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The higher classification of the ant subfamily Leptanillinae (Hymenoptera: Formicidae)

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Abstract. Until now the ant subfamily Leptanillinae has been closely linked with the army ant subfamilies Dorylinae and Ecitoninae, but on relatively tenuous evidence. The current phylogenetic study strongly indicates that this view is incorrect and that the leptanillines really constitute the sister-group of subfamily Ponerinae, and are at a considerably greater taxonomic distance from the Army Ant subfamilies. Three tribes are now recognized within the Leptanillinae (Leptanillini; Anomalomyrmini, new tribe; and Apomyrmini, transferred here from Ponerinae: Amblyoponini), containing a total of eight genera with fewer than fifty species in all. The subfamily and its component tribes are diagnosed and discussed here, and a key to genera provided. New taxa described include *Anomalomyrma* Taylor **gen.n.**, type-species *A.taylori* Bolton **sp.n.** and *Protanilla* Taylor **gen.n.**, type-species *P.rafflesi* Taylor **sp.n.**

Introduction

To the present, the history of the ant subfamily Leptanillinae has consisted almost entirely of the history of the single genus *Leptanilla* Emery. Over the years a few very small or monotypic male-based genera have been described as related to *Leptanilla*, but so little is known of these peripheral forms that they have hardly figured in the literature beyond their original descriptions.

Leptanilla, first described by Emery (1870), was usually treated in the early literature as a member of the subfamily Myrmicinae (e.g. Emery, 1895: 769). In an analysis of the genus and its affinities Emery (1904) changed the situation and linked *Leptanilla* to the Dorylinae, later going so far as to create a tribe Leptanillini (Emery, 1910), within the Dorylinae, to hold this genus. Later authors (Wheeler, 1923; Wheeler & Wheeler, 1930) elevated the tribe to subfamily status, a rank it has since retained apart from a rather aberrant elevation to family-level by Bernard (1951). A good historical account of the early taxonomic perambulations of *Leptanilla* has been given by Wheeler & Wheeler (1965).

Without doubt *Leptanilla* workers and queens, those few of the latter that are known, do show a number of characters that are also displayed by the dorylines (Wheeler, 1922: 632–633). These features, and the opinions of early authors such as Emery (1904), are no doubt the reason why both Baroni Urbani (1977) and Wheeler & Wheeler (1985) maintain that *Leptanilla* shows an 'indisputable doryline affinity.' I intend here to dispute this indisputability, and to demonstrate that leptanillines, whilst deserving subfamily status, are in truth the sister-group of the subfamily Ponerinae, and are at a considerably greater taxonomic distance from the army ant subfamilies Dorylinae and Ecitoninae. Obviously this implies that those doryline attributes exhibited by *Leptanilla* have been evolved convergently, as a

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result of the adoption of similar lifeways.

Strong doubts about the doryline affinity of *Leptanilla* first arose when Wheeler & Wheeler (1965) gave detailed descriptions of the larvae of three species. These larvae showed striking differences from the dorylines and exhibited some remarkable apomorphies not shown in any other poneroid group. So impressive were these characters that Baroni Urbani (1977), in his revision of the Leptanillinae as it was then understood, stated that the larvae were the main reason for separating leptanillines from dorylines. The apomorphies, as given by Wheeler & Wheeler (1965), were '(1) the peculiar projection from the ventral surface of the prothorax; (2) the reduction of the spiracles from the normal ten pairs to a single pair, which is located on abdominal somite III; and (3) the shape and stance of the mandibles.' Masuko (1987) has since discovered the function of some of these characters, as mentioned in the discussion of leptanilline larvae, below.

These strong characters isolating larval leptanillines from larval army ants prompted a closer look at the adult morphology of the leptanillines. As with the cerapachyines (Bolton, 1990) the abdominal segments of workers and females were quickly seen to display a wealth of previously unnoticed characters. As the analysis advanced it became apparent that not only were the leptanillines not particularly close to the dorylines, but that they were in fact the sister-group of the Ponerinae. Further, *Apomyrma*, a West African genus originally placed in the ponerine tribe Amblyoponini, was found to be a leptanilline. My current concept of subfamily Leptanillinae is completed by the inclusion of a third, new, tribe which contains two genera from the Oriental and Indo-Australian regions.

Thus the concept of subfamily Leptanillinae outlined below is much expanded and considerably different from earlier understanding. Previous phylogenies have all tended to place leptanillines somewhere near the army ant groups, although most of them clearly indicate that such a placement was tentative and dubious, and lacking adequate characterization. Brown (1954) summed it up quite nicely when he said that the Leptanillinae, in the sense of *Leptanilla* alone, 'has suffered such drastic anatomical reduction in most of the usually valuable phylogenetic characters that it is doubtful whether we shall ever be certain of its true affinities.' He concluded that opinion at the time 'seems to favor relating the group to the Dorylinae.'

Later phylogenies, such as those of Wilson *et al.* (1967), Taylor (1978) and Dlussky (1988), all bring out the Leptanillinae with the army ant subfamilies, but all indicate clearly that the decision is not supported by strong evidence.

Another major problem which has dogged our understanding of the group, as also in the dorylines, has been the development of a dual taxonomy. By this I mean that one system has been developed for workers (and females where known), and a separate and unrelated system has been adopted for males. Within the Leptanillini this has resulted in the description of many isolated species-level taxa based solely on males, and has also led to the diagnosis of whole genera based solely on individuals of this sex, a process which unfortunately is still continuing (Kugler, 1987). Petersen (1968) and Baroni Urbani (1977) give systematic notes on these male-based genera. This is an unhappy state of affairs which needs to be cleared up by the acquisition of whole-colony samples, so that the various castes and sexes can be associated. I feel sure that when this has been accomplished the number of nominal species-level taxa now recognized in Leptanillini (thirty-six) will fall to a lower figure, and a number of names currently assigned generic status within Leptanillini will fall as synonyms.

The biology of the leptanillines is little understood. All presently known species are hypogaeic and, for the most part, that is all that is known. *Leptanilla* has been claimed to be a nomadic mass-forager for many years (e.g. Wheeler, 1910), probably because of its doryline-like dichthadiiform female, but published evidence showing details of such a lifeway has been lacking until relatively recently.

Masuko (1987) has found that *Leptanilla japonica* feeds exclusively on geophilomorph centipedes, in the soil. Colonies are small, with only about 100 workers, a single queen, and 100–200 brood. Perhaps the strangest biological feature he discovered is that queens feed only on exudations of larval haemolymph, secreted from a special gland on abdominal segment 3. This gland was thought to be a spiracle by Wheeler & Wheeler (1965), as discussed below in the notes on leptanilline larvae. The colony cycle is summarized thus by Masuko (1987). 'In the growing phase of larvae, intensive hunting of centipedes is conducted. The larvae consume the victims and grow quickly. During this period the queen's gaster remains constricted. When the larvae mature, colonies go into the oviposition phase. The queen performs LHF [larval haemolymph feeding] actively and becomes physogastric. Prey consumption ceases and larvae pupate all at once while eggs are laid in mass.'

