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ANEURETUS SIMONI EMERY, A MAJOR LINK IN ANT EVOLUTION

by E. O. WILSON, T. EISNER, G. C. WHEELER and J. WHEELER

WITH THREE PLATES

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No. 3 — ANEURETUS SIMONI *Emery, a Major Link in Ant Evolution*

By E. O. WILSON,[1] T. EISNER,[1] G. C. WHEELER,[2] and J. WHEELER[2]

INTRODUCTION

To students of ants, the genera of the tribe Aneuretini (*Aneuretus, Protaneuretus, Paraneuretus,* and *Mianeuretus*) have always been of primary interest because of their supposed intermediate phylogenetic position between the most primitive known ants (Myrmeciinae, Ponerinae) and the advanced subfamily Dolichoderinae. Few tribes of ants have been more deserving of careful study, and yet few have been so little known or so inaccessible to myrmecologists. *Aneuretus simoni*,[3] the only living species of the tribe, is known only from Ceylon and has been reported from only three collections made there. Until recently the total number of specimens in the museums of the world numbered no more than five or six. Published descriptions have contained only sketches of the gross features of external morphology, and no information whatsoever has been available concerning the internal anatomy, ecology, or behavior of this ant.

During a recent visit to Ceylon one of us (Wilson) made a special attempt to find *Aneuretus simoni* and study it in the field. This attempt was successful to an unexpected degree. Not only were large series of *A. simoni* collected, including all brood stages and adult castes, but a strong beginning was made in the study of the ecology and behavior of the species. Upon his return to the United States in September, 1955, Wilson turned over part of his collection of *Aneuretus* to the Wheelers, who are currently engaged in comparative anatomical studies of ant larvae, and to Eisner, who at that time was in the process of completing a comparative anatomical study of the ant proventriculus. The present paper is the product of the cooperative effort of the four authors, each of whom has concentrated on

[1] Biological Laboratories, Harvard University, Cambridge, Mass.
[2] Department of Biology, University of North Dakota, Grand Forks, N. D.

[3] Equals *Aneuretus butteli* Forel, 1913, Zool. Jahrb. (Abt. Syst.), *36:* 87, fig. A1, queen, *NEW SYNONYMY.* This species was based on an isolated queen, which we have now definitely associated with the *A. simoni* worker. Types of both species have been recently examined by Wilson in the Museum d'Histoire Naturelle, Geneva.

those aspects of special interest to himself. Specifically, Eisner and Wilson have collaborated in the section on adult morphology, the Wheelers have contributed the section on larval morphology, and Wilson has contributed the sections on distribution, ecology, and phylogeny.

ADULT MORPHOLOGY

Worker. (Pl. 1, figs. E, F, H, I; Pl. 2, fig. B; text-figs. 1, 2). A surprising discovery, made when the first nests of *Aneuretus simoni* were opened, was that the worker caste of this species is dimorphic. As shown in the size-frequency histogram of Figure 1, this is true *complete* dimorphism, with intermediates lacking. While the distribution given represents only a single colony, it is probable that if all the colonies collected were compounded, two completely discrete size-distributions would still be obtained. As shown in Plate 1, the major worker differs from the minor primarily in its proportionately larger and broader head, and in its relatively shorter, stouter propodeal spines. In the queen, it will be noted, both of these allometric trends are carried a bit further. The head is wider with respect to its length than in the worker castes, and the propodeal spines are reduced to mere angles.

The following description is based on the minor worker. Eyes small, containing only about 30 ommatidia. Antennae 12-segmented, with the segments of the flagellum increasing distally both in length and width. Clypeus broad and flat, lacking a median carina, the anterior border strongly emarginate in full-face view. Mandible as shown in Plate 2*B*. Mandibular dentition reminiscent of *Dolichoderus* (*s. str.*), relatively constant except in the following two characters: (1) the shapes of all the individual teeth vary somewhat, and (2) the number of the reduced median teeth (located between the three apical and three major basal teeth) varies from four to eight. Maxillary palp 3-segmented, the terminal segment showing a variable median constriction or local cuticular thickening, which may well indicate a phylogenetically recent fusion site. Labial palp 4-segmented.

Alitrunk as figured. Propodeal spines spike-like, tapering abruptly near the tips to form sharp points; seen from above,

they diverge from one another strongly. Metasternal gland bulla prominent, its openings supplied with a small number of coarse guard hairs originating from both the dorsal and ventral lips.

Anterior peduncle of petiole long and slender, somewhat narrowed toward its anterior attachment. The petiolar node well differentiated from the anterior peduncle by dorsal and lateral swellings. Seen from above, the node proper is nearly twice as broad as long. Posteriorly, it narrows abruptly to the point of attachment to the gaster.

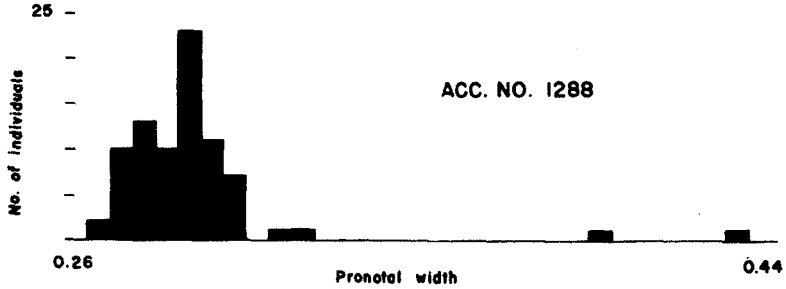

Fig. 1. Size-frequency histogram of the entire worker population of a single colony of *Aneuretus simoni* from Ratnapura, Ceylon, showing worker dimorphism.

The gaster lacks any form of intersegmental constriction whatsoever. The sting is well-developed, sclerotized, and exsertile.

