The ant subfamily Pseudomyrmecinae (Hymenoptera: Formicidae): generic revision and relationship to other formicids

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Abstract. Three genera are recognized in the ant subfamily Pseudomyrmecinae: *Myrcidris* new genus (monotypic; type species *M.epicharis*, new species, from Amazonas, Brazil); *Pseudomyrmex* Lund (*c.* 150 nominal taxa; southern Nearctic and Neotropical regions); and *Tetraponera* F. Smith (*c.* 110 nominal taxa; Palaeotropical region). New generic synonymies are: *Pseudomyrmex* Lund = *Ornatinoda* Enzmann = *Clavanoda* Enzmann = *Triangulinoda* Enzmann = *Apendunculata* Enzmann = *Latinoda* Enzmann; and *Tetraponera* F. Smith = *Pachysima* Emery = *Viticicola* Wheeler = *Sima* Emery (nec Roger) = *Parasima* Donisthorpe. Autapomorphies are identified for the subfamily and for its constituent genera, indicating the monophyly of all four taxa. Based on available character-state information, *Myrcidris* is most parsimoniously interpreted as a sister-group to all other Pseudomyrmecinae (*Pseudomyrmex* + *Tetraponera*), although there is almost equally strong support for an alternative grouping: *Tetraponera* + (*Myrcidris* + *Pseudomyrmex*). Phylogenetic relationships of the Pseudomyrmecinae and other ant subfamilies within the 'poneroid complex' (*sensu* Taylor, 1978) were assessed by a cladistic analysis of eleven representative ant genera. At the level of subfamily relationships the results suggest that: (1) The Myrmicinae and the Pseudomyrmecinae are sister groups. (2) Within the 'poneroid complex' is an unresolved trichotomy composed of: (i) Pseudomyrmecinae + Myrmicinae, (ii) Myrmeciinae, and (iii) Ponerinae + Leptanillinae + (Cerapachyinae + Dorylinae (s.l.)). (3) The Nothomyrmeciinae are a basal lineage within the 'poneroid complex', rather than being allied with the 'formicoid complex' (Formicinae, Dolichoderinae and Aneuretinae).

Introduction

The subfamily Pseudomyrmecinae constitutes a distinct group of large-eyed, slender, agile ants, common in tropical and subtropical regions,

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and living predominantly in arboreal situations. Some species have developed mutualistic associations with particular plants: the ants nest in modified cavities (domatia) of the living plant, and provide protection against herbivores (Wheeler, 1942; Janzen, 1966, 1972; reviewed in Ward, 1990). However, most species are less specific in their choice of nest-sites, inhabiting hollow dead stems or branches of a variety of

plants. The principal pseudomyrmecine genera are *Pseudomyrmex* (Neotropical, southern Nearctic) and *Tetraponera* (Paleotropical), each containing numerous described species, subspecies, and 'varieties' (Emery, 1921; Kempf, 1972). Two additional genera (*Pachysima* and *Viticicola*, with two and one species, respectively) have been described from equatorial Africa. The taxonomy of these ants is in a rather unsatisfactory state: there are many unresolved species-level problems, and the generic limits have not been critically appraised. Moreover, although the subfamily itself is quite distinct and undoubtedly monophyletic (discussed below), the relationship of the Pseudomyrmecinae to other major groups of ants has not been clarified. This partly reflects general uncertainty about the relationships among the ant subfamilies (cf. Wilson, 1971; Taylor, 1978; Lutz, 1986; Baroni Urbani, 1989).

In this paper, I redefine and diagnose the pseudomyrmecine genera, and consider possible sister-group relationships with other formicids, with emphasis on the 'poneroid complex' of subfamilies (*sensu* Taylor, 1978). Ongoing studies deal in greater detail with the taxonomy of particular species groups within the Pseudomyrmecinae (Ward, 1985, 1989, and in prep.).

