsum of the fourth antennal segment there are usually (always?) several thick, elliptical, thin-walled, short setae, much thicker than other setae on the segment, in addition to typical smooth ciliate setae found in *Entomobrya*.

The unguis and empodial appendage have normal lamellae and teeth, except that the apical inner tooth is lacking (or so minute as to be invisible with normal microscopic procedure). The furcula is much as in *Entomobrya*, except for a number of dental spines along the basal portion of the dorsointernal edge of dens. These vary somewhat in shape, but are usually considerably thicker and shorter than the normal setae of furcula, and are finely striate. The mucro has the subapical tooth considerably larger than the apical one, which is directed forward (rarely slightly upcurved at apex). The uncrenulated portion of the dens is always subequal in length to, or shorter than, the mucro.

Discussion

This genus appears to be very well delimited. From the descriptions and figures available, it appears to be quite homogeneous. Those characters in the diagnosis above, which are given as "usually (always?)," are present in the species examined, but it is not known whether or not they are present in the other species. The genus is related to the *Entomobrya bicolor* group of the genus *Entomobrya*, but also appears to be somewhat distantly connected with the subfamily Paronellinae.

Only one species is known so far from the Nearctic, and that is *Homidia sauteri*.

HOMIDIA SAUTERI Börner

Plate 23, figs. 1-7

Homidia sauteri, 1909, Börner, Sitz. Ges. naturf. Freunde, (2):101-103.
Entomobrya (Homidia) sauteri, 1934, Bonet, Eos, **9**:155; 1944, Gisin, Verh. Naturf. Ges. Basel, **55**:71.

Color and pattern. Background color orangish yellow. Pigment blue-black to purple-brown as follows: apical one-third and external line on third segment and all of remaining antennal segments dark. Thin black line around antennal bases and wide dark band connecting bases and running back over anterior half of area between eyepatches. Slight irregular darkening ventral of eyepatches. Anterior margin of mesothorax and anterior halves of leg bases irregularly darkened. Metathorax with irregular scattered pale spots. Second abdominal segment with mediolateral dark spot on either side, ventrally washed with blue. Most of third segment dark. Fourth segment with two narrow broken transverse bands of dark, one at midsegment. A second, at posterior margin, is continued on parafurcular lobes where it is slightly expanded. Fifth segment dark except for two medioanterior semicircular, pale spots. Sixth segment dark. Metathoracic femora each with a lateral external dark stripe for apical half of length, expanded apically. Mesothoracic femora with apices internally black. Remainder pale.

Antennae. Segments cylindrical, subequal. Apical organ of third segment of two large elliptical rods, definitely thicker than neighboring ciliated setae, about seven times as long as wide, situated in individual shallow folds, with a small peg beside each. Apical organ of second segment of three pegs, largest twice the size of third segment.

Head. Seen from above elliptical, one and two-fifths as long as broad. Labral papillae blunt, rounded, lacking setae. Labial appendages with external differentiated seta small, three-fourths as wide as longest normal seta of same papilla, smoothly tapered, and only attaining two-thirds of distance from base of seta to apex of same papilla.

Body. Seen from above elliptical, not compressed.

Clothing. Typical five types of setae. Type one long, abruptly and greatly expanded at apex, and strikingly bent. Setae of type five slender, multilaterally ciliate for four-fifths of length.

Legs. Tibiotarsus internally with four to six very large ciliate setae, swollen just above point of insertion and then gradually tapered toward apex, more than three times as thick as remaining setae. Trochanteral organ atypical, with a dorsal triangular group of setae, mixed short and long, separated from a ventral row of very long setae by a double row of short stout setae. Unguis with external side strikingly curved. All teeth large and subequal. Empodial appendage normal, acuminate, that of prothoracic legs smaller in comparison to corresponding unguis than those of meso- and metathoracic legs.

Furcula and genital plate. Dental spines thirty-two, the basal two on either side thinner and longer than remainder. Genital plate not seen.

Discussion

On some of the specimens the median transverse band on the fourth segment is reduced to a series of spots, and on others the basal portions of antennal segments two and three are pale. The number of setae on the trochanteral organ decreases in the smaller specimens. On a few specimens the apical bulbs on the fourth antennal segment have apical indentations. The external differentiated setae of the labial appendages may be as long as three-fourths of the distance from the base of the seta to the apex of the same papilla. The number of the dental spines varies most strikingly, the smallest number 18 (specimen length 1.6 mm.), the largest 53 (specimen length 2.7 mm.).

Borner's short description is insufficient, but Denis' redescription under the variety *sinensis* (1929) is so complete that I feel certain of a very close relationship between the Nearctic specimens here described and the Oriental species. It is entirely possible that this has been introduced into North America, but the localities of collection lend no support to such a thesis.

Distribution

Louisiana: Harahan, Norco.
Type locality: Yokohama, Japan, 1909.

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INDEX

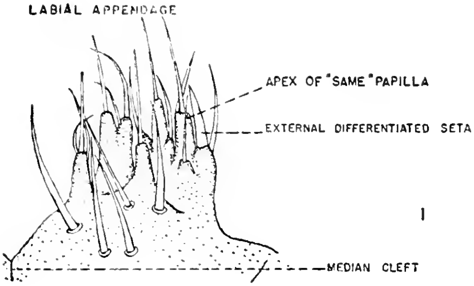
Italicized pages refer to descriptions and distributions.

PLATES

Plate 1

All figures of organs important for the identification of members of the genus *Entomobrya*.

1. Typical left labial appendage, seen from below.
2. Typical habitus showing location of parafurcular lobe, lateral suture, and male genital plate. Lines indicate method of limitation for segmental measurements.
3. Labral papillae of type seen in *nivalis* group.
4. Typical empodial appendage, semi-diagrammatic.
5. Typical unguis, semi-diagrammatic.
6. Head, ventral view, showing location of labral and labial papillae.
7. Typical trochanteral organ showing location of different types of setae referred to in text.



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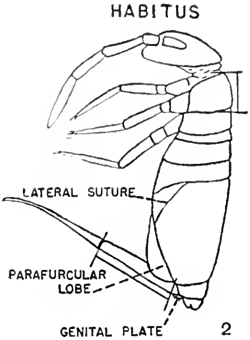

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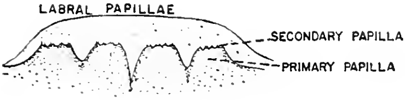

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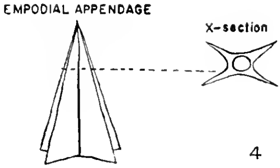

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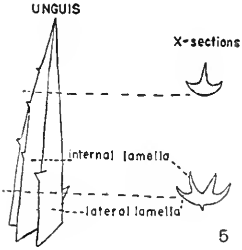

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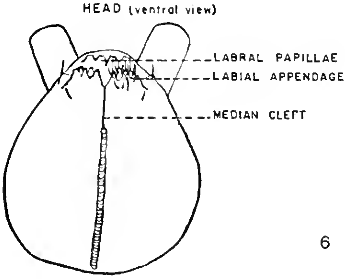

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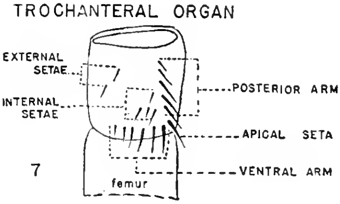

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PLATE 1

Plate 2

All figures of *Entomobrya nivalis* (Linné).

1. Habitus, x 48
2-8. Patterns on specimens taken from one locality on one date, x 38 (approx.).
9, 10. Specimens from same locality taken on different dates, x 38 (approx.).
11. Male genital plate, ventral view, x 445.
12. Right labial appendage, seen from below, x 1010.
13. Right hind unguis and empodial appendages, x 1120.
14-16. Left mucrones, lateral view, x 1150.
17. Body setae, type five, x 1000 (approx.).
18. Labral papillae, seen from below, x 1000 (approx.).

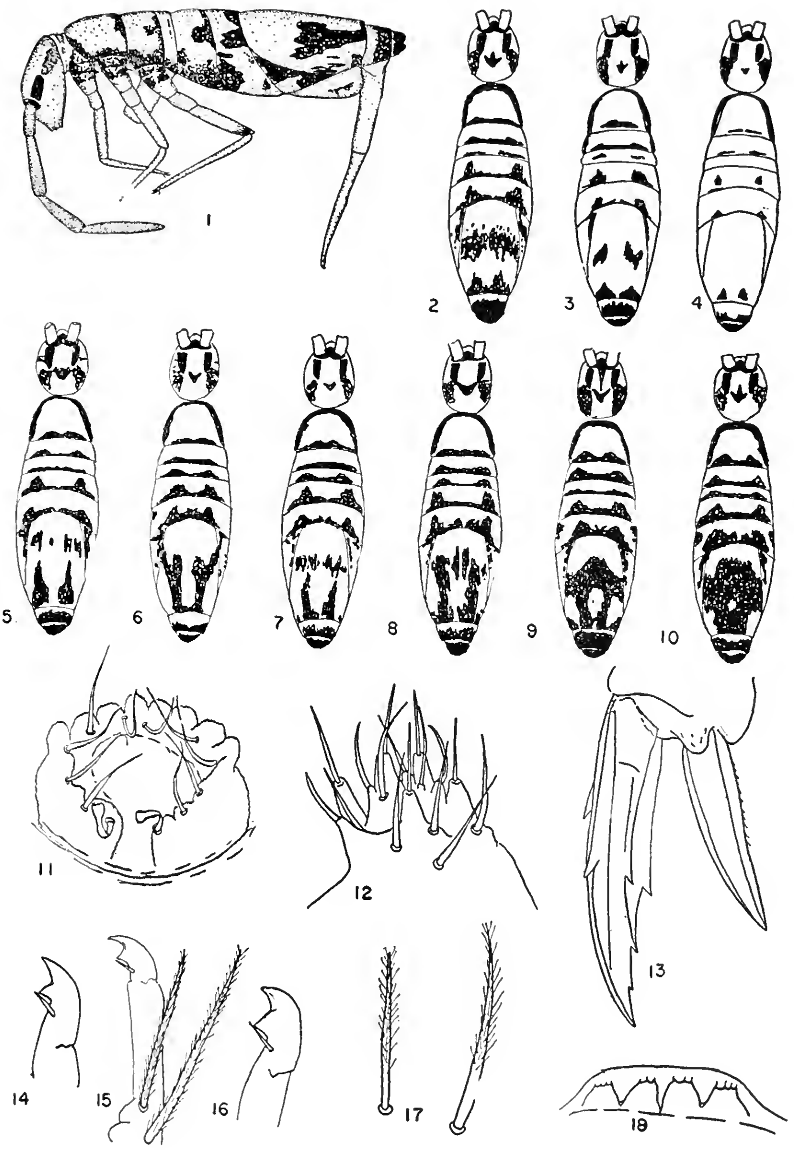


PLATE 2

Plate 3

All figures of *Entomobrya atrocincta* Schött.