Integument relatively thin and collapsible, resembling in this respect that of the higher dolichoderines and formicines. Color of living and fresh alcoholic material varies within most nest series from light yellow (in callows) to medium yellowish orange. Body lightly shagreened overall, subopaque to feebly shining; the dorsal and most of the lateral surfaces of the propodeum are in addition transversely rugulose.

Pilosity generally sparse. Appendages covered with abundant short, oblique pubescence, but lacking longer hairs except on the coxae and tarsal claws. Body supplied with scattered, relatively long, pointed erect hairs distributed as shown in Plate 1; body pubescence appressed and sparse.

Proventriculus as shown in Text-figure 2. Because of its extremely small size and flaccid framework this organ is easily deformed during preparatory handling, and it accordingly varies

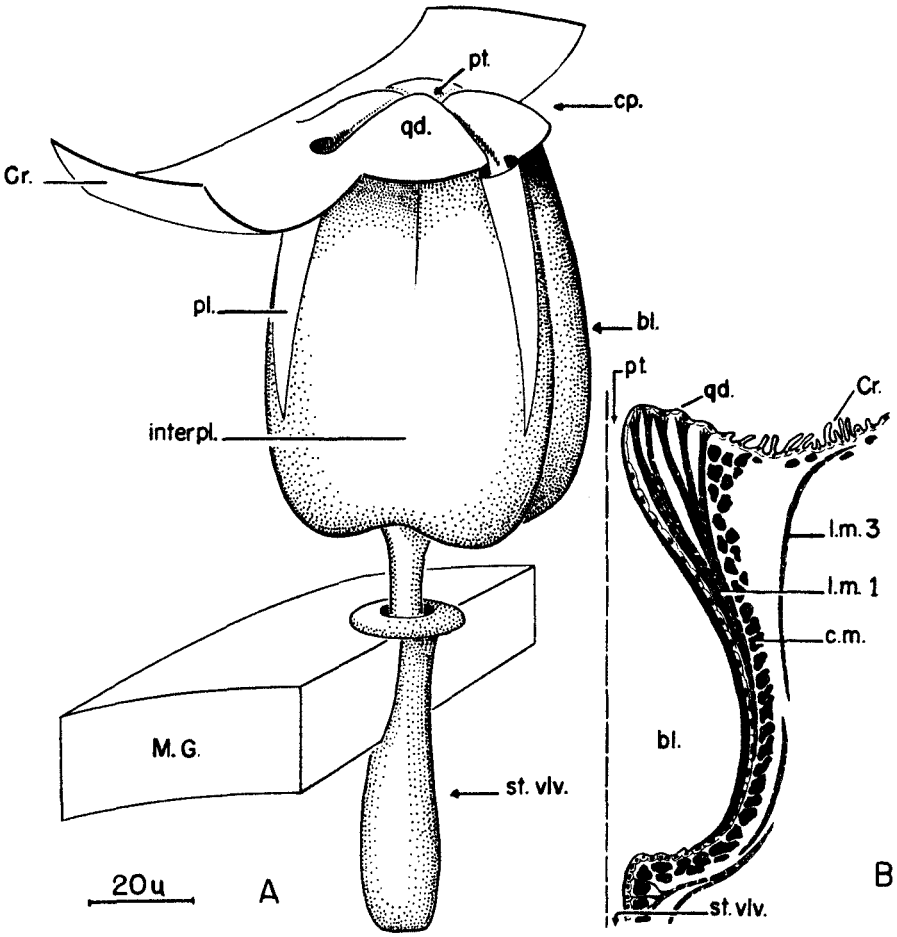

Fig. 2. Worker proventriculus of *Aneuretus simoni*. *A*, cuticular framework with musculature removed. *B*, longitudinal section through interplicary plate and portal quadrant, showing musculature. *Bl.*, bulb; *c. m.*, circular muscles; *cp.*, cupola; *Cr.*, crop; *interpl.*, interplicary plate; *l. m.* 1 and *l. m.* 3, longitudinal muscles; *M. G.*, midgut; *pl.*, plica; *pt.*, portal; *qd.*, cupolar quadrant; *st. vlv.*, stomadaeal valve. Further explanation in the text.

from one preparation to the next; for this reason, the habitus portrayal of Text-figure 2 must be considered semidiagrammatic. The terminology of the following description is the same as that adopted in the forthcoming monograph on the formicid proventriculus by Eisner. The cuticular framework consists of a thin-walled, flask-shaped bulb (*bl.*), opening anteriorly into the crop (*Cr.*) through a relatively wide cruciform portal (*pt.*). The walls of the bulb are four broad, sclerotized, inwardly curved interplicary plates (*interpl.*), joined basally and merging into a slender, tubular stomodaeal valve (*st. vlv.*). The thin and flexible cuticle of the valve, after extending into the midgut, folds back upon itself so as to constitute a compound tube. The interplicary plates of the bulb are separated from one another by relatively narrow longitudinal strips of thin, flexible cuticle, the pleats or plicae (*pl.*), and extend anteriorly into the lumen of the crop as four apically rounded lobes or quadrants (*qd.*), which collectively constitute the cupola (*cp.*). Actually, the cruciform shape of the portal is determined by the presence of the cupolar quadrants. The bulb is surrounded by a strongly developed layer of circular muscles (*cm*, Text-fig. 2B). The longitudinal muscles are arranged in two distinct groups (*l. m.* 1 and *l. m.* 3). The more strongly developed of these muscles (*l. m.* 1) originate on the interplicary plates of the bulb, extend over the plates and insert anteriorly on the quadrants of the cupola. The second group (*l. m.* 3) consists of a few scattered fibers that extend from the crop to the midgut outside the circular muscles. Some of these fibers terminate at the base of the proventriculus, where they insert on the cuticle at the point of origin of the stomodaeal valve.