Materials and Methods

This study is based on a character analysis of a large sample of pseudomyrmecine ants, including the type species of all available genus-group names and the type specimens of the great majority (90%) of named taxa. As outgroups, I examined members of the 'primitive' subfamilies Myrmeciinae (genus *Myrmecia*) and Nothomyrmeciinae (genus *Nothomyrmecia*), in addition to six poneroid genera with rather generalized features: *Amblyopone*, *Paraponera* and *Ectatomma* (Ponerinae); *Cerapachys* (Cerapachyinae); and *Pogonomyrmex* and *Myrmica* (Myrmicinae). These genera were comprehensively surveyed for morphological variation; others examined in a more perfunctory manner included *Melophorus*, *Oecophylla* (Formicinae); *Dolichoderus*, *Leptomyrmex* (Dolichoderinae); *Messor*, *Aphaenogaster*, *Myrmicaria* (Myrmicinae); *Sphinctomyrmex*, *Simopone* (Cerapachyinae); *Eciton*, *Neivamyrmex*, *Cheliomyrmex* (Eciton-

inae); *Dorylus*, *Aenictus* (Dorylinae); *Typhlomyrmex*, *Rhytidoponera*, *Platythyrea*, and *Pachycondyla* (Ponerinae). Information on these outgroups was also gleaned from the literature.

Material was examined in the forty-seven collections listed in Ward (1989), which should be consulted for collection abbreviations, and in the following: AMNH: American Museum of Natural History, New York, N.Y., U.S.A.; ANIC: Australian National Insect Collection, Canberra, Australia; MRAC: Musée Royal de l'Afrique Centrale, Tervuren, Belgium; OXUM: Hope Entomological Collections, University Museum, Oxford, U.K.; ZMAS: Zoological Institute, Academy of Sciences, Leningrad, U.S.S.R.; ZMUM: Zoological Museum, Moscow State University, Moscow, U.S.S.R.

Particular scrutiny was given to the following characters or character systems in the workers: shape and dentition of the mandibles, palpal segmentation, shape of the clypeus, configuration of the frontal carinae and the antennal sclerites, position of the eyes and ocelli, suturation of the mesosoma, mesosternal and metasternal morphology, articulation of the petiole and postpetiole, tubulation and fusion of the abdominal segments, and morphology of the sting apparatus. The same characters were examined in male and female alates, along with caste- and sex-specific features such as wing venation and male genitalia.

The following metric measurements (in millimetres) and indices are cited (details on these measurements can be found in Ward, 1989): HW: head width: maximum width of head, including the eyes, measured in full-face dorsal view; VW: vertex width: width of the posterior portion of the head (vertex), measured along a line drawn through the lateral ocelli; (HL): head length: midline length of head proper, from the anterior clypeal margin to the midpoint of a line drawn across the occipital margin; EL: eye length: length of compound eye, measured with the head in full-face, dorsal view; OD: ocellar distance: distance from the middle of the median ocellus to the midpoint of a line drawn between the lateral ocelli; OOD: oculo-ocellar distance: distance from the middle of the median ocellus to the midpoint of a line drawn across the posterior margins of the compound eyes; MD3: maximum measurable length

of the mandible, from the dorsal abductor swelling to the apical extremity; MD5: length of the basal margin of the mandible; MD9: length of the masticatory margin of the mandible; MFC: minimum distance between the frontal carinae; ASD: maximum distance between the lateral margins of the median lobes of the antennal sclerites; ASO: maximum distance between the outer, lateral margins of the antennal sclerites; EW: eye width: maximum width of compound eye, measured along the short axis, in an oblique dorso-lateral view of the head; EL2: eye length: maximum length of compound eye, measured along its long axis in the same plane of view as EW; SL: scape length; LF1, LF2, LF3: lengths of the first, second and third funicular segments, respectively; WF2: width of second funicular segment; FL: forefemur length; FW: forefemur width; BF: length of the basal (=dorsal) face of the propodeum; DF: length of the declivitous face of the propodeum; MP: depth of metanol groove ('mesopropodeal impression'); PL: petiole length; PND: petiolar node distance: distance from the lateral flanges of the anterior petiolar peduncle to the maximum height of the node; PH: petiole height; PPL: postpetiole length; DPW: dorsal petiolar width: maximum width of the petiole, measured in dorsal view; MPW: minimum petiolar width: minimum width of the petiole, measured in dorsal view, anterior to DPW; PPW: dorsal postpetiolar width; CI: cephalic index (HW/HL); OI: ocular index (EW/EL); OI2: ocular index, using EL2 (EW/EL2); REL: relative eye length (EL/HL); REL2: relative eye length, using HW (EL/HW); OOI: oculo-ocellar index (OOD/OD); VI: vertex width index (VW/HW); FCI: frontal carinal index (MFC/HW); ASI: antennal sclerite index (ASD/ASO); SI: scape index (SL/HW); SI2: scape index, using EL (SL/EL); FLI: funicular length index [(LF2 + LF3)/WF2]; FI: forefemur index (FW/FL); PDI: propodeal index (BF/DF); MPI: Metanotal index (MP/HW); NI: petiole node index (PND/PL); PLI: petiole length index (PH/PL); PWI: petiole width index (DPW/PL); PWI3: petiole width index, using MPW (MPW/DPW); PPWI: postpetiole width index (PPW/PPL).