The reorganized and redefined subfamily Leptanillinae, as discussed in this paper, is still small, containing less than fifty species unevenly distributed through eight genera; thirty-one species of which are placed in *Leptanilla*. The subfamily is restricted to the Old World and most species are found in the tropics and subtropics, although some occur in more temperate latitudes. A synopsis of the subfamily and its distribution is outlined later in this paper, but readers interested in the taxonomy of individual species of *Leptanilla* should consult Baroni Urbani's (1977) excellent account.

Subfamily Leptanillinae

Leptanillini Emery, 1910: 32 [as tribe of Dorylinae]. Type-genus: *Leptanilla* Emery, 1870: 196.
Leptanillinae: Wheeler, 1923: 335. [Raised to subfamily.]

Diagnosis

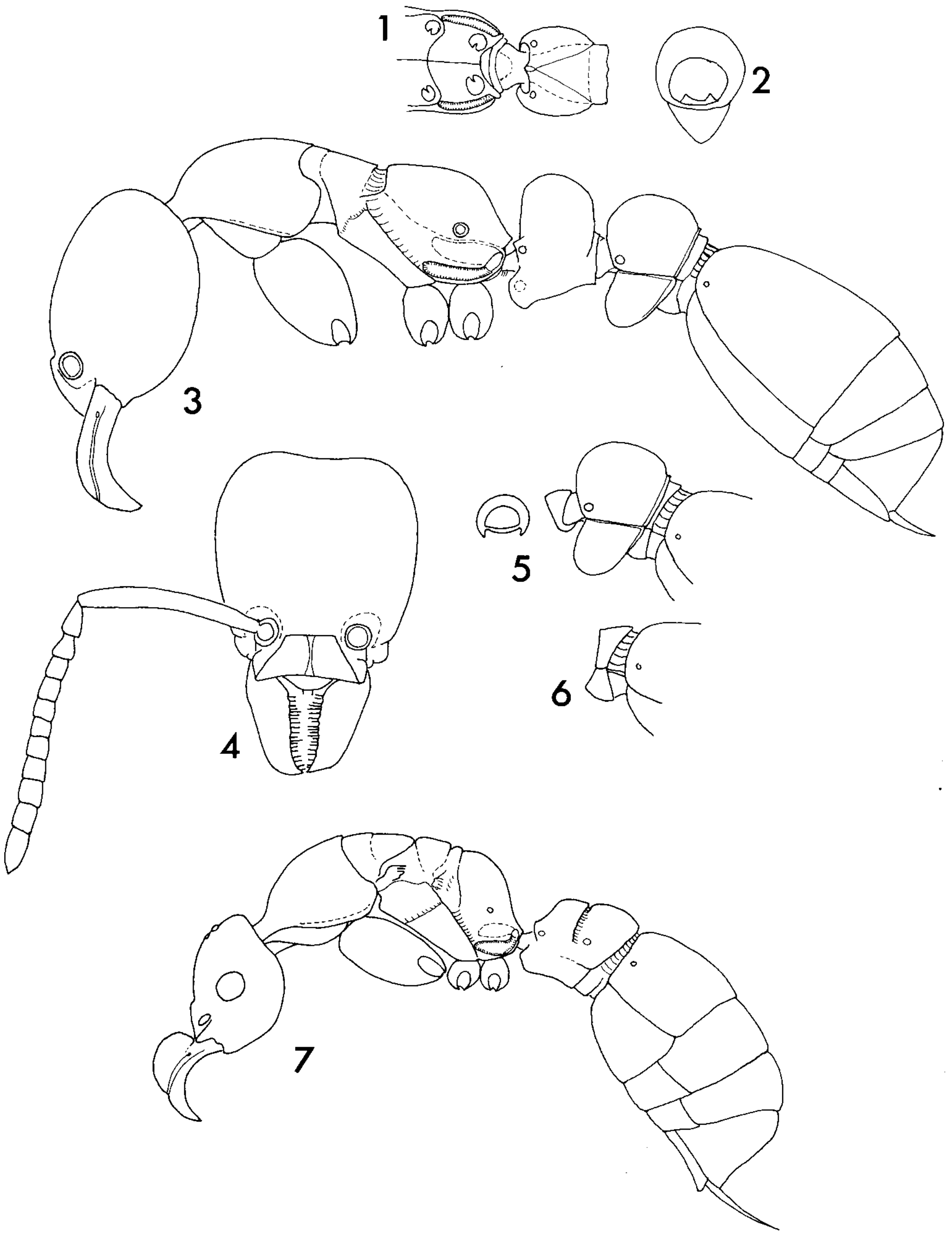
Worker

Small to minute monomorphic subterranean ants with the following combination of characters.

1 Eyes absent (Figs 3, 9, 13).
2 Frontal lobes absent, the antennal sockets directed dorsally and completely exposed (Figs 4, 11, 15).
3 Antennae with 12 segments (in all known species).
4 Promesonotal suture present and mobile, usually deeply constricted.
5 Metapleural lobes absent.
6 Metasternal process absent.
7 Metacoxal cavities closed; with a complete cuticular annulus surrounding each cavity (Figs 1, 8, 12).
8 Propodeal spiracle circular and far back on side of sclerite, low on side (except in a few minute species of *Leptanilla* where the dorsum is very depressed) (Figs 3, 9, 13).
9 Tergite and sternite of petiole fused, without trace of a suture; or sternite reduced to a vestigial sclerite posteromedially (Fig. 8).
10 Helcium with sternite reduced, not visible in profile; sternite seen in frontal view as a transverse strip between the arms of the inverted U-shaped tergite; helcial tergite and sternite fused (Figs 5, 10, 14).
11 Spiracle of abdominal segment 3 large and far forward, very close to or even on anterior face of posttergite.
12 Abdominal segment 4 without tergosternal fusion, the posttergite broadly overlapping the poststernite laterally.
13 Stridulatory apparatus absent from posttergite of abdominal segment 3 and pretergite of segment 4 dorsally.
14 Spiracles of abdominal segments 1–4 exposed, of 5–7 concealed by preceding tergites (Figs 3, 9, 13).
15 Pygidium (tergite of abdominal segment 7) large, unarmed, convex across and downcurved posteriorly.
16 Sting long strong and powerfully developed.

Female

Known from only six species, four of which belong to genus *Leptanilla*. Larger than conspecific workers and like them with the pronotum extensively represented on the dorsal alitrunk. Characters 2, 3, 5 and 7–15, as worker. Character 6 of workers presumably also applies throughout females, but has been proved by dissection only in *Apomyrma*. Character 1 of workers is variable in females as eyes are present in *Apomyrma* (Brown *et al.*, 1971: 266, Fig. 6) and *Anomalomyrma* (Fig. 7), but vestigial to absent in *Leptanilla* females. Character 4 of workers is present in females of *Leptanilla*, which are dichthadiigyne; known females of other genera are alates with a full complement of flight sclerites. *Apomyrma* has moderately complete venation but lacks a pterostigma. In *Leptanilla* females have only one separated waist segment, abdominal segment 2 (petiole), whilst conspecific workers have segments 2 and 3 separated (petiole + postpetiole). Elsewhere



Figs 1–7. 1–6, *Protanilla*, worker of undescribed species [scale: HW=0.56 mm]: 1, ventral view of posterior alitrunk and second abdominal segment; 2, posterior view of second abdominal segment; 3, whole body profile; 4, full-face view of head (left antenna omitted); 5, third abdominal segment to show profile of helcium (right) and frontal view (left); 6, fourth abdominal segment to show presclerites. 7, whole body profile of *Anomalomyrma taylori* female (queen) [scale: AL= 1.92 mm]. Sculpture and pilosity omitted from Figs 1–7.

in the subfamily both castes have the same number of separated waist segments, namely one in *Apomyrma* and two in *Anomalomyrma* (the female of *Protanilla* remains unknown).