The glandular system has not yet been studied, but it is noteworthy that in the field the workers defending their nests were never observed to produce anal droplets, nor did they produce the "Tapinoma-odor," resembling rancid butter or coconuts, which is supposed to characterize most Dolichoderinae.

Queen. (Plate 1.) The queen is much larger in size than either of the worker subcastes and differs further in its proportionately broader head and greatly reduced propodeal spines. In addition, it is much darker, being overall dark brown. It is essentially similar to the workers in petiolar structure, mandibular dentition, pilosity, sculpturing, etc.

The wing venation (of both the queen and the male) is relatively generalized and similar to that of the most generalized true dolichoderine, *Dolichoderus s. str.*, as typified by *D. attelaboides* (Fabr.). The latter species, as pointed out by Brown and Nutting (1950) in their important review of formicid wing venation, possesses all of the venational elements of the primitive ponerine pattern except for the first radial cross-vein. *Aneuretus simoni* shows two significant further advances. First, Mf2 is completely contracted, so that the ends of Rs2 and the cross-vein

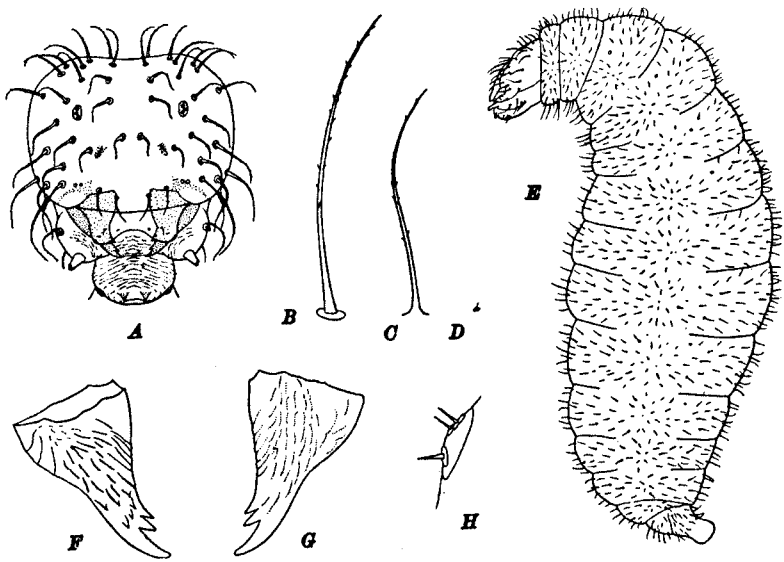

Fig. 3. Larva of *Aneuretus simoni* (immature). *A*, head in anterior view, X 130. *B-D*, three types of body hairs, X 546. *E*, larva in side view, X 43. *F*, left mandible in posterior view, X 325. *G*, left mandible in anterior view, X 325. *H*, left antenna in lateral view, X 546.

m-cu are contiguous. Second, Rs4 has contracted to bring about the alignment of the cross-veins 2r and r-m.

Male. Plates 1 and 2 show almost all of the important features of external morphology of this caste. Especially noteworthy are the conservation of the "myrmecioid" petiolar structure shown also by the worker and queen, the relatively generalized structure

of the mandible, and the generalized structure of the genitalia, especially the volsella. One perhaps significant advanced feature is the absence of serration on the ventral edge of the penis valve.

LARVAL MORPHOLOGY

Immature larva. (Text-fig. 3.) Body length (through spiracles) 1.1-2.1 mm. Straight length 0.8-1.6 mm. Somewhat sigmoidal in side view; thorax forming a stout neck which is bent ventrally at 90°; abdomen rather stout, diameter greatest at abdominal somite IV; abdominal somites IX and X small and directed posterodorsally, the tenth forming a terminal naked knob. Anus posterior. Leg and wing rudiments present. Spiracles small, decreasing in diameter posteriorly. No spinules seen on the integument. Body hairs short, moderately numerous, uniformly distributed, of three types: (1) 0.027-0.045 mm. long, slightly curved or flexuous, with a few minute denticles, without alveolus and articular membrane, the most numerous type; (2) 0.045-0.072 mm. long, longest and most numerous anteriorly, slightly curved or flexuous, with a few minute denticles, with alveolus and articular membrane; (3) minute (about 0.001 mm. long), few, widely scattered. Head moderately large, feebly cordate; cranium transversely subelliptical, with the occipital border impressed and the corners rounded. Mouth parts large. Antennae small, each with three sensilla, each of which bears a moderately long spinule. Head hairs moderately numerous, uniformly distributed, slightly curved or flexuous, long (0.027-0.072 mm.), with numerous minute denticles on the distal 2/3. Labrum short and broad (breadth 2.8 times the length), bilobed due to a rather deep impression of the ventral border; anterior surface of each lobe with one minute hair and three sensilla; ventral border with two sensilla near the middle and with a few minute spinules; posterior surface of each lobe with one large and three minute sensilla; posterior surface spinulose, the spinules minute and in numerous short arcuate rows, the rows radiating from each dorsolateral corner. Mandibles moderately large, heavily sclerotized and subtriangular in anterior view, longer than broad; slightly curved posteriorly; apex forming a rather long tooth which is slightly curved medially, two rather large subapical teeth on the medial border; anterior surface

with numerous short longitudinal ridges (rows of exceedingly minute spinules?); posterior surface with several acute denticles on the distal half and numerous ridges on the basal half, some of the ridges bearing a row of minute spinules. Maxillae lobose, with the apex a small conoid directed medially, with minute spinules in short rows which are arranged in longer rows encircling the galea; palp a frustum bearing four apical (two encapsulated and two with a spinule each) and one lateral (with a spinule) sensilla; galea a tall peg with two apical sensilla. Labium hemispheroidal and protruding; with all surfaces spinulose; the spinules more numerous and in more numerous rows on the anterior surface, and larger, fewer, and in short rows or isolated on the posterior surface; palp a slight elevation with five sensilla, three encapsulated and two bearing a spinule each. Opening of sericteries wide and salient. Hypopharynx spinulose, the spinules so long that those in adjacent rows overlap; the rows numerous and radiating from each dorsolateral angle.