1. Habitus, x 80.
2-5. Patterns on specimens from California, x 45 (approx.).
6. Right half of male genital plate, ventral view, x 800 (approx.).
7. Left hind unguis on different specimen, turned to show both basal internal teeth, x 1000 (approx.).
8. Left hind unguis and empodial appendage, x 1000 (approx.).
9. Left trochanteral organ, x 1000 (approx.).
10. Variation in mucronal shape (all specimens from Calif.), x 1000 (approx.).
11. Body setae, type five, x 1580.
12. Labral papillae, seen from below, x 1240.

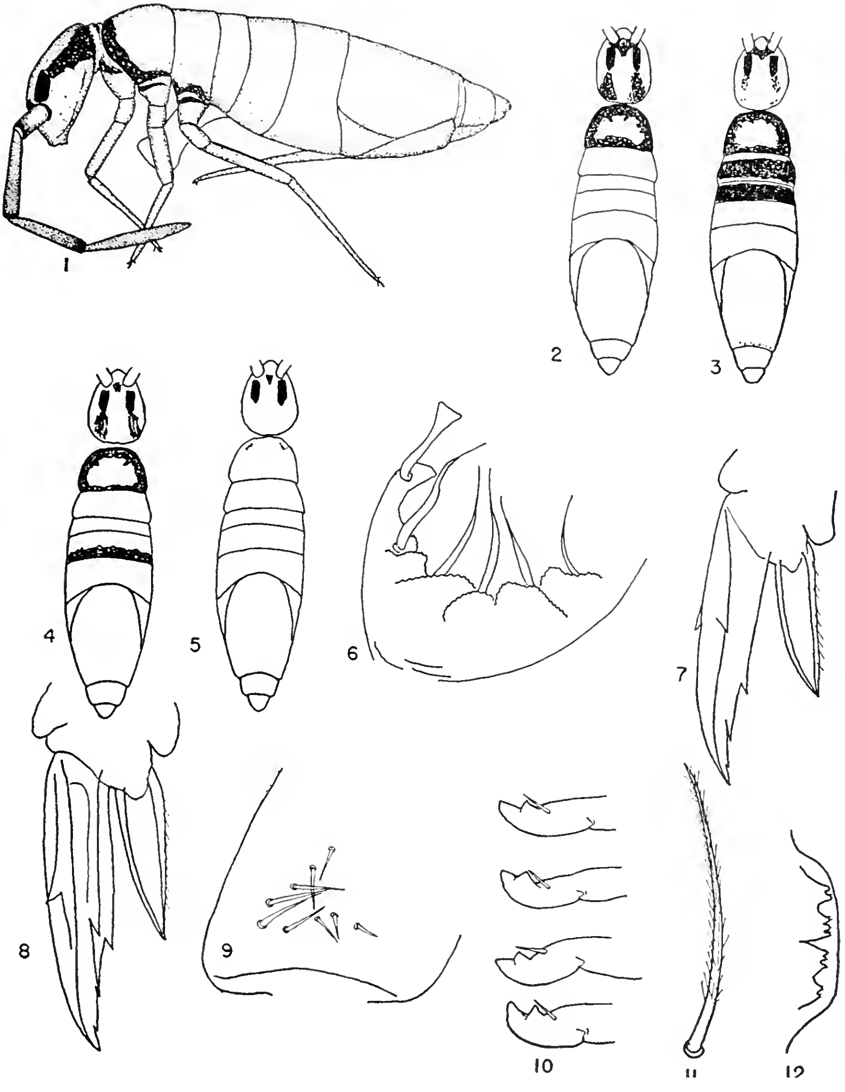


PLATE 3

Plate 4

All figures of *Entomobrya griscoolivata* (Packard).

1. Habitus (part of legs and furcula omitted), x 40.
2-5. Pattern on dorsum of heads of specimens from one locality.
6. Right half of male genital plate, ventral view, x 1200.
7. Three pairs of basal setae of above organ, showing variation, x 1200.
8-12. Ends of right dentes and mucrones, x 1500 (approx.).
13. Left hind unguis and empodial appendage, x 1340.
14. Left trochanteral organ, x 1000 (approx.).
15. Labral papillae, seen from below, x 1280.

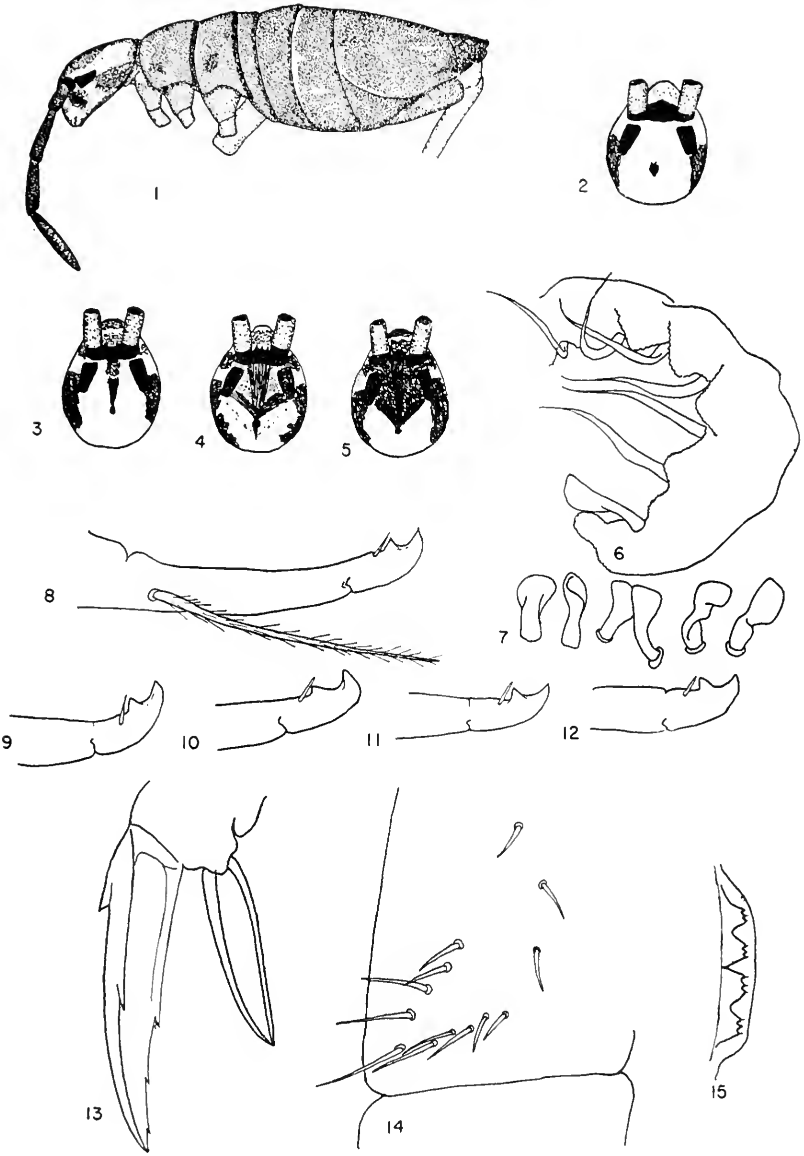


PLATE 4

Plate 5

All figures of *Entomobrya unostrigata* (Stach).

1. Habitus, x 60.
2-5. Pattern variation, all specimens from one locality x 25 (approx.).
6. Right half of male genital plate, lateral view, x 940.
7. Left hind unguis and empodial appendage, x 1540.
8, 9. Left mucrones, x 1300.
10. Heavy seta from internal surface of tibiotarsus, x 1540.
11. External papilla of left labial appendage, x 1000 (approx.).
12. Right trochanteral organ, x 800 (approx.).
13. Labral papilla, seen from below, x 1300.

PLATE 5

Plate 6

All figures of *Entomobrya assuta* Folsom.

1. Habitus, x 47.
2. Pattern on specimen from Massachusetts, x 35 (approx.).
3. Pattern on specimen from Iowa x 35 (approx.).
4. Pattern on specimen from New York, x 35 (approx.).
5. Pattern on specimen from Utah, x 35 (approx.).
6. Pattern on specimen from Massachusetts, x 35 (approx.).
7. Left hind unguis and empodial appendage, x 1500.
8. Male genital plate, seen from front and slightly below, x 1000 (approx.).
9. Right mucro, x 1300.
10. Labral papillae, seen from below, x 1000 (approx.).

11, 12. Patterns on specimens from Louisiana, x 35 (approx.).

13. Male genital plate, ventral view (anterior papillae and setae foreshortened), x 1000 (approx.).

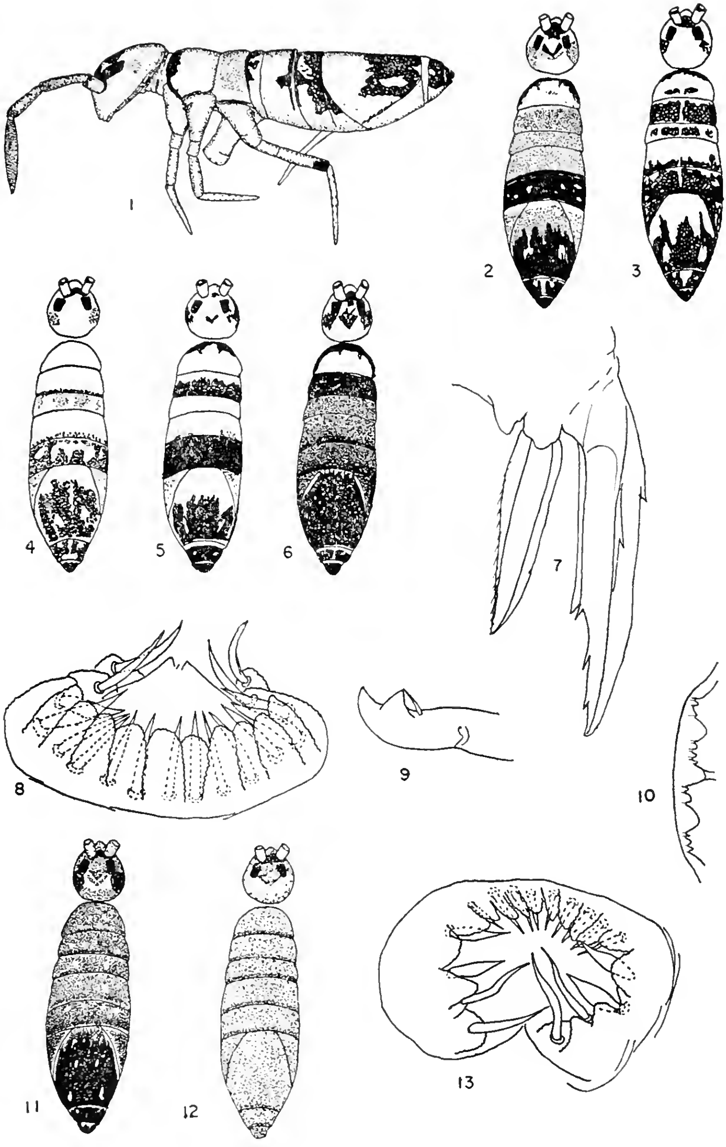


PLATE 6

Plate 7

All figures of *Entomobrya comparata* Folsom.