Male

Apart from a single pharate male of *Apomyrma* noted by Brown *et al.* (1971), no worker-associated males have ever been described in Leptanillinae. Numerous isolated males (eighteen species), assumed to belong in Leptanillini, have been described in *Leptanilla* and its satellites *Phaulomyrma*, *Noonilla*, *Scyphodon* and *Yavnella*. Indubitably some of these will eventually be found to be conspecific with worker-based species within *Leptanilla* when collections containing workers in association with males are made. Petersen (1968) gives a good synopsis of this sex; see also Baroni Urbani (1977) and Kugler (1987).

Males of *Protanilla* and *Anomalomyrma* remain unknown, or just possibly may be represented by one of the male-based genera mentioned above, and the pharate male of *Apomyrma* provides very little information. Thus the diagnosis below is both tentative and unsatisfactory, and applies with certainty only to members of tribe Leptanillini, in the sense of this publication.

1. Mandibles usually reduced, represented by a pair of small, apparently non-opposable lobes; more rarely the lobes larger and plate-like.
2. Antennal sockets exposed; antennae with 13 segments.
3. Alate; venation absent or reduced to a single vein just behind the leading edge (probably a fusion of $Sc+R+Rs$), or with apical abscissa of *Rs* free. More rarely *Cu* and the basal abscissae of *Rs* and *M* may be visible as spectral veins.
4. Pterostigma absent.
5. Waist with only abdominal segment 2 (petiole) separated.
6. Abdominal segment 4 without tergosternal fusion.
7. Genitalia large to enormously hypertrophied, often bizarre; not retractile.

Larva

As with the males, larval descriptions have only been accomplished for a few species of *Leptanilla* (five), and for *Apomyrma stygia*. For details see Wheeler & Wheeler (1965, 1971, 1989), Kugler (1987), and the synoptic larval study by Wheeler & Wheeler (1976).

Larvae belonging to genus *Leptanilla* are very distinctive, possessing the three remarkable characters mentioned in the introduction. Masuko (1987) has recently discovered the function of two of these. The peculiar projection from the ventral surface of the larval prothorax is now known to be a specialized carrying device, which workers grip with their lower mouthparts, but not the mandibles. Masuko also notes that the enlarged 'spiracle' on abdominal segment 3, as described by Wheeler & Wheeler (1965, 1976), is not a spiracle at all but a specialized organ for feeding haemolymph to the queen, as mentioned in the introduction to this paper. Masuko adds that under SEM observation normal spiracles can be seen.

Larvae of *Apomyrma* are leptanilline in shape but lack the diagnostic features of *Leptanilla*. Despite the sterling efforts of the Wheelers' it is apparent that comparative studies of many more leptanilline larvae need to be undertaken before authoritative synapomorphies can be worked out.

Phylogeny of Leptanillinae

The construction of the helcium (articulatory pretergite and presternite of abdominal segment 3) is proposed here as a strong synapomorphy of the clade Ponerinae + Leptanillinae. The Ponerinae in this instance excludes the cerapachyine tribes Cerapachyini, Cylindromyrmecini, and Acanthostichini, which are now regarded as a discrete subfamily Cerapachyinae (Bolton, 1990).

The Ponerinae and the Leptanillinae share the same very specialized and characteristic helcial structure, which is unique among all the poneroid subfamilies. It may be postulated that this structure has evolved twice, once in each subfamily, but as it appears exactly the same in both subfamilies and is unlike that of any other poneroid subfamily, it seems most parsimonious to accept a common origin for the articulation, to accept that it has arisen only once during the course of poneroid evolution, and to conclude that Leptanillinae and Ponerinae diverged after the evolution of this specialised articulation.

The helcium in Leptanillinae and Ponerinae consists of a thickened, inverted U-shaped collar formed from the pretergite (Figs 5, 10, 14). The helical sternite is reduced to a thin transverse strip, which may be shallowly convex to concave, running between the arms of the U-shaped tergal collar, some distance up from their apices and completely fused to the inner face of the tergite on each side. In both anterior and profile view the helcial sternite does not project ventrally below the apices of the tergite.

The two subfamilies within this clade are distinguished as follows in workers and females. After each apomorphy the corresponding plesiomorphic state, applicable to the alternative subfamily, is given in square brackets.

1 Apomorphies of Ponerinae.
Abdominal segment 4 with tergosternal fusion. [Tergosternal fusion of abdominal segment 4 absent in Leptanillinae.]
Metapleural lobes present. [Metapleural lobes absent in Leptanillinae.]

2 Apomorphies of Leptanillinae.
Spiracles of abdominal segment 3 large and far forward, very close to or on anterior face of post-tergite (Figs 2, 5, 9, 10, 13, 14). [Spiracles small and more posteriorly sited in Ponerinae.]

Apart from the above, the Leptanillinae have closed metacoxal cavities, with a complete cuticular annulus (Figs 1, 8, 12), and eyes are universally absent in all known workers (Figs 3, 4, 9, 11, 13, 15). In the Ponerinae the metacoxal cavities are open or, more usually, the cuticular annulus is interrupted by a mobile suture. Metacoxal cavities are closed only in a few very specialized small genera. Among the Ponerinae eyes are generally retained, being lost only in individual species of a few genera and lost independently in one or two extremely specialized small genera.

Separation from army ant subfamilies

The morphological characters which underlie the decision to uncouple Leptanillinae from its traditional association with the army ant subfamilies are as follows. First and foremost, the helcium in the army ant subfamilies (and in Cerapachyinae) is differently specialized. The helcial sternite in these groups is large, thick, and strongly convex, so much so that it bulges ventrally and is clearly visible in profile without dissection; it can normally be seen in ordinarily point-mounted specimens. In this condition it bears a strong resemblance to a reduced, fused, but otherwise normally constructed dorsal and ventral pair of abdominal sclerites, and hence is plesiomorphic at this level of analysis. The condition seen in leptanillines and ponerines, described above, is a modification of this state, with enlargement of the tergite and reduction and specialization of the sternite, and hence is apomorphic.

Apomorphic developments common to workers of the army ant subfamilies (and also the Cerapachyinae), but lacking in the Leptanillinae and Ponerinae, include the posterior migration of the spiracles of abdominal segments 5–7 so that all abdominal spiracles are visible. Specialization of the army ant pygidium (tergite of abdominal segment 7) has taken place, either by extreme reduction in size, development of a transverse furrow subapically, or by flattening its dorsum and arming it with teeth or denticles. Leptanillines and ponerines retain the plesiomorphic state here, having abdominal spiracles 5–7 concealed by the preceding tergite (Figs 3, 9, 13) and having a simple large pygidium which is convex and evenly curved.