Discussion of characters

Some general aspects of pseudomyrmecine morphology are discussed in Ward (1989). Further elaboration on some of the more important character systems is given here.

1. Mandibular dentition. The number and position of teeth on the masticatory and basal margins varies characteristically among species-groups and genera. When counting teeth, the apico-basal tooth (the tooth at the juncture of the masticatory and basal margins; see Ward, 1989, Fig. 1) is arbitrarily considered to be part of the dentition of the masticatory margin. Of particular interest is the presence or absence of a proximal tooth on the basal margin of the mandibles in workers and queens (Figs 15, 16). Mandibular teeth, including the proximal basal tooth, can become abraded, so it is important to check several individuals of a nest-series when evaluating this character complex.

2. Mandibular measurements. Measurement of the lengths of the basal and masticatory margins of the mandibles (MD5 and MD9, respectively) presents no problem when the juncture between the two is marked by a distinct apico-basal tooth or angle. In a few *Tetraponera* workers, however, it may be difficult to determine whether the tooth closest to the base of the mandible is the apico-basal tooth or a tooth on the distal half of the basal margin; I count such a tooth as the apico-basal tooth (and hence the juncture of the basal and masticatory margins) if it lies roughly in the same line as the remaining dentition on the masticatory border. In some *Tetraponera* males the apico-basal angle is replaced by a rounded corner; the middle of this convexity is considered to represent the proximal and distal limits of the masticatory and basal margins, respectively.

For making some measurements (e.g. overall length: MD3) it is helpful to remove the mandibles and mount them separately on points. This is also useful when assessing the condition of the ventral mandibular ridges.