1. Habitus Taiga pattern, x 60.
2. Pattern on specimen from Colorado, x 30 (approx.).
3. Pattern on specimen from Idaho, x 30 (approx.).
4. Pattern on specimen from New Hampshire, x 30 (approx.).

5-7. Intermediates between taiga form and tundra form from Grinnell Glacier, Montana, x 30 (approx.).

8. Pattern on specimen from Colorado, x 30 (approx.).
9. Right hind unguis and empodial appendages, x 1400.
10. Same, from small specimen, x 1400.
11. Tip of right fourth antennal segment, x 935.
12. Body seta, type one, x 460.
13. Body seta, type five, (a) x 460, (b) x 1400.
14. Another seta of type five, x 1400.
15. Male genital plate, ventral view, x 860.
16. Left mucrones, (a) x 650, (b) and (c) x 1300.
17. External papilla of right labial appendage, x 1000 (approx.).
18. Labral papillae, x 1000 (approx.).

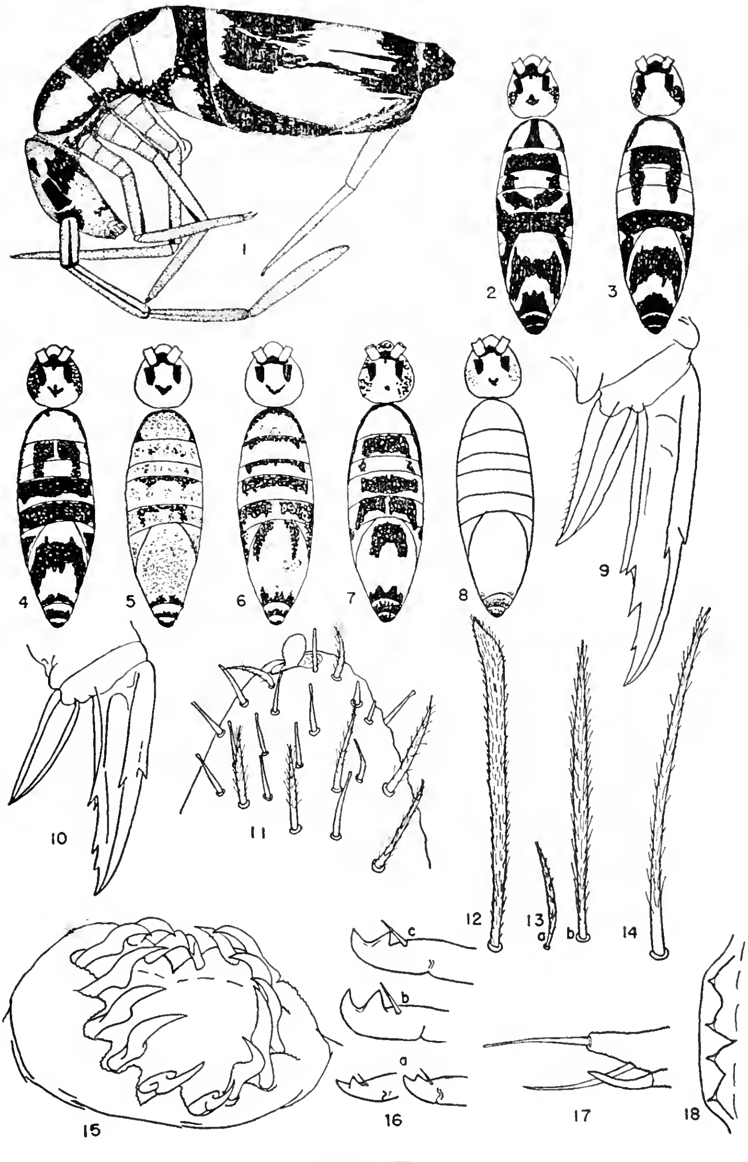


PLATE 7

Plate 8

All figures of *Entomobrya clitellaria* Guthrie.

1. Habitus, x 45.
2. Pattern variation, specimen from Massachusetts, x 40 (approx.).
3. Pattern variation, specimen from Iowa, x 40 (approx.).
4. Pattern variation, specimen from New York, x 40 (approx.).
5. Pattern variation, specimen from Ontario, x 40 (approx.).
6. Pattern variation, specimen from New York, x 40 (approx.).

7-8. Left hind unguis and empodial appendages, x 1250.

9. Male genital plate, ventral view, x 780.
10. End of left dens and left mucro, x 1000.
11. Apical organ of third antennal segment, x 1200.
12. External papilla of right labial appendage, x 1000 (approx.).
13. Body setae, type five, x 1500 (approx.).
14. Labral papillae, seen from below, x 1200.

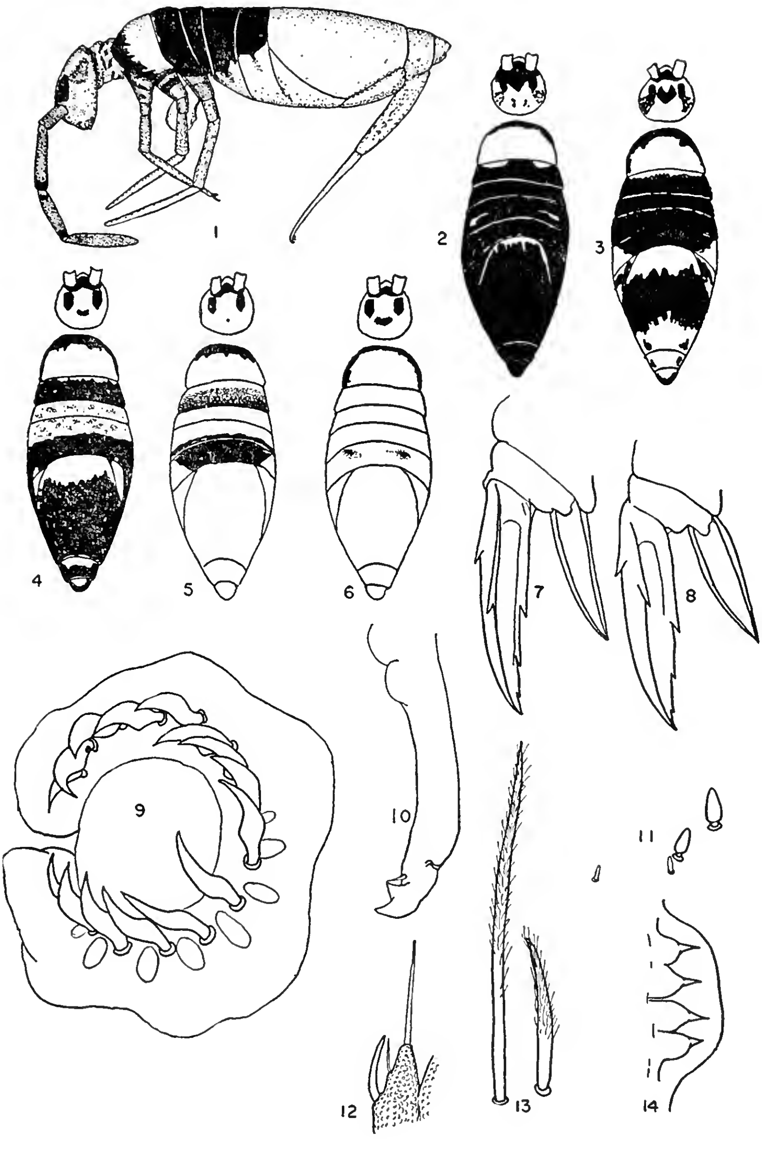


PLATE 8

Plate 9

Figures 1-8 of *Entomobrya kincaidi* Folsom.

1. Male genital plate, ventral view, x 970.
2. Body setae, type five, (a) normal, (b) slightly twisted, x 1000.
3. Similar seta, seen from different angle, x 1000.
4. Differently shaped seta of type five, x 1000.
5. Body seta, type two, x 900.
6. Hind unguis and empodial appendage, x 1200.

7, 8. Left mucrones, x 150.

Figures 9-16 of *Entomobrya troglodytes* n. sp.

9. Right half of male genital plate, ventral view, x 1000.
10. Left hind unguis and empodial appendage, x 1280.

11, 12. Left mucrones, x 1280.

13. Labral papillae, seen from below, x 1000 (approx.).
14. External papilla, right labial appendage, x 1350.
15. Apical sensory organ of left third antennal segment, x 1500 (approx.).
16. Same, of second antennal segment, x 1500 (approx.).