Apart from these features, which cover all the subfamilies concerned, it should also be pointed out that the Ecitoninae and the aenictines have the poststernite of abdominal segment 3 much reduced (apparently independently) relative to the third posttergite, and that the Dorylinae and Ecitoninae both retain the plesiomorphic state of having the propodeal spiracles situated far forward. In leptanillines the poststernite of abdominal segment 3 is not drastically reduced relative to the size of posttergite 3, and the propodeal spiracles are shifted backwards on the sclerite.

Finally, leptanilline males, whilst unique in several ways (lobate mandibles, strange to bizarre genitalia, much-reduced venation), do not show any of the 'sausage-fly' habitus associated with the army ant subfamilies, nor do they have the completely retractile genitalia characteristic of army ant males. Petersen's (1968) excellent review of leptanilline males shows just how different they are from the males of army ants.

Other considerations

A number of characters at first considered useful in this survey later proved to be of little or no value, and a couple of these merit a comment.

I first thought that the lack of a stridulatory system (dorsally on posttergite of abdominal segment 3 and pretergite of segment 4) in leptanillines may have value in the phylogenetic analysis. Unfortunately this is a character which comes and goes with baffling irregularity, not just in ants but in the Vespoidea (*sensu* Gauld & Bolton, 1988) in general. The stridulatory system occurs in all Myrmicinae examined so far, but appears to be universally absent in the army ant subfamilies and the cerapachyines, as well as the leptanillines. Among the Ponerinae it is present in Ponerini, Platythyreini, and the 'lower' Ectatommini, but seems wholly absent from the Amblyoponini and also missing from some 'higher' ectatommine genera.

Some characters important in the diagnosis of tribe Leptanillini are of no value at subfamily level as they are autapomorphies of the tribe. Included here are the larval characters mentioned above and the reduced wing venation. Even within the Leptanillini in its older sense the reduced venation, supposedly characteristic of the males, has been compromised, as *Yavnella* (Kugler, 1987: 54, Fig. 14) shows a much fuller vein system than is usually encountered in *Leptanilla* (Baroni Urbani, 1977: 473, Figs 43, 44). *Apomyrma* has an even more complete venation in the female (Brown *et al.*, 1971: 267, Fig. 7).

The occurrence of dichthadiiform females in genus *Leptanilla* and in the army ant subfamilies is not a synapomorphy. It seems most likely that the condition has arisen independently in each group as a nomadic and mass-predatory lifeway was evolved. Outside the aenictines, dorylines, ecitonines and genus *Leptanilla*, dichthadiigynes also occur in some *Leptogenys* (Ponerinae) (e.g. Wilson, 1958; Bolton, 1975), in *Onychomyrmex* (Ponerinae) (Brown, 1960), in *Simopelta* (Ponerinae) (Gotwald & Brown, 1967), and in at least one species of *Sphinctomyrmex* (Cerapachyinae) (Brown, 1975), where nomadism is known or suspected. Standing apart from this, other leptanillines such as *Apomyrma* and *Anomalomyrma* have normal alate females, although the peculiar fusion of abdominal sternites 2 and 3 in *Anomalomyrma* females (Fig. 7) may indicate the beginnings of yet another independent evolution of dichthadiigyny.

The leptanilline tribes and genera

Until now this subfamily has only contained the single tribe Leptanillini, but the current study indicates that three tribes are present: Leptanillini, Apomyrmini (transferred here from subfamily Ponerinae) and Anomalomyrmini, a new tribe from the Oriental and Indo-Australian regions, which is closer related to Leptanillini than either is to Apomyrmini.

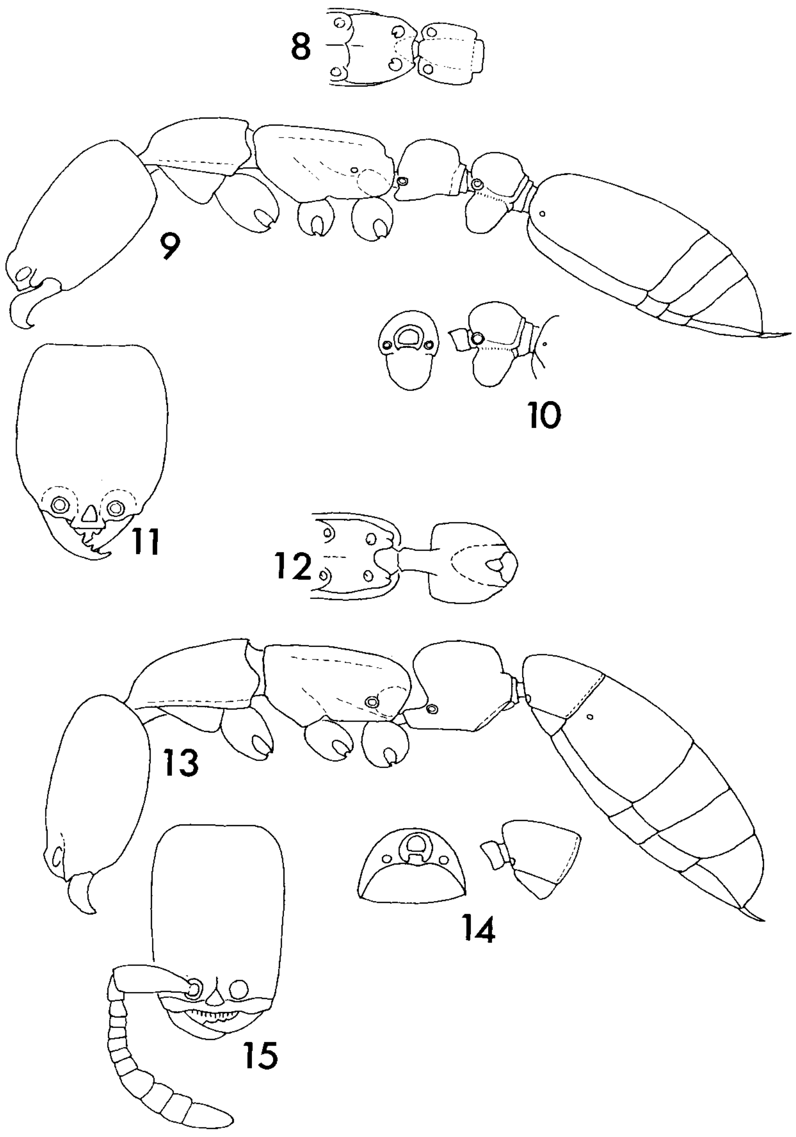
A synopsis of the subfamily is given below, followed by a discussion of the phylogenetic relationships of the three tribes, and preliminary keys to genera have been drawn up. Following this the tribes are diagnosed and descriptions of their abdominal external morphologies are given.