The larva of *Aneuretus* shows only one dolichoderine character —— the short, broad labrum ——— and even this is not distinctive. The one and only character that affiliates it with the Dolichoderinae is, strangely enough, one which is not characteristic of the subfamily at all, namely the terminal knob projecting posteriorly or posterodorsally. Now, a terminal knob occurs in the larvae of several genera in other subfamilies, but there it projects posteroventrally, ventrally, or anteroventrally. Only in the most advanced dolichoderine genera *Engramma, Tapinoma* and *Technomyrmex* have we previously found it projecting posteriorly or posterodorsally. (See G. C. and J. Wheeler, 1951.)

In marked contrast are the many non-dolichoderine characters of *Aneuretus* larvae. These are given in the accompanying table. It will be seen that all the non-dolichoderine characters of *Aneuretus* except 3 and 4 are more generalized than their dolichoderine counterparts. Thus we find *Aneuretus* standing out conspicuously as a generalized ant larva when considered in reference to the Dolichoderinae.

TABLE

Larval Characters of the Subfamily Dolichoderinae	Non-dolichoderine Larval Characters of *Aneuretus*
1. No neck	1. Neck present
2. Body and head usually almost naked, hairs typically very few and widely scattered	2. Body and head hairs moderately numerous and uniformly distributed
3. Hairs of only one type (one exception)	3. Hairs of three types
4. Hairs simple (one exception)	4. Hairs denticulate
5. Mouth parts small, spinules sparse or lacking	5. Mouth parts moderately large, with moderately abundant spinules
6. Mandibles small (ratio of head width to mandible length ranges between 4 and 10)	6. Mandibles moderately large (head width divided by mandible length=2.6)
7. Mandibles feebly sclerotized	7. Mandibles heavily sclerotized
8. Mandibles with the basal portion inflated; distal portion slender, acuminate	8. Mandibles subtriangular in anterior view (not divided into two distinct portions)
9. Mandibles without teeth on the medial border (rarely with a single small tooth)	9. Mandibles with two rather large subapical teeth on the medial border
10. Maxillary palp and galea represented by clusters of sensilla; never paxilliform	10. Maxillary palp and galea paxilliform
11. Opening of sericteries small and inconspicuous	11. Opening of sericteries wide and salient.

PHYLOGENETIC POSITION AND TAXONOMIC STATUS OF THE ANEURETINES

Like so many archetypal or annectant forms, *Aneuretus simoni* by itself shows a remarkable mixture of primitive and specialized characters. In some of these characters the species seems to have remained close to the mainstream of dolichoderine evolution; in others, it has moved off on a branch of its own. Before commenting on the totality of *Aneuretus* morphology and attempting to place the genus phylogenetically, let us review briefly the principal aneuretine characters and attempt to assess them with respect to their evolutionary significance.

Female mandibular dentition. In the form and placement of the basal teeth, *Aneuretus* closely resembles the primitive true dolichoderines, especially *Dolichoderus s. str.* At the same time, the set of reduced, semicircular median teeth represents a specialization not shared with any of the living dolichoderines.

Integument. The adult integument is relatively thin and collapsible, as in the higher dolichoderines and formicines.

Clypeus. In shape and proportionate size, the clypeus resembles the Dolichoderinae-Formicinae more closely than the Myrmeciinae-Ponerinae. The prominently emarginate anterior border is highly characteristic of the Dolichoderinae.

Palpal segmentation. The reduction of the number of segments in the maxillary palp is a specialization peculiar to *Aneuretus;* it is not shared by *Protaneuretus* or any primitive dolichoderine or formicine genus.

Petiole structure. The *Aneuretus* petiole, with its long anterior peduncle and low, rounded node, is undoubtedly of a very primitive type. It is in fact most similar to that of *Nothomyrmecia*, probably the most primitive of all the known living ant genera. There is nothing comparable to it anywhere in the Dolichoderinae or Formicinae.

Gaster. The absence of any constriction behind the postpetiolar segment constitutes an important difference from most unspecialized Ponerinae, and makes it unlikely that the aneuretines could have been derived from any of the known ponerine tribes. *Nothomyrmecia*, on the other hand, also lacks any form of gastric constriction.

Sting. The well-developed, exsertile sting of *Aneuretus* is a primitive character not shared by any of the Dolichoderinae or Formicinae.

Wing venation. In this character, *Aneuretus* is generalized with respect to the Dolichoderinae and Formicinae as a whole, but is more advanced than *Dolichoderus*, having undergone reductions in two important venational elements (Mf2, Rs4).

Male genitalia. Until a much-needed survey of formicid male genitalia is available, the most that can be said about *Aneuretus* is that it is unspecialized, having undergone no important reductions or modifications beyond the loss of serration on the ventral penial valve blades. By contrast, some of the higher dolichoderines have undergone such changes as partial reduction of the volsellae and complete loss of the pygostyles.

Proventriculus. The proventriculus of *Aneuretus simoni* conforms closely to the primitive formicid type, as seen in the Myrmeciinae, Pseudomyrmicinae, Ponerinae, and Cerapachyinae, which in turn does not differ much from the generalized aculeate pattern. Specifically, there is a mobile portal associated with flexible plicae in the bulb, with no suggestion of the portal growth and reinforcement through plical sclerotization seen in the higher Dolichoderinae and Formicinae. At the same time, there is apparently lacking in *Aneuretus* a group of longitudinal muscles (*l. m.* 2) which is characteristic of the lower ant groups. This lack of *l. m.* 2 is surprising in view of the otherwise primitive structure of the *Aneuretus* proventriculus, and may represent an important evolutionary step toward the proventricular type of the higher Dolichoderinae and Formicinae.