3. Ventral mandibular ridges. The venter of the mandible frequently possesses a submarginal ridge or escarpment, which parallels the masticatory margin, the basal margin, or both. Three conditions are seen in the Pseudomyrmecinae (Figs 1–4): (i) in *Myrcidris* both the masticatory and basal margins are preceded by ridges which converge angularly at the apico-basal tooth; (ii) in *Pseudomyrmex* there is a linear, trenchant escarpment, paralleling the masticatory margin, which terminates at the
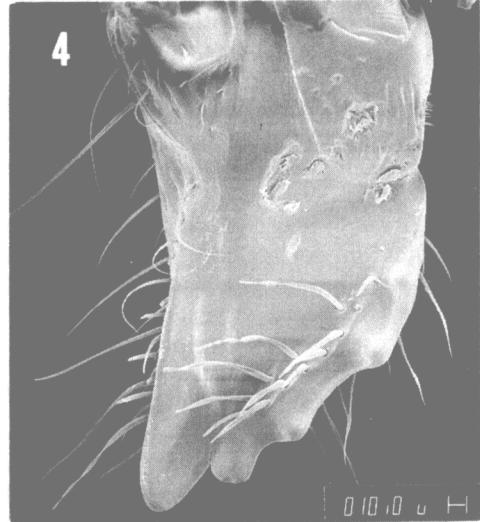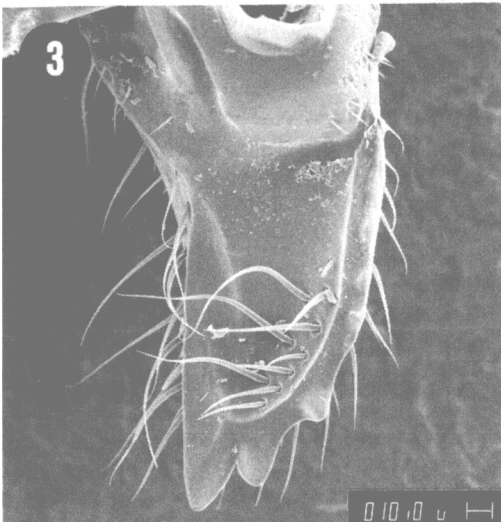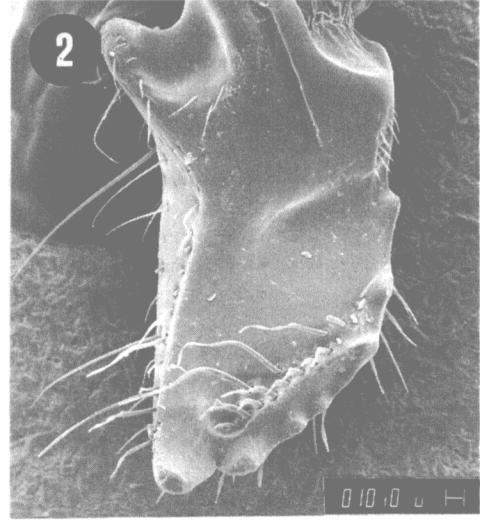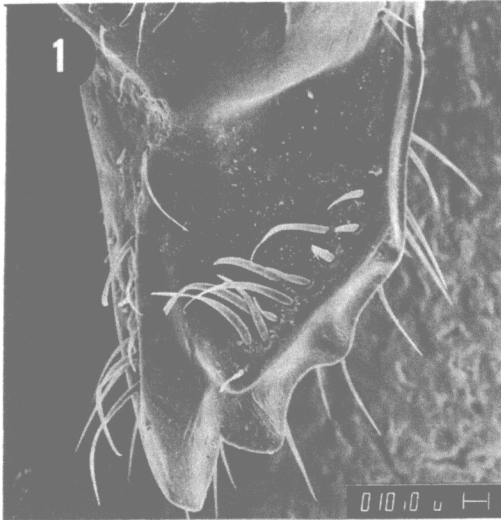
Figs 1−4. Venter of worker left mandible. 1, *Myrcidris epicharis*; 2, *Pseudomyrmex* sp. PSW-44; 3, *Tetraponera tessmanni*; 4, *Tetraponera nitida*.

apico-basal tooth; the corresponding ridge under the basal margin is weak or absent; (iii) in *Tetraponera* there is a single, non-trenchant ridge which is continuous and broadly rounded behind the masticatory and basal margins; in some species it is quite weakly developed.

4. Median clypeal lobe. The anterior margin of the clypeus is variably developed as a lobe-like protrusion (median clypeal lobe) in pseudomyrmecine workers and queens. The upper (anterodorsal) surface of this lobe has a number of conspicuous, anteriorly-directed setae. In those species in which the upper surface of the median clypeal lobe is continuous and broadly convex, the insertions of the lowermost clypeal setae are visible in a full-face (frontal) view of the head (e.g. Fig. 7); below these insertions the upper surface forms a (usually sharp) juncture with the lower anteroventral surface; in an anterior view of the clypeus the setae are confined to the area above this juncture (Figs 9,

31). However, in *Pseudomyrmex* the upper surface of the median clypeal lobe is discontinuous and truncate (at least laterally), and the insertions of the lowermost clypeal setae occur below this truncation. As a result they are often hidden in a full-face view of the head (Fig. 8); in an anterior view of the clypeus the setae thus occur *below* the apparent anterodorsal margin (Fig. 10), and the surface below the truncation often merges inconspicuously into the true ventral surface without a sharp juncture.

5. Antennal sclerites. In pseudomyrmecines the antennal sclerite (the sclerite which encircles the antennal fossa) is developed mesially as a dorsolaterally-directed median lobe which arches over part of the basal condyle of the antenna. The pair of median lobes is visible in a full-face (frontal) view of the head, because the frontal carinae, with which the median lobes usually fuse anteriorly, are not expanded laterally to cover them. Nevertheless the extent to which the median lobes of the antennal sclerites protrude laterally differs between the two principal genera.

6. Hind coxal cavities. These are said to be closed when they are fully enclosed by sclerotized integument (e.g. Fig. 5). To assess this and other metasternal characters the legs are removed and the ant is mounted upside down.