Synopsis of subfamily

Leptanillinae Emery
Tribe Leptanillini Emery
    Genus *Leptanilla* Emery (=*Leptomesites* Kutter)
    Genus *Noonilla* Petersen
    Genus *Phaulomyrma* Wheeler & Wheeler
    Genus *Scyphodon* Brues
    Genus *Yavnella* Kugler
Tribe Apomyrmini Dlussky
    Genus *Apomyrma* Brown, Gotwald & Levieux
Tribe Anomalomyrmini Taylor
    Genus *Anomalomyrma* Taylor
    Genus *Protanilla* Taylor

Phylogeny of the leptanilline tribes

The characters cited below are necessarily based on the worker caste. Worker-associated females and males are scanty and far too poorly known to provide characters which can be proved to be universal. In queens, however,



Figs 8–15. 8–11, *Leptanilla*, worker of undescribed species [scale: HW= 0.34 mm]: 8, ventral view of posterior alitrunk and second abdominal segment; 9, whole body profile; 10, third abdominal segment to show profile of helcium (right) and frontal view (left); 11, full-face view of head (antennae omitted). 12–15 *Apomyrma stygia*, worker [scale: HW= 0.36 mm]: 12, ventral view of posterior alitrunk and second abdominal segment; 13, whole body profile; 14, third abdominal segment to show profile of helcium (right) and frontal view (left); 15, full-face view of head (left antenna omitted). Sculpture and pilosity omitted from Figs 8–15.

a few possibilities occur which may prove valuable. For instance, known queens of Leptanillini are dichthadiigyne (Baroni Urbani, 1977), a derived condition, whilst those of Apomyrmini and Anomalomyrmini are alates. The queens of apomyrmines and anomalomyrmines have the same number of separated abdominal segments as the workers, but in *Leptanilla* there is dimorphism, with queens having one separated segment (petiole) and conspecific workers two (petiole + postpetiole).

Plesiomorphic states are given in square brackets following each apomorphy, the plesiomorphy occurring in the alternative group in each case.

1 Apomyrmini *versus* Leptanillini + Anomalomyrmini.
  (a) Apomorphies of Apomyrmini.
    Antennae clavate (Fig. 15) [filiform in 1b].
    Petiole pedunculate (Figs 12, 13) [sessile in 1b].
    Tergite of petiole hypertrophied (Figs 12, 13) [of normal size in 1b].
    Helcium attached low on anterior face of abdominal segment 3 (Figs 13, 14) [attached at midheight in 1b].
    Anterior face of abdominal tergite 3 expanded ventrally, inserted as transverse strip between pre- and poststernites [tergite not expanded ventrally, not inserted between pre- and post-sternites in 1b].
    Transverse sulcus present on abdominal sternite 3 (Fig. 14) [sulcus absent in 1b].
  (b) Synapomorphies of Leptanillini + Anomalomyrmini.
    Spur formula reduced from 1, 2, 2 [formula 1, 2, 2 in 1a].
    Petiole tergite and sternite completely fused (Figs 3, 9) [unfused in 1a].
    Abdominal segment 3 reduced and isolated from segment 4 by posterior constriction, to form a discrete postpetiole [segment 3 not isolated from segment 4 in 1a].
    Abdominal segment 4 tubulate anteriorly (Figs 3, 6, 9, 10) [not tubulate anteriorly in 1a].

2 Leptanillini *versus* Anomalomyrmini.
  (a) Apomorphies of Leptanillini.
    Median portion of clypeus narrowed and raised (Fig. 11) [broad and flat in 2b].
    Metanotal groove absent (Fig. 9) [present in 2b].
    Articulatory foramen of petiole in posteroventral alitrunk closed by a floor of thin cuticle (Fig. 8) [foramen open, no cuticular floor in 2b].
    Constriction between abdominal segments 3 and 4 almost or quite as narrow as helcium (Figs 9, 10) [much broader than helcium in 2b].
  (b) Apomorphies of Anomalomyrmini.
    Mandibles with bizarre armament [bizarre armament lacking in 2a].
    Median portion of clypeus sharply marginate laterally (Fig. 4) [immarginate in 2a].
    Metapleural gland bulla longitudinal and running forward below propodeal spiracle (Fig. 3) [bulla semicircular and behind spiracle in 2a].
    Metapleural trench present (Figs 1, 3; see description of ventral alitrunk) [trench absent in 2a].

Key to tribes and genera (workers)

Note. Keys to males and females which have any real meaning cannot yet be constructed. Apart from the fact that males remain unknown in Anomalomyrmini and insufficiently known in Apomyrmini, too many of those small genera already described in Leptanillini are based only upon the morphological peculiarities of the males of single species. Scanning the available data on males it seems that a number of morphoclines exist in this sex, among which are shortening, broadening and flattening of the head, reduction of venation, elongation and specialization of the genitalia, and location of antennal sockets. Until the mutual relationships of these 'genera' can be examined in detail, and whilst no worker-related males are known, very little can be done. But one point must be stated. I most strongly urge a cessation in the description of vague genera based on isolated males as they tend to increase confusion rather than enlightenment, and create problems that may be decades in the solving. For species-level information on leptanilline males the reader is referred to Petersen (1968), Brown *et al.* (1971) Baroni Urbani (1977), Kugler (1987) and their included references.

1 Petiole pedunculate (Figs 12, 13). Differentiated postpetiole absent (Fig. 13) Helcium attached low down on anterior face of abdominal segment 3. (Apomyrmini) .... *Apomyrma*

– Petiole sessile (Figs 3, 9). Differentiated pospetiole present (Figs 3, 9). Helcium attached at midheight of abdominal segment 3 2

2 Mandible with 3–5 teeth, all located on distal half of masticatory margin (Fig. 11). Maxillary palp with 1 segment. Metanotal groove vestigial to absent (Fig. 9). Bulla of metapleural gland rounded, located behind level of spiracle (Fig. 9). Meta-

pleural trench absent (Figs 8, 9). (Leptanillini) .... *Leptanilla*

– Mandibles with many more than 5 peg-like to hook-like teeth (Fig. 4). Maxillary palp with 4 segments. Metanotal groove present, strong and impressed (Fig. 3). Bulla of metapleural gland elongate and narrow, running below the spiracle (Fig. 3). Metapleural trench present (Figs 1, 3). (Anomalomyrmini) 3

3 Mandibles elongate, narrowly triangular and downcurved, equipped with numerous peg-like teeth on inner surface (Figs 3, 4) .... *Protanilla*

– Mandibles surmounted by a large erect convex lamella (cf. Fig. 7) which is lined internally with numerous short recurved cuticular teeth .... *Anomalomyrma*

Tribe Leptanillini

Leptanillini Emery, 1910: 32 [as tribe of subfamily Dorylinae]. Type-genus: *Leptanilla* Emery, 1870: 196.

Leptanillini: Wheeler, 1923: 335 [sole tribe of subfamily Leptanillinae].