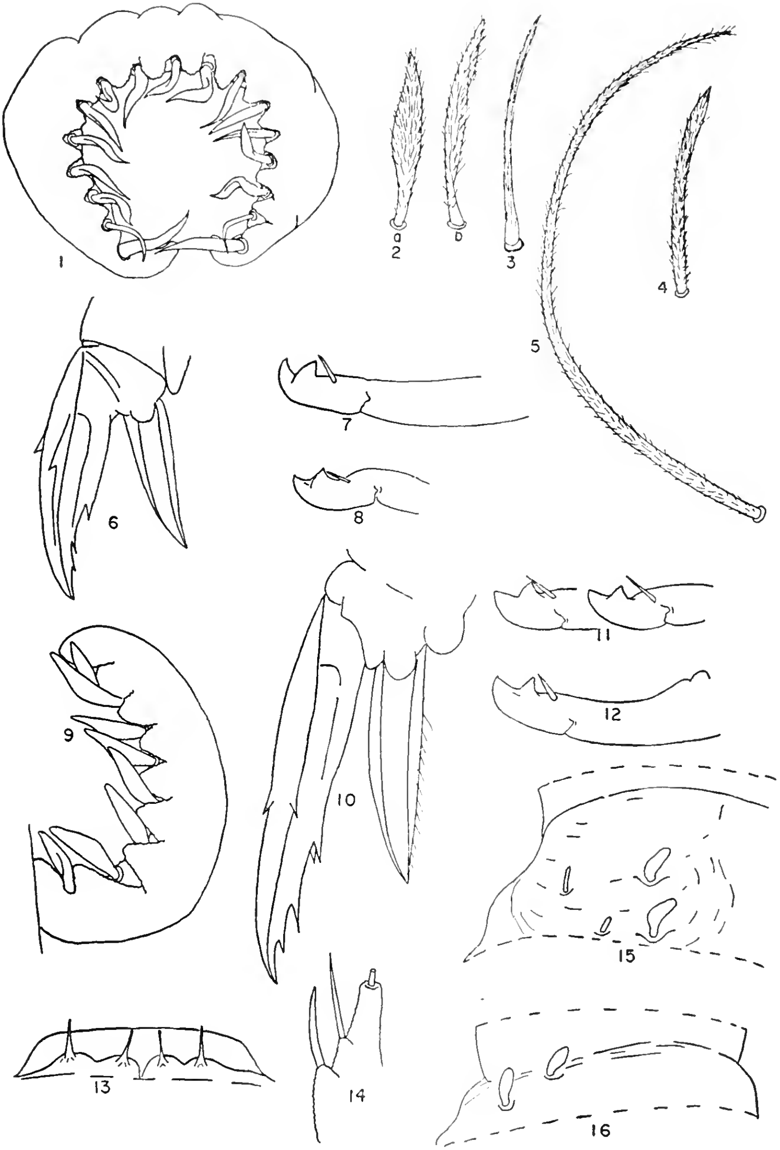


PLATE 9

Plate 10

All figures of *Entomobrya triangularis* Schött.

1. Habitus, x 46.
2-8. Pattern variations, same locality, same date, x 30 (approx.).
9. Hind unguis and empodial appendage, x 1480.
10. Hind empodial appendage, x 1480.
11. Hind empodial appendage and unguis of small specimen, x 1400.
12. Right mucrones of three specimens, x 1480.
13. External papilla of right labial appendage, x 1000 (approx.).
14. Right half of male genital plate, ventral view, x 630.
15. Left half of another male genital plate, lateral view, x 630.
16. Right trochanteral organ, setae omitted (*a* is apical seta), x 720.
17. Labral papillae seen from below, x 940.

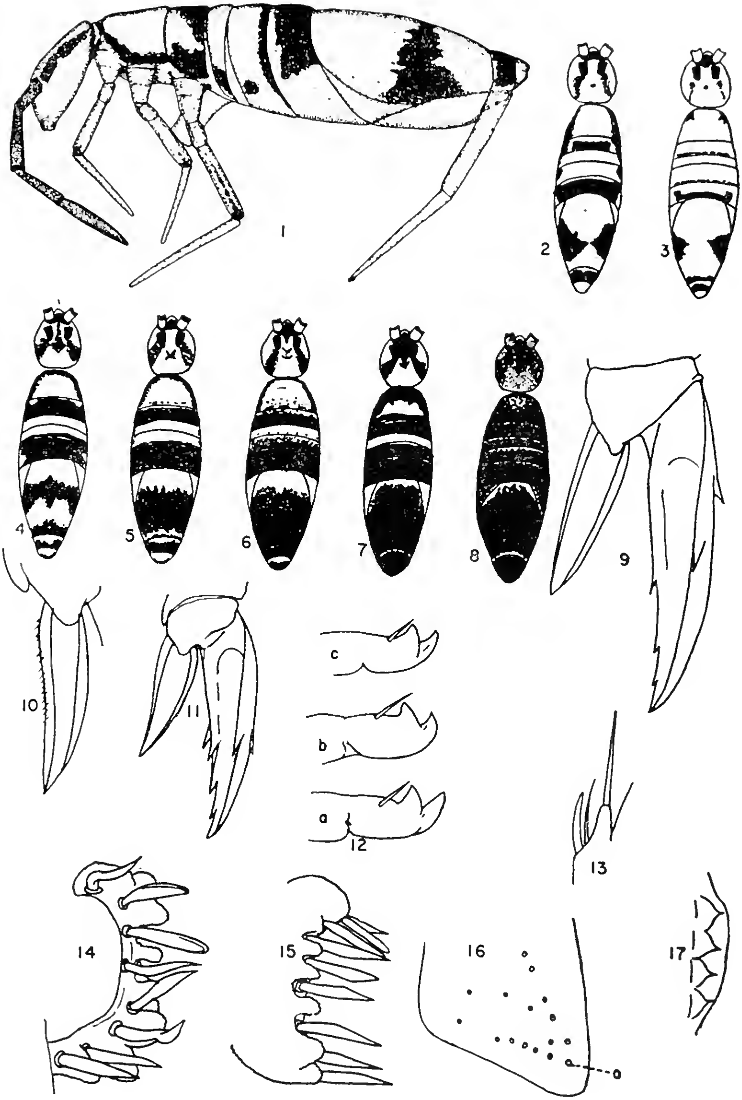


PLATE 10

Plate 11

Figures 1-7 of *Entomobrya ligata* Folsom.

1. Habitus, x 47.
2. Male genital plate, lateral view, x 1000.
3. Hind unguis and empodial appendage, small specimen, x 1520.
4. Hind unguis and empodial appendage, larger specimen, x 1520.
5. Left mucro, x 1300.
6. Left mucro, x 1300.
7. Apex of body seta, type one, x 1680.

Figures 8-16 of *Entomobrya washingtonia* Mills.

8. Dorsal view, pattern of specimen from Vancouver Island, x 55.
9. Same, specimen from Yakima, Washington, x 45.
10. Same, another specimen from Yakima, Washington, x 45.
11. Left half, male genital plate, side view, x 700.
12. Left hind unguis and empodial appendage, x 1420.
13. External papilla, right labial appendage, x 850.

14-16. Right mucro, x 1250.

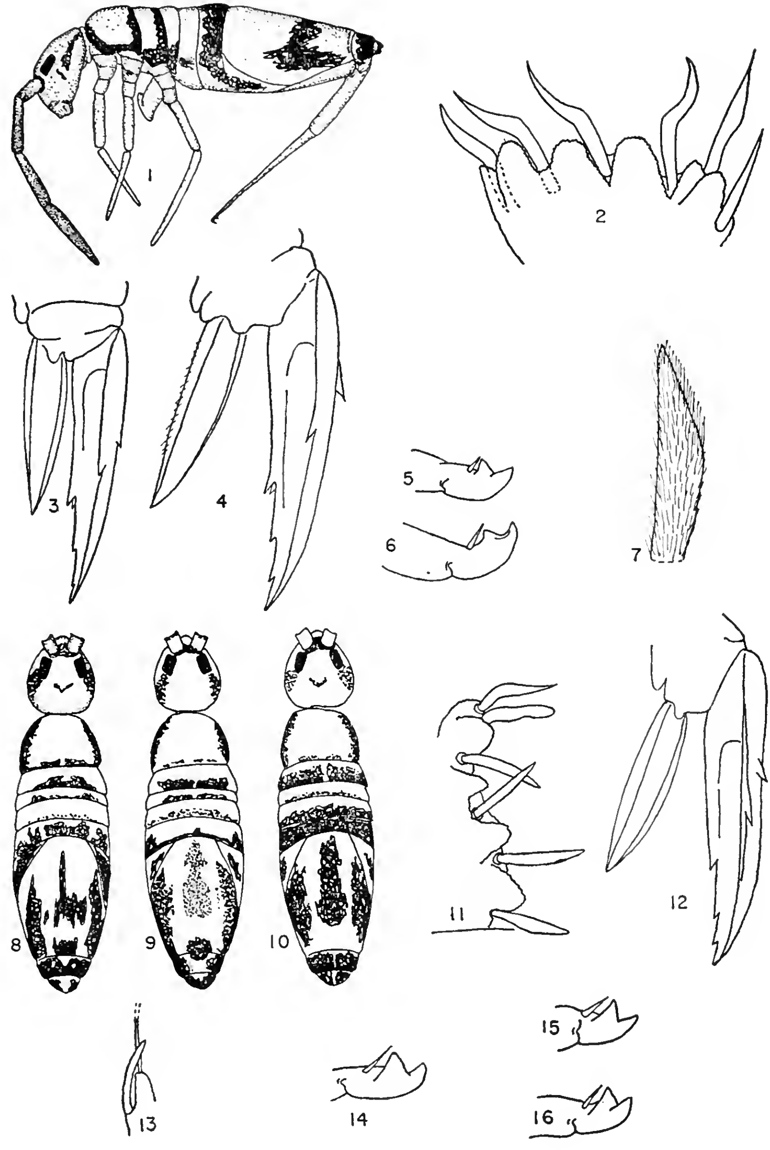


PLATE 11

Plate 12

All figures of *Entomobrya confusa* n. sp.

1. Habitus (apical three antennal segments omitted), x 80.
2. Variation in head pattern, specimen from Idaho, x 80 (approx.).
3. Same, specimen from Colorado, x 80 (approx.).
4. Same, specimen from Montana, x 80 (approx.).
5. Same, specimen from Montana, x 80 (approx.).
6. Hind unguis and empodial appendage, x 1250.

7-10. Ends of right dentes and mucrones, x 1250.

11. Labral papillae, seen from below, x 500 (approx.).
12. Male genital plate, ventral view, x 780.
13. Left trochanteral organ, x 1200.
14. Same, of another specimen, x 1200.