7. Hind basitarsal sulcus. This is a longitudinal impression which (when present) is situated on the anterior face of the first (basitarsal) segment of the hind tarsus (e.g. Fig. 6). An equivalent structure often appears on the mid basitarsus.

8. Propodeal lobes. These are the posterior lobes of the propodeum which flank the propodeal foramen. They are rounded in Pseudomyrmecinae; in other ants they may be rounded, tooth-like, reduced or absent. In the ant taxonomic literature they are usually termed 'metapleural lobes' although they are not part of the metapleuron.

9. Fusion of abdominal terga and sterna. This was assessed for the petiole (abdominal segment II) and two succeeding segments, by dissecting freshly-killed or relaxed specimens. The segment of interest was isolated from the others. If the tergum and sternum could not be teased apart, at least posteriorly, and if there
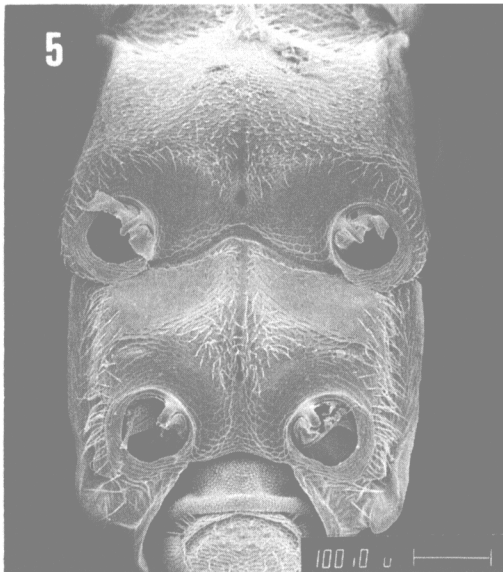

Fig. 5. *Tetraponera penzigi*, ventral view of worker mesosoma, with legs removed, showing closed hind coxal cavities.
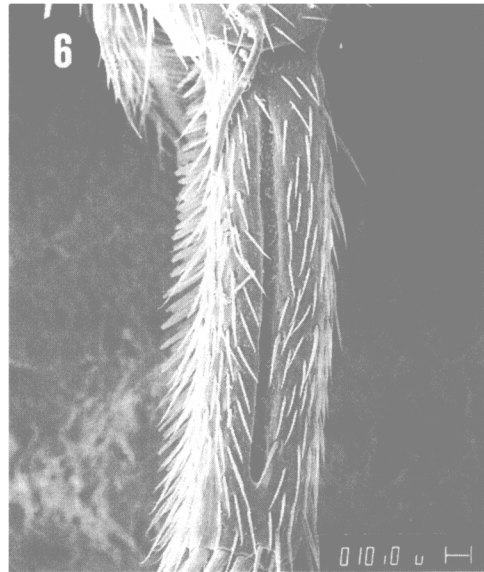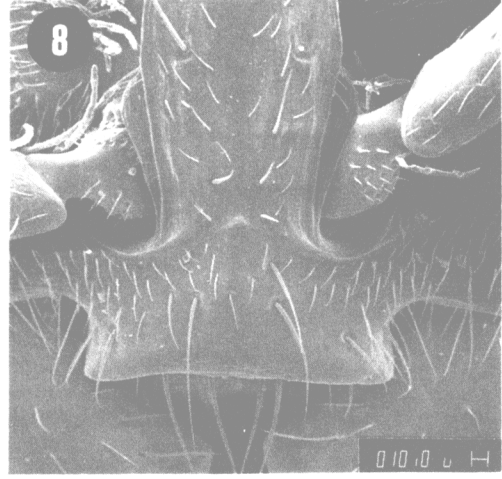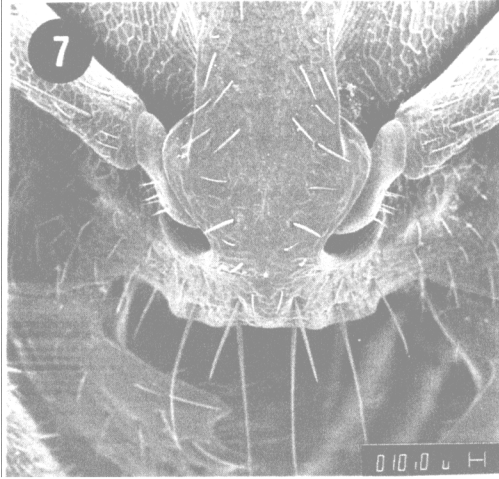
Fig. 6. *Myrcidris epicharis*, worker, anterior view of left hind basitarsus, showing basitarsal sulcus.