Diagnosis

Worker

1 Mandibles elongate, narrowly blade-like and curved, with a relatively large tooth at about the midlength; blade unarmed proximal to this tooth but with 1–2 smaller teeth distally before the apical tooth (Fig. 11).
2 Labrum without peg-like teeth.
3 Palp formula 1, 1.
4 Clypeus narrow between antennal sockets, raised medially (Fig. 11).
5 Antennae not clavate.
6 Middle leg with one spur; hind leg with 1–2 spurs.
7 Metanotal groove absent to vestigially present (Fig. 9).
8 Metapleural gland bulla rounded in outline, situated behind and below level of propodeal spiracle (Fig. 9).
9 Metapleural trench absent (Figs 8, 9).
10 Articulatory cavity of petiole in postero-ventral alitrunk closed by a secondary floor of cuticle, the cavity not running forward toward the metacoxal cavities (Fig. 8).
11 Petiole sessile, the tergite and sternite fused, without trace of suture (Figs 8, 9).
12 Abdominal segment 3 isolated from segments 2 and 4 by strong anterior and posterior constrictions to form a separated postpetiole (Figs 9, 10).
13 Poststernite of abdominal segment 3 (postpetiole) strongly prominent ventrally, without a transverse sulcus behind the helcium (Figs 9, 10).
14 Helcium attached at midheight of anterior face of abdominal segment 3.
15 Presclerites of abdominal segment 4, which articulate in posterior foramen of segment 3, very small, the same size as or only fractionally larger than the helcium in profile.

Female

Dichthadiigyne. Eyes vestigial to absent, ocelli absent. Abdominal segment 3 broadly attached to 4, no postpetiole separated. Hypopygium prominent posteriorly, projecting beyond apex of pygidium in dorsal view. Mandibles narrower and more falciform than in worker. Otherwise characters 2–9, 11 and 14 as worker; condition of character 10 not known.

Male

See characterization of subfamily.

Component genera of Leptanillini

1 *Leptanilla* Emery, 1870: 196 (=*Leptomesites* Kutter, 1948: 286; synonymy by Baroni Urbani, 1977: 433).

The genus currently contains thirty-one species, of which eighteen are based on workers (four with known females). The remaining thirteen are based solely on males. Distributed throughout the Old World, primarily in the tropics and subtropics but several species are known from the temperate zones. Numerous undescribed species of the genus are present in museum collections.

2 *Noonilla* Petersen, 1968: 582.

A monotypic male-based genus from the Philippines. To the best of my knowledge the genus is known only from the type-collection.

3 *Phaulomyrma* Wheeler & Wheeler, 1930: 193.

A monotypic male-based genus from Java, Indonesia; again known only from the type-collection.

4 *Scyphodon* Brues, 1925: 93.

A monotypic male-based genus from Sumatra, Indonesia. Only known from the type-collection.

5 *Yavnella* Kugler, 1987: 52.

This genus is based on the males of two species, one from India and the other from Israel. Both known only from type-material.

Abdominal morphology of Leptanilla worker

Ventral alitrunk and abdominal segment 1 (propodeum) (Figs 8, 9).

Metacoxal cavities closed, with a complete cuticular annulus surrounding each cavity. No metasternal process. Foramen in which petiole articulates has a secondarily developed floor. Original U-shape of the articulation cavity visible, extending between posterior ends of metacoxal cavities, but instead of being open the area has a solid floor of thin cuticle. In posterior view the foramen in the alitrunk where the petiole articulates is almost circular because of this secondary cuticular development. Propodeal spiracle moderate to small, circular, usually low on the side and always far back on the sclerite; with a thick annular sclerite. Bulla of metapleural gland subcircular, situated in lower posterior corner of alitrunk, behind and below the level of the spiracle. Metanotal groove vestigial to absent; metapleural lobes absent.

Abdominal segment 2 (petiole) (Figs 8, 9).

Petiole moderate to large in size, sessile, and with a deep posterior face to the node. Proprioceptor zone visible in profile. Spiracle large, anterior on side of tergite, with a broad annular sclerite. Tergite and sternite completely fused, usually without trace of a suture but in some the suture replaced by a fine ridge. Sternite forming a large ventral process. Posterior foramen almost circular, without distinction between tergite and sternite around the rim, but internally the latter sometimes expanded into a lip or flange.

Abdominal segment 3 (postpetiole) (Figs 9, 10).

Sternite of helcium invisible in profile. In front view the helcial sternite visible as a transverse plate which runs between the inner surfaces of the arms of the collar-shaped helcial tergite, some distance up from the apices of the arms. Helcium attached at mid-height of segment, tergite behind helcium with a declivitous anterior face; post-helcial neck present. Tergite and sternite fused, the suture running the length of the segment in most, but in a few species all trace of the suture has been lost. Posttergite slightly larger than poststernite, the latter strongly prominent and rounded, bulging ventrally. Abdominal segment 3 reduced in size and separated as a discrete postpetiole, bounded by narrow anterior and posterior constrictions. Segment 3 the same size as 2 or slightly larger, much smaller than segment 4. Posttergite of 3 with a posterior declivity and anterior face of poststernite concave. Spiracle large and very conspicuous, with a broad annular sclerite. Spiracle situated far forward on posttergite, on the curve where the side rounds into the anterior declivity.

Abdominal segment 4 (first gastral) (Fig. 9).

Strongly tubulate anteriorly, with a deep girdling constriction between pre- and postsclerites. The presclerites, which articulate in the posterior foramen of segment 3, are very small, usually only marginally larger than the helcium. In some species they are so small that they may be regarded as a second helcium. Posttergite with a short declivitous anterior face, the anterior face of the poststernite transversely concave. Tergosternal fusion absent, the posttergite broadly overlapping the poststernite laterally. Largest segment of abdomen, its spiracle conspicuous anteriorly on the posttergite, much smaller than the spiracle on segment 3.

Abdominal segments 5–7 (Fig. 9).

Tergites and sternites not fused, the former broadly overlapping the latter. Spiracles far forward on segments, invisible, each concealed by the posterior section of the preceding tergite. Pygidium (tergite of segment 7) large, rounded and unarmed, unspecialised; its dorsum strongly downcurved posteriorly. Sting long and strongly developed, very conspicuous and fully functional.

Diagnosis of tribe Anomalomyrmini

Anomalomyrmini Taylor tribe n.

Type-genus: *Anomalomyrma* Taylor gen.n., see below.

Diagnosis

With characters of the subfamily diagnosis, and as follows.

Worker

1 Mandibles either long, narrowly triangular and downcurved (Figs 3, 4), with numerous peg-like to pencil-like teeth on inner faces (Fig. 4); or dorsal surface with a large erect lamella (cf. Fig. 7) which is lined internally with many short recurved cuticular teeth.
2 Labrum with or without peg-like spiniform teeth.
3 Palp formula 4, 1, the labial palpomere large and swollen (*in situ* counts of *Protanilla* species).
4 Clypeus broad medially, raised and with a sharply keeled edge running from the mandibular insertion to the junction with the frons (Fig. 4).
5 Antennae not clavate (Fig. 4).
6 Middle legs without spurs, hind legs each with a single pectinate spur.
7 Metanotal groove present, strongly developed and impressed (Fig. 3).
8 Metapleural gland with an elongate narrow bulla which runs below the propodeal spiracle (Fig. 3).
9 Metapleural trench present below and paralleling metapleural gland bulla, the trench running the length of the segment (Figs 1,3).
10 Articulatory cavity of petiole in posteroventral alitrunk open and U-shaped, running forward toward metacoxal cavities (Fig. 1).
11 Petiole sessile, the tergite and sternite fused, without trace of suture (Fig. 3).
12 Abdominal segment 3 isolated from segments 2 and 4 by strong anterior and posterior constrictions to form a separated postpetiole (Figs 3, 5).
13 Poststernite of abdominal segment 3 (postpetiole) strongly prominent ventrally, without a transverse sulcus behind the helcium (Figs 3, 5).
14 Helcium attached at midheight of anterior face of abdominal segment 3.
15 Presclerites of abdominal segment 4, which articulate in posterior foramen of segment 3, constricted but much larger than the helcium in profile (Figs 5, 6).