Odor. It was established in the field that *Aneuretus simoni* adults lack the "*Tapinoma-odor*" which is supposed to characterize the Dolichoderinae.

Larval morphology. The larva of *Aneuretus simoni* has only one character that definitely affiliates it with the Dolichoderinae: the posterodorsally projecting terminal knob, which is characteristic only of several of the most specialized dolichoderine genera. Otherwise, larval morphology is so generalized as to set *Aneuretus* off from the Dolichoderinae as a group. Phylogenetically the larva could have been derived from that of the Myrmeciinae, but so could the larvae of most other primitive ant groups. More immediately, it can be linked to the larvae of the more primitive

formicine genera such as *Melophorus,* which it resembles in number and shape of body and head hairs, size of mouth parts, shape and sclerotization of mandibles, and size and shape of maxillary palp and galea. *Melophorus* in turn resembles very closely the larvae of some of the Ponerinae, especially *Ectatomma* (see Wheeler and Wheeler, 1953). At the present time, however, the interrelationships of these last two genera are poorly understood, and it is not known to what extent larval morphology by itself can be used as a phylogenetic standard.

Summing up the above information, it is clear that the aneuretines, as exemplified by *Aneuretus simoni,* are a group of paramount significance in the evolution of the ants. Their relationship to the Dolichoderinae is undeniable. Some characters in both adult and larval morphology are shared exclusively with the Dolichoderinae. But in other characters, the aneuretines are so generalized as to seem to place them closer to the Myrmeciinae and Ponerinae than to the Dolichoderinae. There is evidence to suggest, and apparently none to deny, that the aneuretines represent the direct ancestors of the Dolichoderinae, and perhaps also of the Formicinae. At the same time it appears, on the important basis of external abdominal anatomy, that the aneuretines are more closely related to *Nothomyrmecia,* the living "archetypal" myrmeciine ant of Australia, than to any other primitive ant group. On the basis of these two major considerations, future phylogenists may feel justified in deriving the Dolichoderinae and Formicinae ultimately from a *Nothomyrmecia*-like stock through the aneuretines.

In the past, the aneuretines have been conventionally considered a tribe of the Dolichoderinae. The totality of anatomical evidence we have presented in this paper should now make it clear that such a taxonomic placement is awkward, since an inclusion of the aneuretines in the Dolichoderinae would make that subfamily heterogeneous out of all proportion to the remainder of the ant subfamilies, and its diagnosis would then have to depend on relatively minor characters in cephalic structure. We consider that the best course is to elevate the aneuretines to subfamily rank, coordinate with the Dolichoderinae.

Subfamily ANEURETINAE Emery

Aneuretini Emery (tribe), 1912, Gen. Ins., 137: 6. Type: *Aneuretus* Emery; monobasic.

Aneuretini, Wheeler, 1914, Schrift. Phys.-ökon. Ges. Königsberg, 55: 71. (Description and inclusion of the Baltic amber genera *Protaneuretus* and *Paraneuretus*).

Aneuretini, Carpenter, 1930, Bull. Mus. Comp. Zool. Harv., 70: 39. (Description and inclusion of the genus *Mianeuretus* from the Florissant shales).

Aneuretinae (subfamily), Clark,[1] 1951, Formicidae of Australia, Genus *Myrmecia* (Commonwealth Sci. Indust. Res. Org., Australia), p. 16.

Diagnosis. (1) Clypeus broad, flat, and anteriorly emarginate, as in the Dolichoderinae.

(2) Petiole with an anterior peduncle at least as long as the basal portion of the node.

(3) Gaster completely lacking constrictions behind the first postpetiolar segment.

(4) Sting well-developed, sclerotized, and exsertile.

(5) Larva primitive in form, with well developed neck, large, sclerotized mandibles, and paxilliform maxillary palps and galeae.

(6) Pupae enclosed in cocoons; larvae with large, salient serictery-openings.

(7) Adult integument relatively thin and collapsible.

(8) Proventriculus generalized, with simple, mobile portal. Proventricular muscle group *l. m.* 2 seemingly lacking.

(9) Fore-wing venation relatively generalized, but with the following specializations: first radial cross-vein lacking, Mf2 and Rs4 completely contracted.

Note on internal classification. The known genera of the subfamily include the nominate genus, with the single species described herein, and the extinct *Protaneuretus*, *Paraneuretus*, and *Mianeuretus*. Together, these four appear to constitute a single tribal entity, to be known as Aneuretini.

[1] While we are in agreement with Clark's elevation of the Aneuretini from tribal to subfamilial rank within the Formicidae, we consider most of his other subfamilial creations unwarranted, e.g., Nothomyrmeciinae, Eusphinctinae, Discothyrinae, and Odontomachinae.

DISTRIBUTION AND ECOLOGY

The present known distribution of *Aneuretus simoni* is shown in Figure 4. At present this species is known only from Ceylon. Here it is apparently more abundant in the southern part of the range, where it is associated with the rather limited rainforest area. Around Kandy and Peradeniya, the two localities from which the species had previously been recorded by other authors, Wilson searched in vain for it during a period of five days (July 10-14), before moving on into the more fruitful Ratnapura area.

The least disturbed forest within the Kandy-Peradeniya area is that of the Udawaddatekele Sanctuary, located just north of Kandy and representing the remains of the old royal gardens of the Kandy kings. This forest is relatively lush, with many large evergreen trees, but it is noticeably drier than the forests of the Ratnapura area and does not have a rainforest aspect. The impression that an insect collector gets here is that the ant fauna is diverse, but that the total population (of individuals) is rather sparse. Scarcity of individuals seems to be due in part to the scarcity of rotting wood on the ground, brought about in turn by the incessant activity of Singhalese wood-gatherers from Kandy. The few nesting sites left for wood-dwelling ants are further diminished by the dense population of termites, which on Ceylon are extremely abundant and more than able to hold their own in competition with the ants.