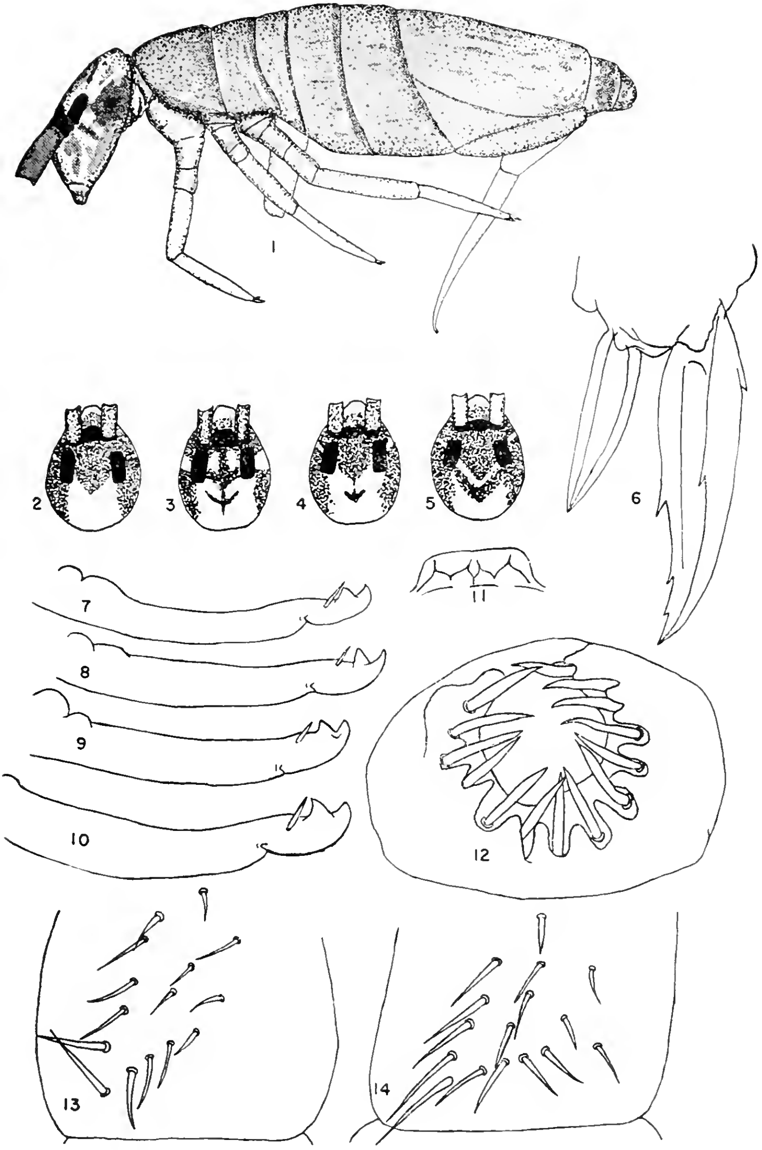


PLATE 12

Plate 13

All figures of *Entomobrya suzannae* Schött.

1. Habitus (type specimen), x 30.
2. Hind unguis and empodial appendage, x 1520.
3. Apices of setae of type one, x 1000 (approx.).
4. Right trochanteral organ, x 600.
5. Male genital plate seen from right side and slightly below, x 1000 (approx.).
6. Male genital plate of another specimen, side view (some setae omitted).
7. External setae of labial appendage, x 1000 (approx.).
8. Tip of fourth antennal segment, x 1000.

9-12. Variations in pattern in specimens from Santa Barbara mountains.

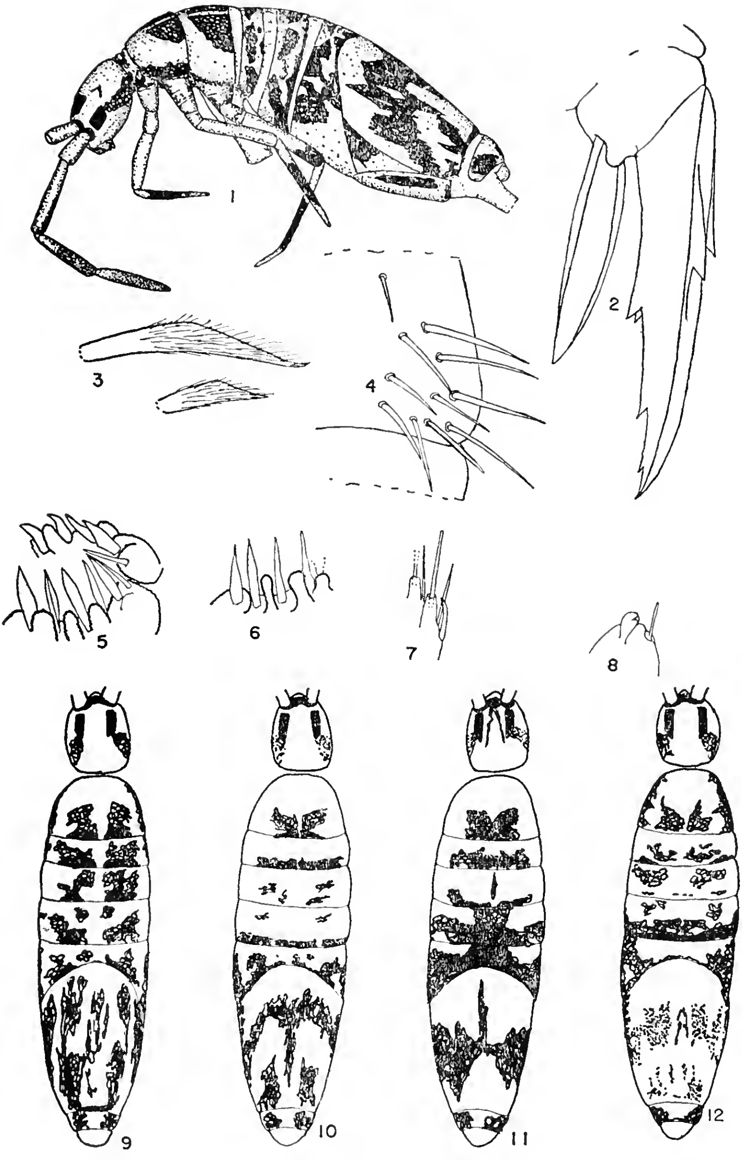


PLATE 13

Plate 14

Figures 1-8 of *Entomobrya bicolor* Guthrie.

1. Habitus, x 29.
2. Hind unguis and empodial appendage, x 1200.
3. Left half of male genital plate, ventral view (seen through covering integumentary flap), x 800 (approx.).
4. Body setae, type five, x 1200.
5. Apices of body setae, type one, x 1200.
6. Apex of fourth antennal segment, x 650.
7. Right mucro, x 1200.
8. Right mucro, x 1200.

Figures 9-16 of *Entomobrya gisini* n. sp.

9. Habitus, x 45.
10. Hind unguis and empodial appendage, x 1350.
11. Hind unguis, another specimen, x 1350.
12. Pattern of dark specimen from Alberta, Canada, x 258.
13. Right half of male genital plate, ventral view (some setae omitted, similar to heavy setae shown), x 740.
14. Apex of fourth antennal segment, x 580.
15. Right mucro, x 1200 (approx.).
16. Labral papillae, seen from below, x 1000 (approx.).

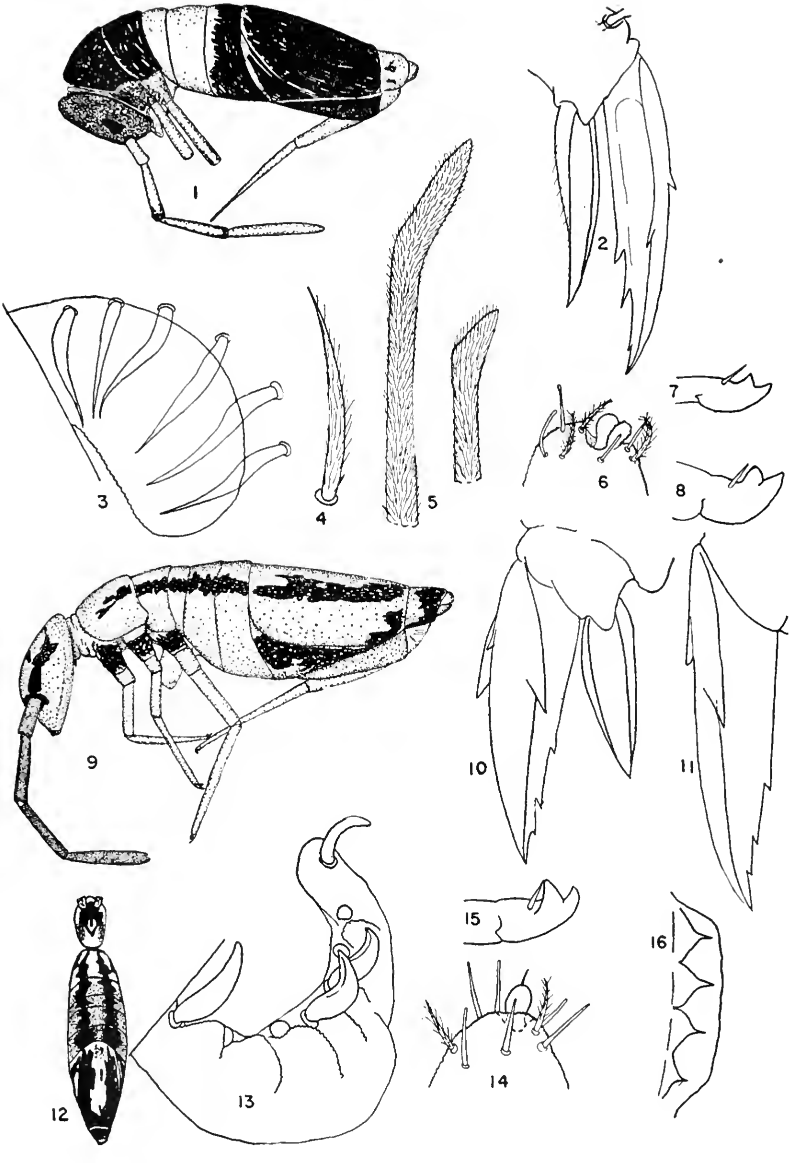


PLATE 14

Plate 15

Figures 1-9 of *Entomobrya nigriceps* Mills.

1. Habitus, x 38.
2-4. Body patterns, specimens from Texas, x 25 (approx.).
5. Left half, male genital plate, ventral view, x 800 (approx.).
6. Right mucro (basal spine broken), x 1000 (approx.).
7. Hind unguis and empodial appendage, x 1000 (approx.).
8. Labral papillae, seen from below, x 1000 (approx.).
9. External papilla of right labial appendage, x 1000 (approx.).

Figures 10-15 of *Entomobrya quadrilineata* Bueker.

10. Habitus, x 42.
11. External papilla of right labial appendage, x 1000 (approx.).
12. Right half of male genital plate, x 750.
13. Pattern, specimen from Illinois, x 25 (approx.).
14. Pattern, specimen from Tennessee, x 25 (approx.).
15. Pattern, specimen from Illinois, x 25 (approx.).