Female (based on a single specimen of *Anomalomyrma* (Fig. 7)).

Alate when virgin, the alitrunk with full complement of flight sclerites. Eyes present, situated behind midlength of sides but not shifted to posterior corners of head. Ocelli present. Pronotum large and occupying a large area of the dorsal alitrunk. Postpetiole separated but sternites of petiole and postpetiole fused together and immobile (may be teratological or a modification towards dichthadiigyny). Hypopygium not prominent posteriorly. Otherwise characters 1, 2, 4–6, 8, 9 and 11–15 as worker; character 7 not applicable as flight sclerites present; characters 3 and 10 unknown.

Male

Unknown.

Component genera of Anomalomyrmini

This new tribe contains two previously undescribed genera. Minimal diagnoses are given below as a full taxonomic study of both genera is being prepared by R. W. Taylor (C.S.I.R.O., Canberra). For this reason the tribe name and the new genera are credited to Taylor in the present paper.

Anomalomyrma Taylor gen.n.

Female (Fig. 7). With characters of subfamily and tribe given above. Mandibles unique, elongate and with blade strongly downcurved in profile. Dorsal surface of each mandibular blade surmounted by a high convex vertical lamella of thick cuticle which has its origin close to the base and extends for about two-thirds the length of the blade. Inner surface of this lamella lined with three longitudinal rows of sharp cuticular teeth which are curved backwards and downwards. Beneath the lowest row of teeth is a longitudinal row of stout spiniform setae, directed ventrally. Outer surface of mandible below lamella with a broad longitudinal groove which runs forward from a small laterobasal pit.

Apically the groove crosses the width of the mandible in front of the anterior termination of the lamella. Distal portion of each blade, beyond end of lamella, with a few denticles on the inner margin and with a truncated apex. Labrum with numerous sharp spiniform cuticular teeth which project forward and downward.

Type-species: *Anomalomyrma taylori* Bolton **sp.n.**

The holotype and only known specimen of this species is a dealate female (Fig. 7) from EAST MALAYSIA: Sabah, Kinabalu Nat. Park, 1400 m, 22.v.1987, no. 35a (*Burckhardt & Löbl*) (MHN, Geneva). It was recovered from a litter sample; no workers attributable to this species were present in the sample.

The structure of the petiole and postpetiole in the holotype is very peculiar. The sternites are fused into a single plate which itself is fused laterally to the tergites, so that there is no possibility of flexion between these segments. The alitrunk is large and has a full complement of flight sclerites (Fig. 7). Vestiges of wing-bases indicate that this female was alate when virgin. As in *Apomyrma* the pronotum is large and forms an extensive part of the dorsal alitrunk. The holotype female is a moderately sized ant, with standard measurements of TL 6.0, HL 0.96, HW 1.08 (immediately behind eyes), SL 1.13, PW 0.98, AL 1.92.

A second species is known from a few workers from Japan, to be described elsewhere by Taylor.

Protanilla **Taylor gen.n.**

Worker. With the characters of subfamily and tribe given above. Mandibles elongate-triangular and strongly downcurved apically, lacking the large dorsal lamella described for *Anomalomyrma*, above. Masticatory margin of mandible unarmed to minutely crenulate, and with 3–4 denticles distally on the downcurved portion close to the narrow apex. Inner surfaces of each mandibular blade with numerous blunt elongate peg-like to pencil-like 'teeth', which appear in reality to be modified stout hairs. Outer margin of mandible with a small laterobasal pit subtended by a distinct longitudinal groove which runs anteriorly, the groove traversing the width of the mandible at a point just before the preapical series of denticles. Labrum with a single pair of minute peg-like cuticular teeth (perhaps lacking in some species). Clypeus with a thin median strip which superficially resembles a longitudinal sulcus (Fig. 4). [Genus illustrated by an undescribed species, from Pakistan (BMNH and MHN, Geneva). Figs 1–6.]

Type-species: *Protanilla rafflesi* Taylor **sp.n.**, from Singapore and East Malaysia. The holotype worker is from SINGAPORE: McRitchie, 1.ix.1970 (*D. H. Murphy*) (NHM, London). It has standard measurements of TL 2.7, HL 0.52, HW 0.40, CI 77, SL 0.43, SI 108, PW 0.36, AL 0.80.

This small genus is widely distributed in the Oriental and Indo-Australian regions. It is known from workers of five or six species, to be described elsewhere by Taylor.

Abdominal morphology of Protanilla worker

Ventral alitrunk and abdominal segment 1 (propodeum) (Figs 1, 3).

Metacoxal cavities closed, with only a thin strip of cuticle separating the cavities from the articulatory foramen which accommodates the petiole. Foramen in which petiole articulates large, broadly U-shaped, open and terminating anteriorly close to a line connecting the posteriormost points of the metacoxal cavities. No metasternal process. Propodeal spiracle large and circular, with a thick annular sclerite, situated low on the side and far back on the sclerite. Bulla of metapleural gland elongate and narrow, running forward as a longitudinal structure below the spiracle on the side of the propodeum. Side of metapleuron with a broad sharply margined longitudinal trench (*metapleural trench*) below and parallel to the metapleural gland bulla. The trench runs the length of the metapleuron, reaching the level of the mesocoxae. Metapleural gland opens into the trench at the posterolateral corner of the alitrunk. Metanotal groove present and impressed.

Abdominal segment 2 (petiole) (Figs 1–3).

Petiole large, sessile, and with a deep posterior face to the node. Proprioceptor zone visible in profile. Spiracle large and conspicuous, anterior on side of tergite. Tergite and sternite completely fused, the suture obliterated. Sternite forming a large anteroventral process. Posterior foramen almost circular, with no distinction between tergite and sternite, but internally the latter forming a thickened shallowly U-shaped flange which is clearly visible in posterior view.

Abdominal segment 3 (postpetiole) (Figs 3, 5).
Sternite of helcium invisible in profile. In front view the helcial sternite visible as a transverse plate which runs between the inner surfaces of the arms of the collar-shaped helcial tergite, some distance up from the apices of the arms. Helcium attached at midheight of segment, tergite behind helcium with a declivitous anterior face; post-helcial neck present and narrow. Tergite and sternite fused, the suture running the length of the segment. Posttergite slightly larger than poststernite, the latter strongly prominent ventrally, bulging and rounded. Abdominal segment 3 reduced in size and separated as a discrete postpetiole, bounded by narrow anterior and posterior constrictions. Segment 3 about same size as 2 or slightly larger, much smaller than 4. Posttergite of segment 3 with a posterior declivity and anterior face of poststernite concave. Spiracle conspicuous, with a broad annular sclerite. Spiracle situated far forward on posttergite, on or almost on the curve where the side rounds into the anterior declivity.