Figs 7, 8. Anterodorsal views of median clypeal lobe of worker. 7, *Tetraponera ophthalmica*; 8, *Pseudomyrmex malignus*.
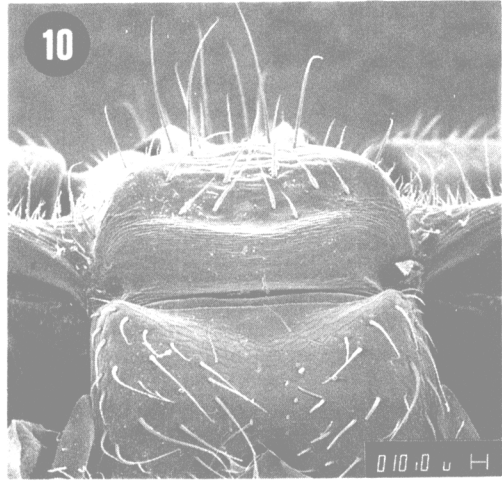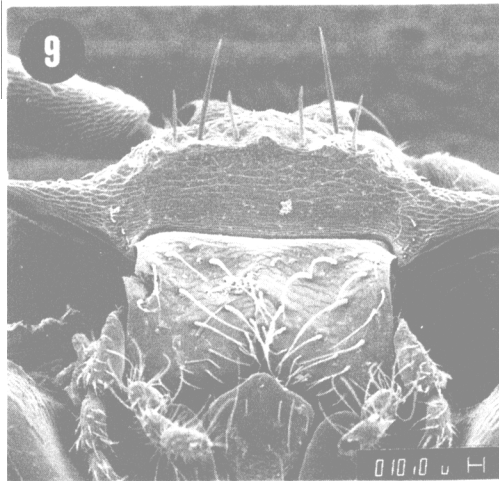
Figs 9, 10. Anterior views of median clypeal lobe of worker, with mandibles removed. 9, *Tetraponera penzigi*; 10, *Pseudomyrmex concolor*.

was no free movement between the two plates, tergosternal fusion was considered to be complete.

10. Presclerites of abdominal segments III and IV. The terms 'presternite' and 'pretergite' are used for the differentiated anterior regions of the sternum and tergum, respectively, which occur in pseudomyrmecines and other ants in the 'poneroid complex' (e.g. Figs 26–28).

11. Male genitalia: parameres. A series of lobes, protuberances and impressions adorns the parameres of pseudomyrmecine males. The principal features are: a mediodorsal impression, a mesial dorsoventral lobe, and a posterodorsal lobe (e.g. Figs 24, 25).
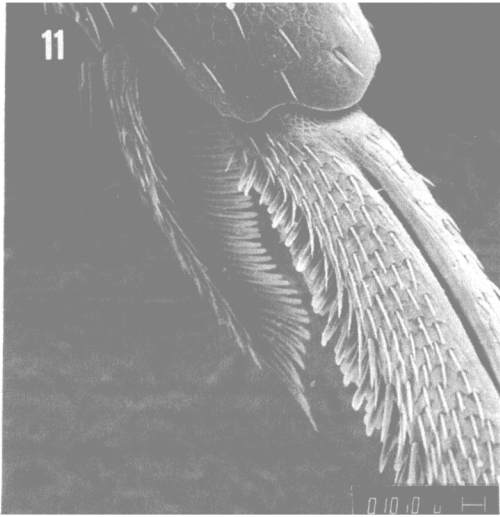
Figs 11, 12. Anterior views of left hind tibial apical spurs and adjacent portion of basitarsus, of worker. 11, *Tetraponera penzigi*; 12, *Pseudomyrmex concolor*.

Analysis of relationships

Following the description and diagnoses of the pseudomyrmecine genera, the results of a genus-level numerical cladistic analysis are presented. Because of uncertainty about the sister-group of the Pseudomyrmecinae, a series of eight other ant genera were included in the data set. The analysis thus provides information not only about the phylogeny of the pseudomyrmecine genera but also about relationships between the Pseudomyrmecinae and other subfamilies in the 'poneroid complex'. For this analysis character states were not explicitly polarized; rather the 'living-fossil' genus, *Nothomyrmedia* (Taylor, 1978), was used as an outgroup to root the tree.