The following general observations were made with respect to the ant fauna of the Udawaddatekele Sanctuary. A great many, perhaps most, of the myrmicines, dolichoderines, and formicines nest on the ground in pieces of rotting wood, and forage both on the ground and up onto low vegetation. Ponerines nest primarily in pieces of rotting wood on the ground also, and confine their foraging to the ground. A high-arboreal fauna is not well developed, either in species or individuals. Judging from the number of individuals seen both in and away from nests, the dominant genera on the ground appear to be *Ponera* and *Pheidole,* followed by *Myrmicaria, Solenopsis* (*Diplorhoptrum*), and *Euponera* (*Mesoponera*), in that order. Also abundant, but considerably less so than the above genera, are *Leptogenys* (*s.*

lat.), *Paratrechina* (*Nylanderia*), and *Pseudolasius*. Among the low vegetation foragers, *Technomyrmex* leads, followed by *Tetramorium* (with *Xiphomyrmex*), and then *Polyrhachis* and *Camponotus* in that order. *Crematogaster* forages on the ground and up into the trees, but is rather scarce in this locality.

While not a single specimen of *Aneuretus simoni* was taken

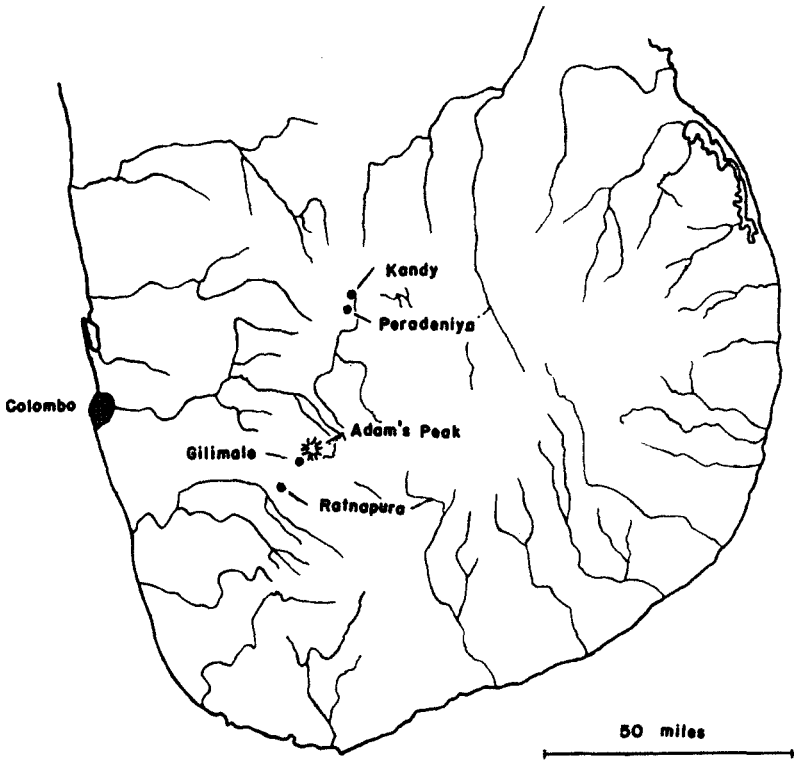

Fig. 4. Map of the southern half of Ceylon, showing the localities where *Aneuretus simoni* has been collected. The port of Colombo is included only for reference.

from the Kandy-Peradeniya forests, where it was most expected, it proved to be one of the dominant ants not far to the south, in the area between Ratnapura and Adam's Peak. At Ratnapura it was found to be extremely abundant in second-growth forest

around the city reservoir, and in similar "scrub" forest just two miles east of the city. It was also discovered in the extensive tract of rainforest that lies northeast of the village of Gilimale and near the foot of Adam's Peak.

The Gilimale forest was made the site of further intensive collecting in order to gain a picture of the natural environment of *Aneuretus*. Although far from being primary over most of its range, this forest is one of the least disturbed in Ceylon, and is probably not greatly different in elementary composition from the virgin rainforest of the nearby Sinharaja district.[1] In at least one spot remote from the main trails, the forest was found to approach what appeared to be a primary condition and exhibited several aspects of the "normal" tropical rainforest: trees forming several stories and a closed canopy, undergrowth sparse, and leaf litter and mold thin. Rotting wood is generally more abundant on the ground than at Kandy, but the total ant population is only slightly denser. The order of genus-dominance in the ant fauna is quite similar to that at Kandy, with the striking introduction of *Aneuretus* among the most prevalent components. On the ground, *Ponera* and *Pheidole* appeared to be the most abundant, as at Kandy. These are followed by *Myrmicaria, Aneuretus, Paratrechina* (*Nylanderia*), *Euponera* (*Mesoponera*), and *Euponera* (*Brachyponera*), in that order. Among the genera foraging on low vegetation, *Technomyrmex* is by far the most abundant, followed by *Polyrhachis* and *Camponotus*. *Tetramorium* occurs, but is far less common than at Kandy. *Crematogaster* is also present but relatively scarce.

In the Gilimale forest, colonies of *Aneuretus simoni* were most abundant at the edge of clearings (see Plate 3). This, coupled with the fact that the species is also successful in the scrubby forests around Ratnapura, may suggest that it is not naturally a dweller of the deep rainforests, but is adapted to clearings and more open forest types.