Abdominal segment 4 (first gastral) (Figs 3, 6).
Strongly tubulate anteriorly, with a deep girdling constriction between pre- and postsclerites; posttergite with a short anterior declivitous face. The presclerites which articulate in the posterior foramen of segment 3 are small but very obviously broader than the helcium. Tergosternal fusion absent, the posttergite broadly overlapping the poststernite laterally, and the postternite transversely concave immediately behind the presclerites. Largest segment of abdomen, its spiracle is conspicuous anteriorly on the posttergite, smaller than spiracle on segment 3.

Abdominal segments 5–7 (Fig. 3).
Tergites and sternites not fused, the former broadly overlapping the latter. Spiracles far forward on segments, not visible, each concealed by the posterior section of the preceding tergite. Pygidium (tergite of segment 7) large, rounded and unarmed, unspecialized; its dorsum strongly downcurved posteriorly. Sting long and strongly developed, very conspicuous and fully functional.

Tribe Apomyrmini subfam. transfer

Apomyrmini Dlussky, 1988: 78 [as tribe in subfamily Ponerinae].

Type-genus: *Apomyrma* Brown, Gotwald & Lévieux, 1971: 259.

Diagnosis

Worker

1 Mandibles short, narrowly blade-like and curved, with 3–4 denticles on distal half of blade; terminating apically in a smaller preapical and larger apical tooth (Fig. 15).
2 Labrum with peg-like teeth present.
3 Palp formula 2, 2.
4 Clypeus narrow between antennal sockets, raised medially (Fig. 15).
5 Antennae clavate apically (club weakly of 4 segments, Fig. 15).
6 Middle and hind legs each with 2 spurs, one pectinate and one simple in each case.
7 Metanotal groove absent (Fig. 13).
8 Metapleural gland bulla subcircular in profile, immediately behind the propodeal spiracle and contiguous with it (Fig. 13).
9 Metapleural trench absent (Figs 12, 13)
10 Articulatory cavity of petiole in posteroventral alitrunk open and U-shaped, running forward toward metacoxal cavities (Fig. 12).
11 Petiole pedunculate anteriorly; sternite of petiole reduced to a minute medioventral sclerite situated at posterior end of segment (Figs 12, 13).
12 Abdominal segment 3 contiguous with, and broadly attached to, segment 4; segment 3 not constricted behind (Figs 13, 14).
13 Poststernite of abdominal segment 3 not prominent; with a transverse sulcus behind the helcium (Figs 13, 14).
14 Helcium attached low down on anterior face of abdominal segment 3.
15 Presclerites of abdominal segment 4, which articulate in posterior foramen of segment 3, broad, not constricted nor helcium-like and enormously larger than the helcium in profile (Fig. 13).

Female

Alate when virgin, with full complement of flight sclerites. Eyes present and large, situated at posterior corners of head. Ocelli present. Pronotum large and extensively present on dorsal alitrunk. Hypopygium not prominent posteriorly in dorsal view. Otherwise characters 1–6 and 8–15 as worker. Character 7 not applicable as flight sclerites present.

Male

Known only from a single pharate adult removed from pupal case. See Brown *et al.* (1971) for short description. Nothing of tribe-level value can currently be gleaned from this specimen.

Component genera of Apomyrmini

Apomyrma Brown, Gotwald & Lévieux, 1971: 259.

A monotypic genus first described from Ivory Coast, since then also discovered in Nigeria and Benin (BMNH). Workers and females are well known but males remain known from the single pharate adult mentioned in the original description.

Abdominal morphology of Apomyrma worker

Ventral alitrunk and abdominal segment 1 (propodeum) (Figs 12, 13)

Metacoxal cavities small, closed, with a complete annulus of cuticle around each cavity. No metasternal process. Foramen in which petiole articulates narrowly U-shaped, open, terminating anteriorly close to a line connecting the posteriormost points of the metacoxal cavities. Propodeal spiracle large and circular, with a thick annular sclerite. Spiracle situated low on side and far back. Spiracle abutting anterior margin of large semicircular metapleural gland bulla. Metapleural trench absent. Metanotal groove and metapleural lobes absent.

Abdominal segment 2 (petiole) (Figs 12, 13).

Petiole with differentiated anterior and posterior faces, short-pedunculate anteriorly. Proprioceptor zone visible in profile, anteroventrally on peduncle. Petiolar spiracle large and conspicuous, on anterior face of node immediately behind peduncle. In profile with a sharp ridge running from lowest point mid-ventrally to side of posterior collar. Sternite reduced to a very small V-shaped sclerite posteromedially. Remainder of petiole composed of the massively expanded tergite. Ridge visible in profile is seen in ventral view as a broadly U-shaped rim which probably represents the boundary between tergite and laterotergite. In posterior view the foramen of segment 2 is almost entirely surrounded by tergite; the sternite is merely a small wedge mid-ventrally.

Abdominal segment 3 (first gastral) (Figs 13, 14).

Sternite of helcium invisible in profile. In front view helcial sternite seen to be very reduced, forming a narrow transverse plate which runs between the inner surfaces of the arms of the collar-like tergite, some distance up from the apices of the arms. Helcium attached low down on anterior face of segment, the low position brought about by a downward expansion of the anterior face of the posttergite. The latter has a sloped anterior face so that the dorsalmost point of the declivity overhangs the helcium. Anterior face of posttergite extends ventrally to such an extent that it intrudes between the helcial sternite (presternite of segment 3) and the main portion of the sternite (poststernite). Immediately behind the intrusive tergal strip is a transverse sulcus, which is a secondary development. The original tergosternal junction, running the length of the segment and including the helcium, has been obliterated anteriorly where it is broken by the intrusive strip of the tergite. (This development has also evolved independently in some groups of Formicinae.) Post-helcial neck present and narrow. Anterior portion of segment with tergosternal fusion. Segment 3 reduced, smaller than 2 and much smaller than 4, its poststernite reduced in size relative to its post-tergite. Segment not constricted behind, broadly attached and not forming a separated postpetiole. Spiracle large and with a broad annular sclerite, the spiracle shifted forward, low down on the anterior, delivitous, face of the posttergite.

Abdominal segment 4 (Fig. 13).

Not tubulate anteriorly, without any trace of a groove, impression or constriction between pre- and postsclerites; the pretergite differentiated only by the presence of some fine microsculpture anteriorly. Tergite and sternite not fused, the former broadly overlapping the latter laterally. Largest abdominal segment, its spiracle conspicuous but much smaller than that of segment 3.

Abdominal segments 5–7 (Fig. 13).

Tergites and sternites not fused, the former broadly overlapping the latter. Spiracles far forward on segments, invisible, each concealed by the posterior section of the preceding tergite. Pygidium (tergite of segment 7) large, rounded and unarmed, unspecialised; its dorsum strongly downcurved posteriorly. Sting long and strongly developed, fully functional.

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