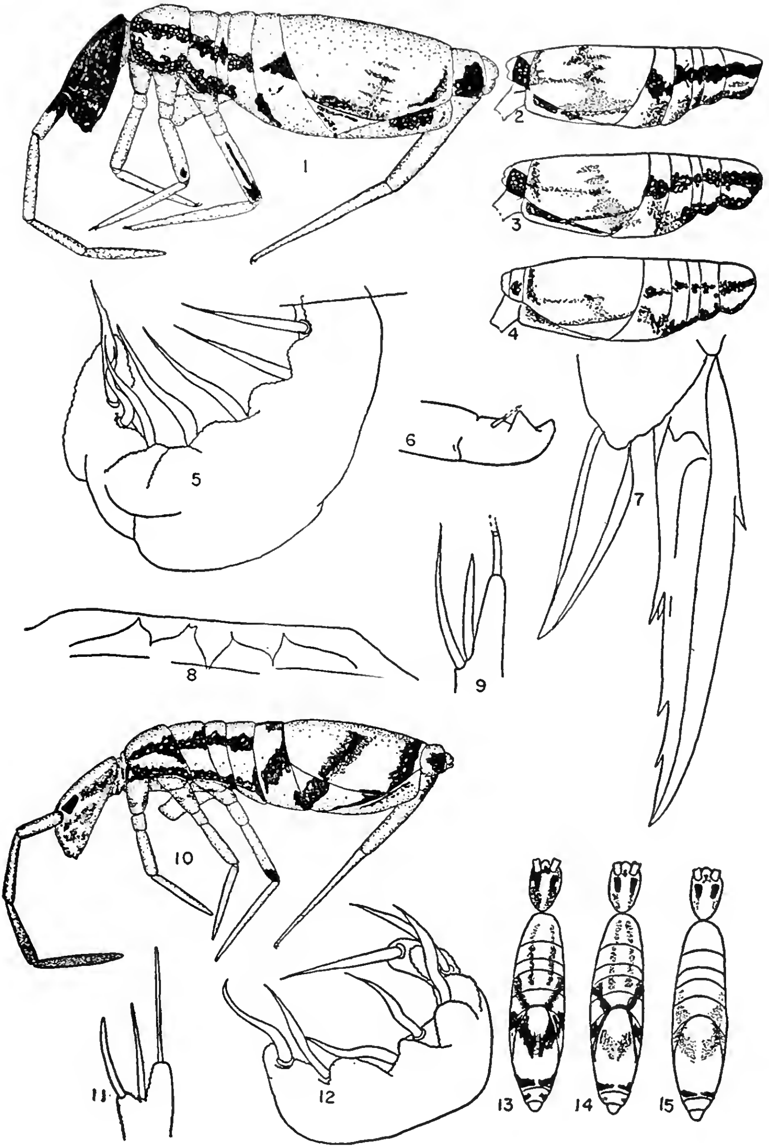


PLATE 15

Plate 16

Figures 1-4 of *Entomobrya quadrilineata* Bueker.

1. End of left dens and mucro, x 1000 (approx.).
2. Left mucro, x 1000 (approx.).
3. Hind unguis and empodial appendage, x 1000 (approx.).
4. Body seta of type one (median portion omitted), x 1280.

Figures 5-16 of *Entomobrya decemfasciata* (Packard).

5. Habitus, x 45.
6. Tip of fourth antennal segment, x 750.

7-9. Patterns, specimens from Texas, x 25 (approx.).

10. Body setae, type one, (a) apex, x 1200; (b) whole seta (ciliations omitted basally), x 750.
11. Male genital plate, seen from front, x 620.
12. Hind unguis and empodial appendage, x 1000 (approx.).
13. Hind unguis, another specimen, x 1000 (approx.).
14. End of left dens and mucro, x 1000 (approx.).
15. External papilla of left labial appendage, x 1200.
16. Labral papillae, seen from below, x 800.

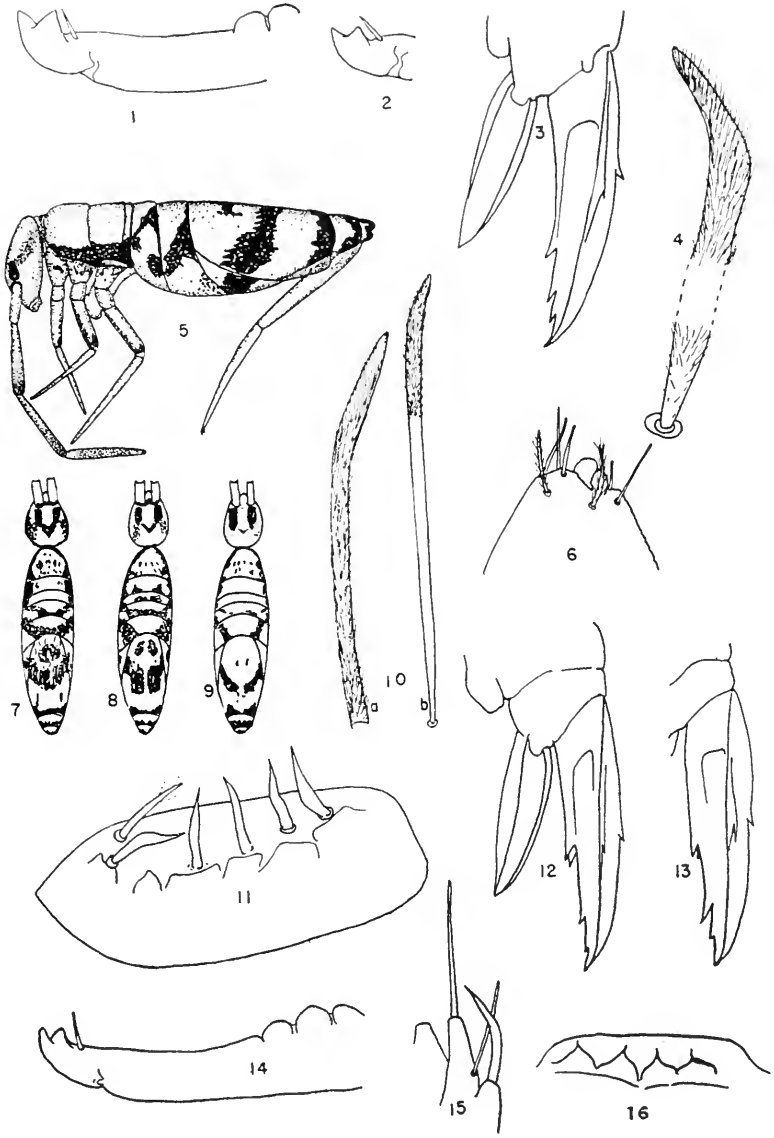


PLATE 16

Plate 17

Figures 1-7 of *Entomobrya sinelloides* n. sp.

1. Habitus, type specimen, x 47.
2. Dorsal view of pattern, specimen from Sioux Falls, South Dakota, x 40.
3. Right half of male genital plate, side view, x 700.

3a, 3b. Different male genital plates, x 700.

4. Hind unguis and empodial appendage, x 1500 (approx.).
5. Right mucro, x 1500 (approx.).
6. External papilla of right labial appendage, x 780.
7. Tip of fourth antennal segment, x 580.

Figures 8-12 of *Drepanura perpulchra* (Packard).

8. Habitus (part of antennae and legs omitted), x 70.
9. Hind unguis and empodial appendage, x 740.
10. Tip of fourth antennal segment, x 740.
11. Right mucro, x 1000 (approx.).
12. Labral papillae, seen from below, x 840.

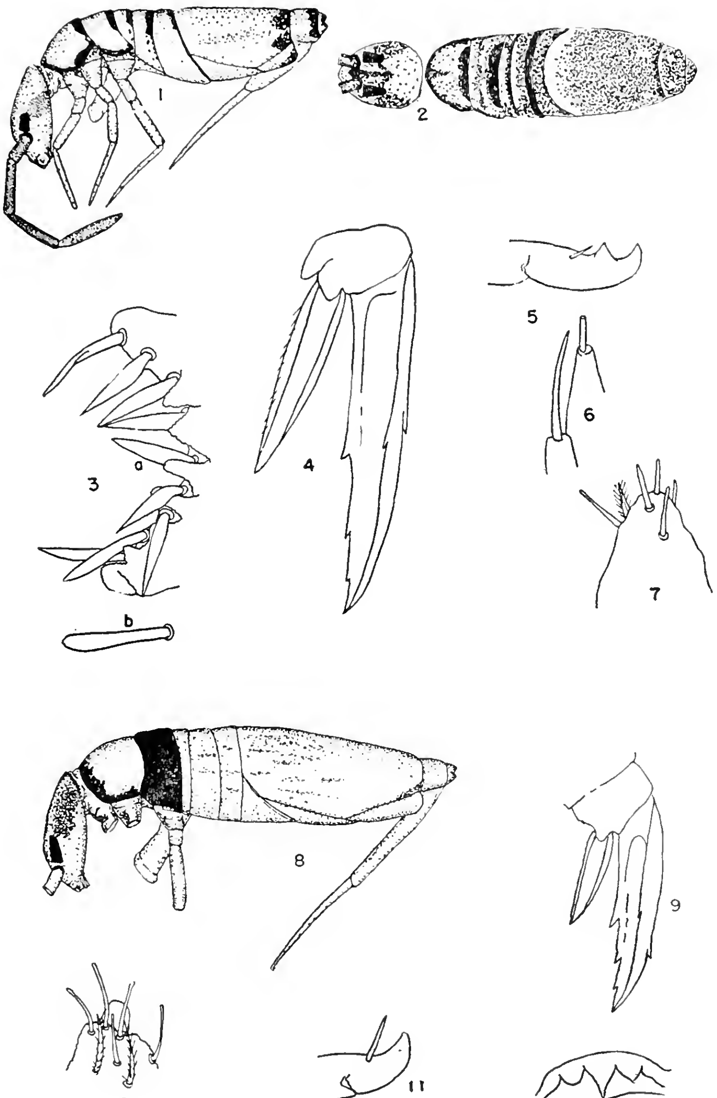


PLATE 17

Plate 18

Figures 1-10 of *Drepanura californica* Schött.

1. Habitus of typical specimen from California, x 40.
2. Male genital plate, side view, x 1000 (approx.).
3. Single seta of genital plate in profile, x 100 (approx.).
4. External setae of labial appendage, x 1000 (approx.).
5. Habitus, after Schött, x 40.
6. Habitus, specimen from Washington, x 38.
7. Hind unguis and empodial appendage, x 1620.
8. Tip of fourth antennal segment, x 780.
9. External papilla of another labial appendage, x 1000 (approx.).
10. End of right dens and mucro, x 840.