Some consideration should be given as to why *Aneuretus simoni* has been able to survive, and indeed flourish locally, in Ceylon, while in other parts of the world the aneuretines have faded to extinction. The general problems of extinction and range delimitation are certainly among the most complicated and least understood in biology, and to attempt to supply an

[1] For a description of the Sinharaja forest, see Baker (1938).

answer in this particular case with any tone of resoluteness would be unwarranted. Nevertheless, it may be of help to future students to mention a special condition of the Ceylon environment which appears to favor the survival of *Aneuretus*. This is the relatively weak development of the two ant genera *Pheidole* and *Crematogaster*. These two groups between them tend to occupy both the preferred nest site and food niche of *Aneuretus* (so far as these are known), and in many other tropical areas of the world they are overwhelming dominants of the ant fauna. On Ceylon, *Pheidole* is, to be sure, quite abundant, but relatively much less so than in comparable forests studied (by Wilson) in tropical Mexico and Melanesia, and it is represented by a smaller number of species. *Crematogaster* is very sparsely represented in both species and individuals.

It is also important to emphasize in this connection that since *Aneuretus simoni* is both ground-dwelling and primarily ground-foraging, its principal competition probably comes not from the dolichoderines, which are the phylogenetic successors of the aneuretines, but rather from the ponerines and myrmicines.

During the course of the field work in 1955 a total of 20 nests of *Aneuretus simoni* were collected. The number of individuals in each ranged from only two to over one hundred. Only two of the nests yielded dealate queens. One of these had, in addition to the queen, 94 minor workers, one major worker, and a quantity of eggs and small-to-medium larvae. The other contained what appeared to be an incipient colony, with eight relatively small minor workers and a quantity of all stages of brood in addition to the queen. Two other nests contained alate queens, and two contained males. Eight contained major workers, but there were never more than two of these to a nest. Nearly all of the twenty nests contained brood of various stages.

Eighteen of the 20 nests were in pieces of rotting wood on the ground. The pieces ranged in size from small twigs up to fallen tree-limbs three inches in diameter. In most cases the wood had decomposed to the extent that it could be easily crumbled in the hands. In two instances the *Aneuretus* were found beneath rather large rotting logs on the ground. No nests at all were found under rocks or in the open soil away from wood.

Numerous workers were found foraging during the daytime, during both overcast and sunny weather. They seemed to prefer shady places, and very likely were nocturnal also, although no field observations could be made during the night to check this supposition.[1] The great majority of workers encountered away from the nest were running over the surface of the ground; a few were taken on herbaceous plants and shrubs at heights of up to four feet.

Only a few observations were made on food habits. As might be expected of a primitive ant, *Aneuretus* is predaceous. On two occasions in the field, workers were found carrying entomobryid collembolans. In an artificial nest, workers of a colony accepted entomobryids readily and on one occasion captured about twenty of these insects in the course of one morning. Most significantly, the larvae were given the entomobryids directly, in the primitive ponerine fashion, and they fed on them separately from the workers. Workers in the artificial nest also accepted sugar water readily, and at each feeding this substance was distributed rapidly around the colony until all the adult individuals had full, distended gasters.

Adult trophallaxis was observed on several occasions. The donor opened its mandibles wide while the acceptor fed with closed mandibles from the donor's lower mouthparts. On one occasion a worker was seen donating to two of its sisters simultaneously. The occurrence of adult-larval trophallaxis was not investigated, although it is perhaps significant in this respect that callow workers in the artificial nest seemed extremely attentive of the brood, remaining close to it at all times.

In life the *Aneuretus* workers have the deceptive appearance of small yellow *Pheidole* minor workers, although to the experienced observer their general behavior is very un-myrmicine. They almost always keep their long petiole folded up against the posterior face of the propodeum, with the gaster correspondingly partly elevated. In foraging, they move at about an average gait for ants of comparable size; very roughly speaking, they are slower than most dolichoderines, such as *Technomyrmex albipes,* but faster than most ponerines, such as *Ponera coarctata.* Like many of the higher dolichoderines, they are much given to

[1] The workers of a colony maintained for a short time in an artificial nest foraged from the brood chamber into the uncovered food chamber during both the day and night.

halting abruptly at intervals, standing motionless for a moment, and then abruptly starting off again, often in another direction. When they are disturbed away from the nest, this behavior is intensified, with the workers dashing for a short distance, then halting and remaining perfectly still for a while, then dashing off again; under these conditions they show themselves capable of considerable speed and agility. When a nest is first broken open, the minor workers swarm out aggressively and run over any alien object offered them, but they do not attempt to bite or sting. Major workers seem to be more timid, and do not venture out in this fashion. The aggressiveness of the minor workers is usually short-lived, and they soon retreat back into the undisturbed part of the nest, leaving unprotected any brood which may happen to be in the exposed chambers. Later, they venture out singly to retrieve the brood.

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PLATES

PLATE 1

A, Wings of queen. *B*, Wings of male. *C*, *G*, Queen. *D*, Male. *E*, *H*, Worker major. *F*, *I*, Worker minor.