The most parsimonious tree(s) was(were) sought using Steve Farris' Hennig86 program (Version 1.5) and David Swofford's PAUP program (Version 2.4.1), with identical results. Bootstrapped confidence intervals were obtained by converting the data to binary form, and employing the program BOOT on Joe Felsenstein's PHYLIP package (Version 3.1); the original multistate characters were identified using the FACTOR option.

The characters used for this analysis are as follows:

1. Worker and queen, mandible, proximal basal tooth (0) present; (1) absent.
2. Worker and queen, mandible, median number of teeth on masticatory margin (0) 3–4; (1) 5–10; (2) >10.
3. Worker, mandible (0) relatively short, maximum measurable length two-thirds or less of head length (MD3/HL 0.30–0.68); (1) relatively long, about three-quarters or more of head length (MD3/HL >0.70).
4. Male, mandible, median number of teeth on masticatory margin (0) 1–6 (if 6 then HW ≥1.00); (1) 6–18 (if 6 then HW <0.98).
5. Male, mandible, basal margin (0) one half or less the length of the masticatory margin (MD5/MD9 ≤0.55); (1) two-thirds or more the length of the masticatory margin (MD5/MD9 >0.65).
6. Worker and queen, mandible, ventral surface (0) descending suddenly along ridge lines which precede the masticatory and basal margins and which converge angularly at the apico-basal tooth; (1) sharply cut off by a linear, trenchant escarpment which precedes the masticatory margin and which terminates at the apico-basal tooth; corresponding ridge under basal margin weak or absent; (2) with a single, non-trenchant ridge or weak rise which is continuous and broadly rounded behind the masticatory and basal margins; or lacking altogether.
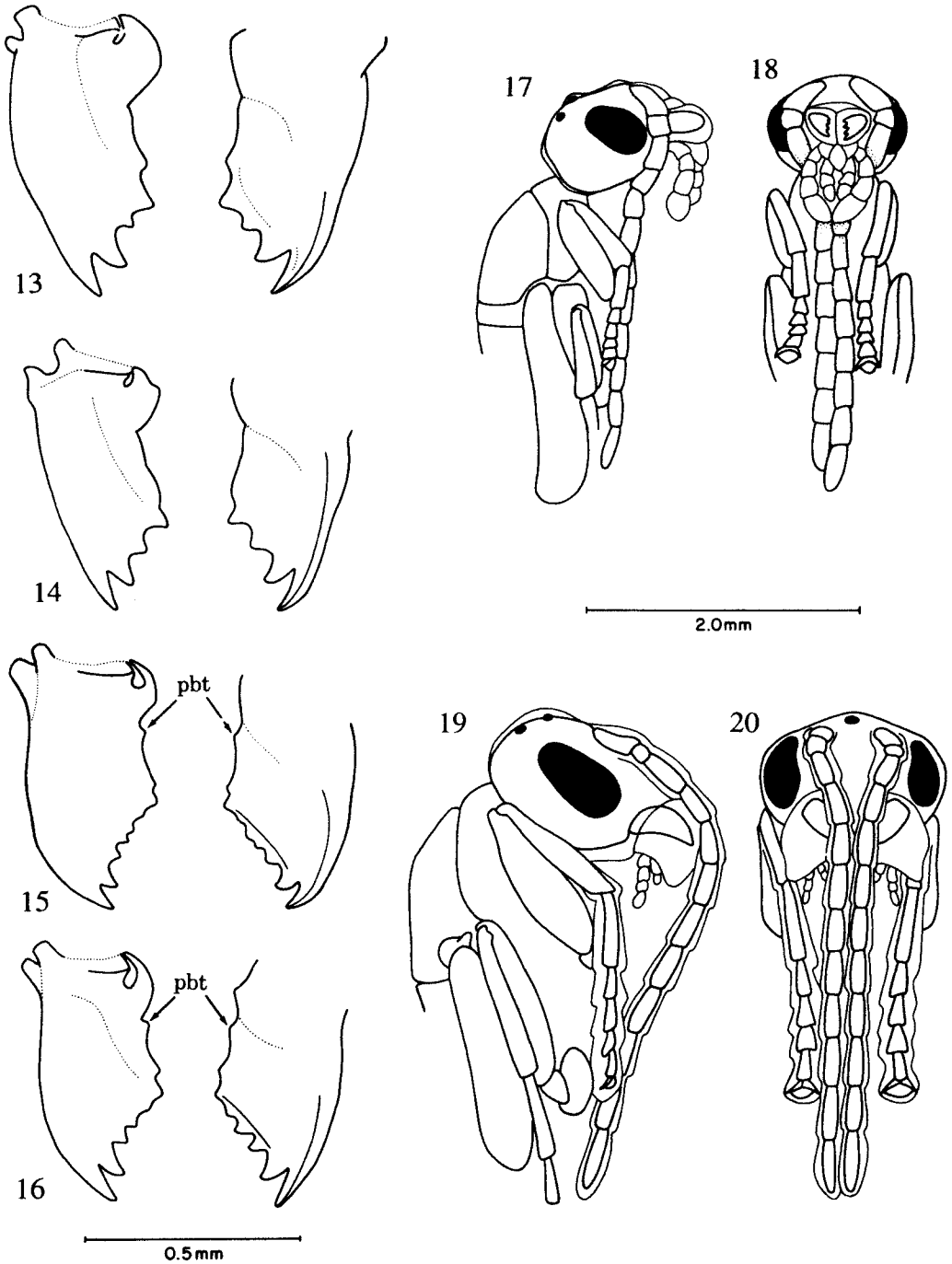
Figs 13–16. Worker right mandible, dorsal surface (left) and ventral surface (right). 13, *Tetraponera pilosa*; 14, *T.nigra*; 15, *Pseudomyrmex triplarinus*; 16, *P.salvini*. pbt = proximal basal tooth.