Figures 11-15 of *Entomobrya arnaudi* Wray.

11. Labral papillae, x 1000 (approx.).
12. Apical and lateral setae, male genital plate, x 1000 (approx.).
13. Apical bulb, fourth antennal segment, x 1000 (approx.).
14. Mucro, x 1000 (approx.).
15. External differentiated seta, labial appendage, x 1000 (approx.).

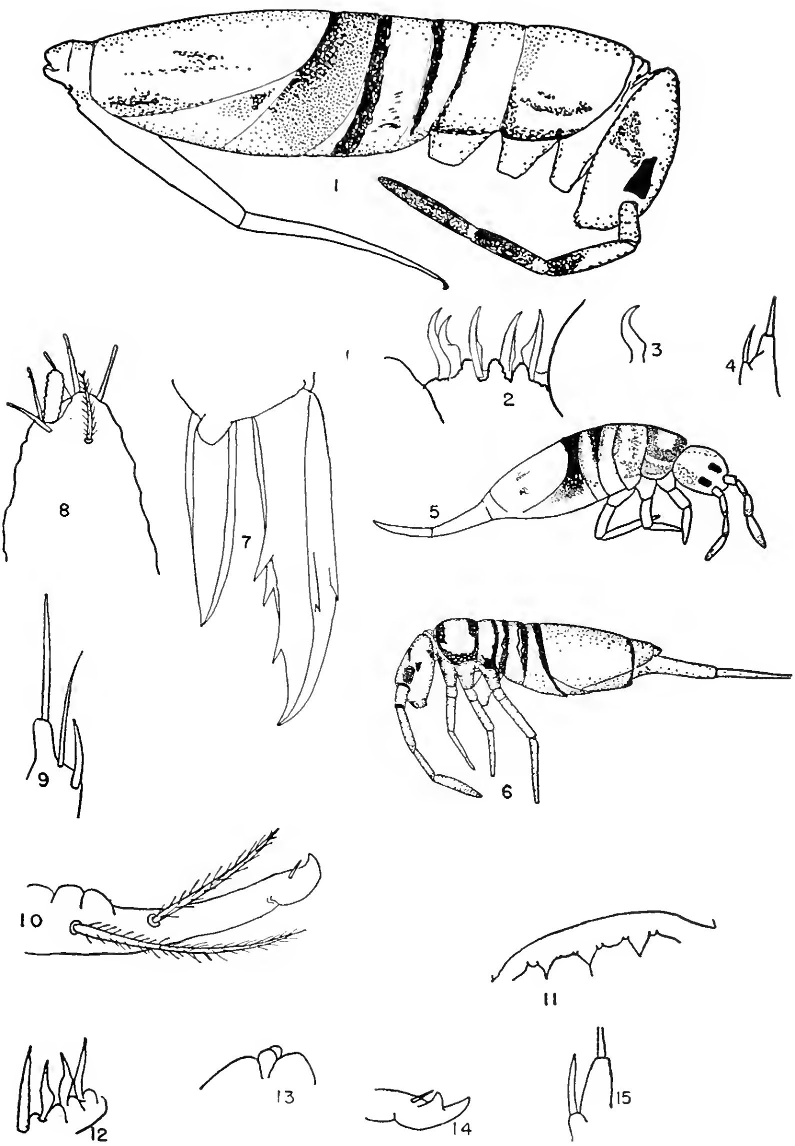


PLATE 18

Plate 19

All figures of *Entomobryoides purpurascens* (Packard).

1. Habitus, northern form, x 65.
2. Male genital plate, side view showing internal integumentary structures and the genital pore, x 1000 (approx.).
3. Pattern, specimen from Massachusetts, x 35 (approx.).
4. Pattern, specimen from Iowa, x 35 (approx.).
5. Pattern, specimen from Illinois, x 35 (approx.).
6. Pattern, specimen from Louisiana, x 35 (approx.).
7. Hind unguis and empodial appendage, specimen from Massachusetts, x 750.
8. Same on specimen from Illinois, x 750.
9. Same on specimen from Florida, x 750.

10, 11. The two extremes of the condition of the external differentiated seta of the labial appendage, x 1000 (approx.).

12, 13. Right mucrones, x 1280.

14. Labral papillae seen from below, x 1000 (approx.).
15. Right trochanteral organ, x 750.

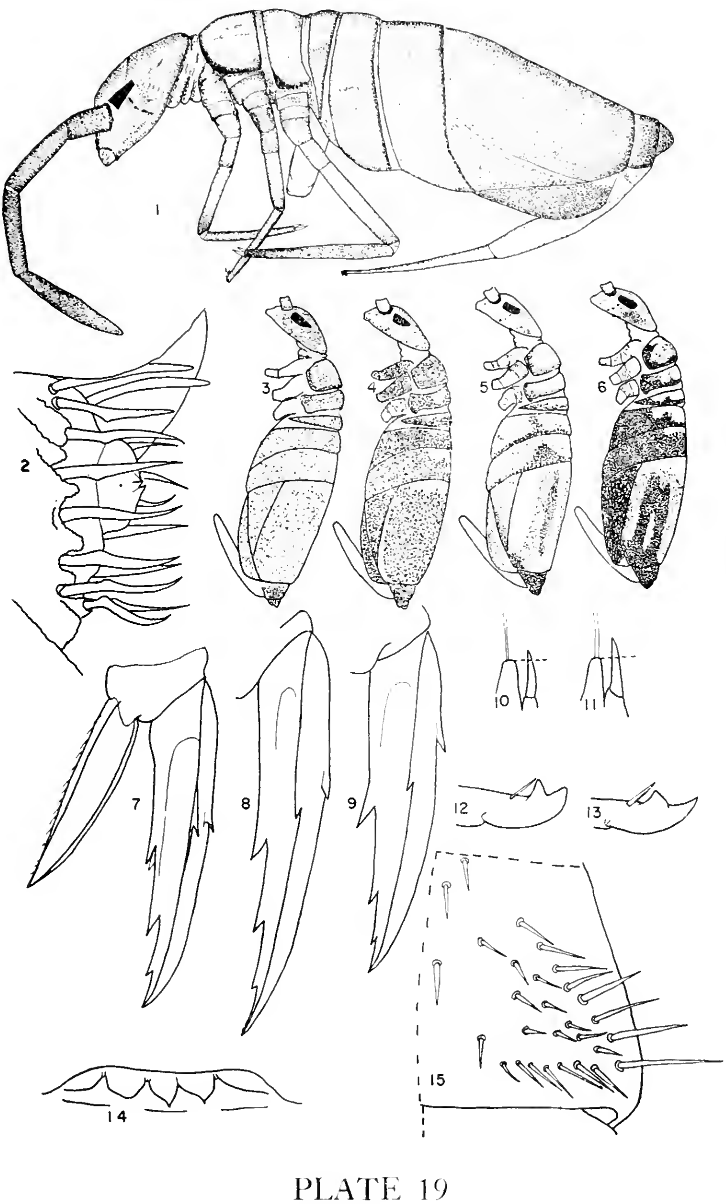


PLATE 19

Plate 20

Figures 1-6 of *Entomobryoides mineola* (Folsom).

1. Habitus, x 52.
2. Hind unguis and empodial appendage, x 1720.
3. Hind unguis of small specimen, x 1720.
4. Normal condition of external labial papilla, x 1200.
5. Unusual extreme of labial papilla, x 1200.
6. Right mucro, x 1000 (approx.).

Figures 7-13 of *Entomobryoides dissimilis* (Moniez).

7. Hind unguis and empodial appendage of large specimen, x 1700.
8. Same of normal size specimen, x 1700.

9, 10. Two extremes of external seta of labial appendage, x 1200.

11. Right mucro, unusual specimen, x 1200.

12, 13. Mucrones of normal specimens, x 1200.

PLATE 20

Plate 21

All figures of *Entomobryoides guthriei* (Mills).

1. Male genital plate of specimen from Oregon, seen from the side and slightly above, x 780.
2. Same of a specimen from South Dakota, x 780.
3. Same of a specimen from Colorado, x 780.
4. Specimen from British Columbia, unguis and empodial appendage, x 1500 (approx.).
5. Same of another specimen of same series, x 1500.
6. Same of a specimen from South Dakota, x 1500.
7. Same of a specimen from Colorado, x 1500.

8-10. Mucrones from different localities, x 800 (approx.)

11. Typical labial appendage, x 800.

12, 13. Extreme conditions of the labial appendage, x 1000.

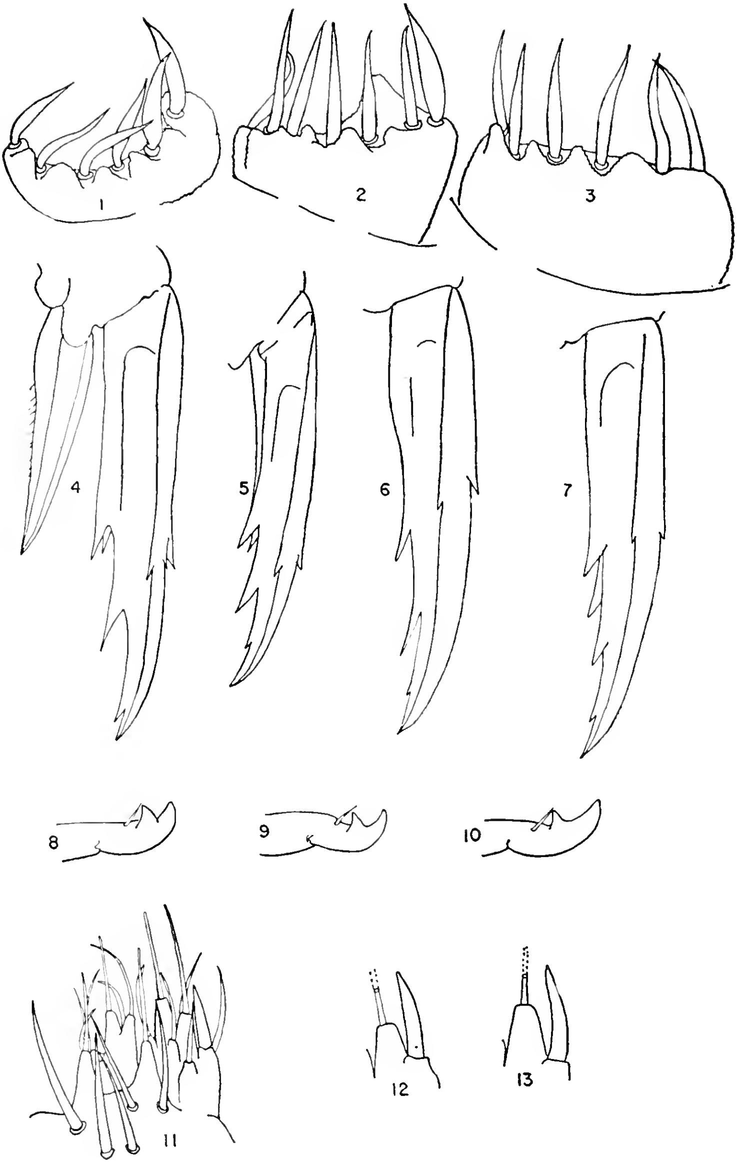


PLATE 21

Plate 22

All figures of *Calx sabulicola* Mills.