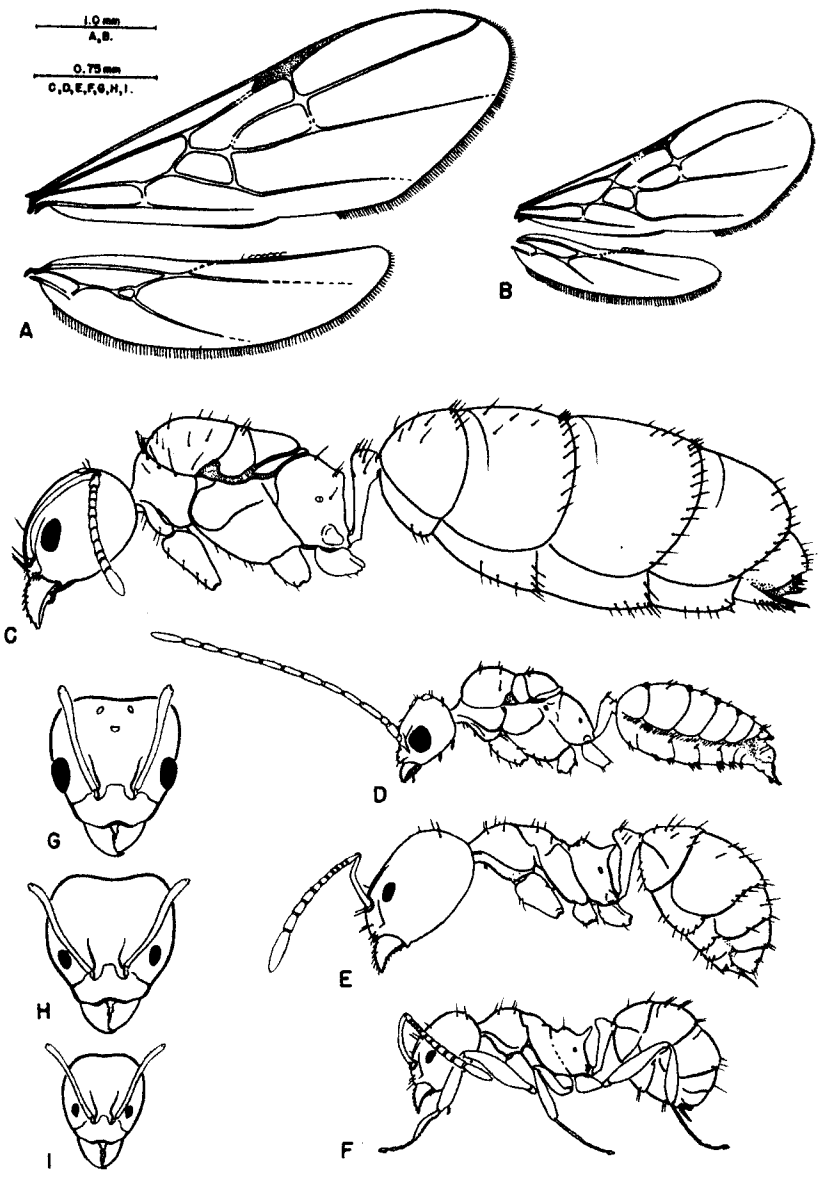

PLATE 1

PLATE 2

A, Male mandible. *B*, Worker mandible. *C*, Terminus of male abdomen, showing intact genitalia. *D-H*, Components of male genitalia isolated: *D*, subgenital plate (sternite IX); *E*, paramere; *F*, volsella; *G*, penis valve; *H*, tergites IX and X with pygostyles.

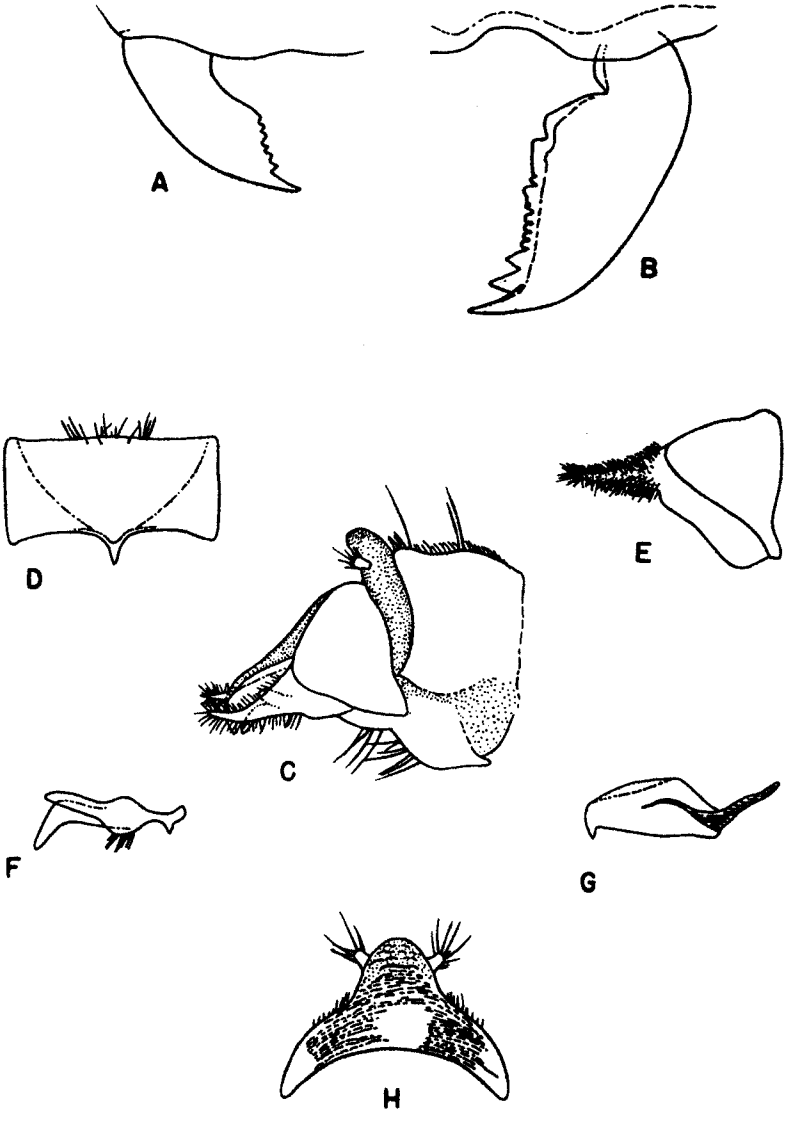

PLATE 2

PLATE 3

1. Rainforest near Gilimale, Ceylon; looking from a hill at the outskirts of Gilimale over the forest canopy toward the cloud-enveloped base of Adam's Peak in the distance.

2. Trail in the interior of the Gilimale forest, at a spot where *Aneuretus simoni* was one of the dominant ants.

PLATE 3