1. Habitus, x 40.
2. Pattern variation, specimen from Arizona, x 35 (approx.).
3, 4. Pattern variation, specimens from Wyoming, x 35 (approx.).
5. Pattern variation, specimen from Colorado, x 35 (approx.).
6. Pattern variation, specimen from Texas, x 35 (approx.).
7. Male genital plate, seen from side and slightly below, x 1000 (approx.).
8. Right trochanteral organ, x 940.
9. Hind unguis and empodial appendage, x 1580.
10. Apex of antennal segment four, x 640.
11. Labral papillae, seen from below, x 800.
12. Body setae, type five, x 1200.
13. End of left dens and mucro, x 1200.

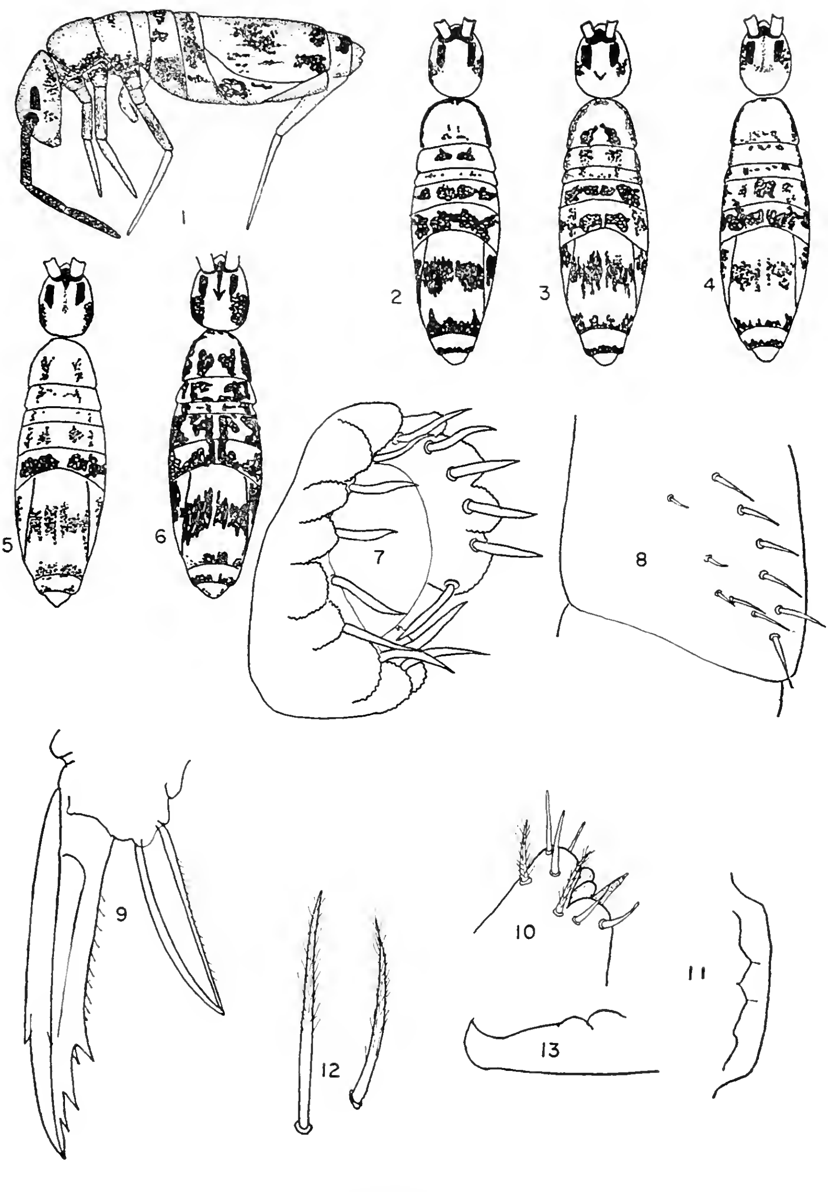


PLATE 22

Plate 23

Figures 1-7 of *Homidia sauteri* Börner

1. Habitus, x 38.
2. Hind unguis and empodial appendage, showing small extra basal tooth, x 1500 (approx.).
3. Apex of body seta, type one, x 1280.
4. Right trochanteral organ, x 1280.
5. External papillae of right labial appendage, x 1560.
6. Basal three-fourths of left dens, showing dental spines, x 115.
7. Apex of right dens and mucro, x 1280.

Figures 8-12 of *Mesentotoma laguna* (Bacon).

8. Apex of body seta, type one, x 1400.
9. Base of second antennal segment, showing subdivision and setae, x 800.
10. Hind unguis and empodial appendage, x 1000 (approx.).
11. Apex of fourth antennal segment, x 800.
12. Mucro, x 1000 (approx.).

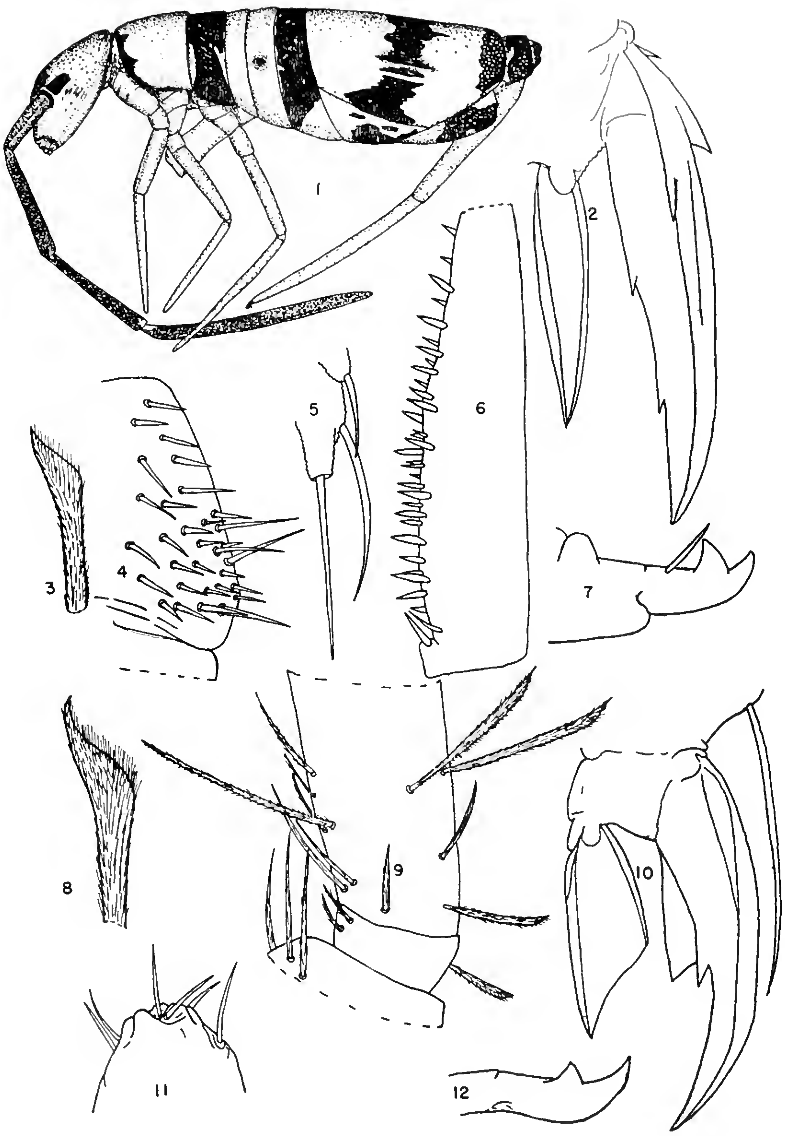


PLATE 23

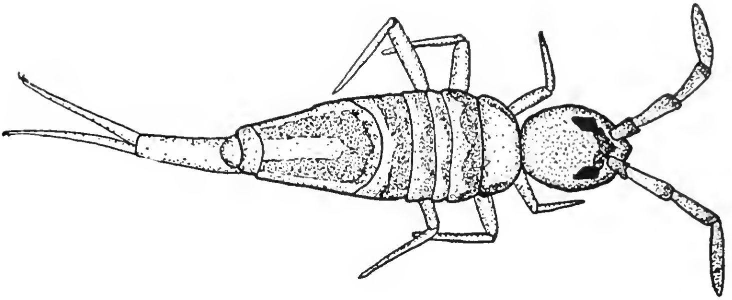
Plate 24

Figure 1 of *Entomobrya pygmaea* Harvey.

1. Habitus (after Harvey), x 50.

Figures 2-4 of *Entomobrya duolineata* Bueker.

2. Habitus (after Bueker), x 25.
3. Unguis and empodial appendage (after Bueker), x 250 (approx.).
4. Mucro (after Bueker), x 250 (approx.).



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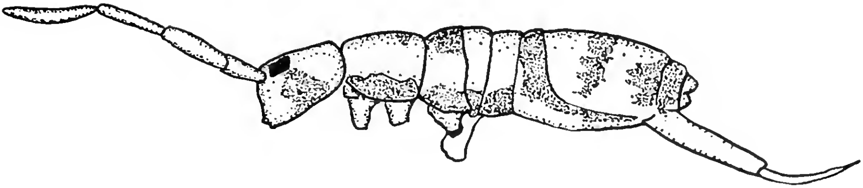

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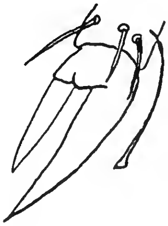

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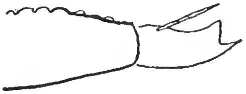

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PLATE 24