Figs 17–20. Paired lateral and ventral views of male pupa. 17, 18, *Tetraponera punctulata*; 19, 20, *Pseudomyrmex gracilis*.

7. Worker and queen, mandible, in lateral view such that the face of the external margin is perpendicular to the plane of view (0) rounded, or at most obtusely angled, above the trulleum; (1) sharply angulate above the trulleum.

8. Worker, queen, and male, number of maxillary palp segments (0) 6; (1) 5; (2) 4.

9. Worker, queen and male, number of labial palp segments (0) 4; (1) 3.

10. Worker and queen, median clypeal lobe, upper (anterodorsal) surface (0) continuous, non-truncate; (1) discontinuous and (at least partially) truncate.

11. Worker and queen, posteromedial margin of clypeus (0) with a conspicuous posterior extension between the frontal carinae; (1) not extending strongly backwards between frontal carinae; or posterior margin obscure.

12. Worker, frontal carina (0) not expanded laterally as a frontal lobe covering the median lobe of the antennal sclerite (in frontal view); (1) so expanded.

13. Worker, queen and male, ring of the antennal sclerite (0) inclined dorsomesially (1) positioned dorsally flat.

14. Worker, median lobe of antennal sclerite (0) slightly to moderately expanded laterally (ASI 0.40–0.74); (1) strongly expanded laterally (ASI 0.75–1.10).

15. Worker and queen, number of antennal segments (0) 12; (1) 11.

16. Male, number of antennal segments (0) 13; (1) 12.

17. Worker, scape length (0) three-quarters or more of head length; (1) shorter (SL/HL 0.20–0.70).

18. Male, scape length (0) about one-third the length of the first two funicular segments (SL/(LF1 + LF2) 0.30–0.40); (1) less than the length of the first two funicular segments, but more than two-fifths (SL/(LF1 + LF2) 0.40–0.90); (2) ≥length of first two funicular segments.

19. Male, scape length (0) less than one-fifth the length of the funiculus (SL/funicular length 0.04–0.15); (1) one-fifth or more of funicular length (SL/funicular length 0.20–0.50).

20. Male, first funicular segment (0) much shorter than second (LF1/LF2 0.10–0.20); (1) one-quarter or more the length of the second (LF1/LF2 0.25–0.90).

21. Worker, compound eye (0) less elongate (≤1.5 times as long as wide, such that OI 0.67–0.95 and OI2 0.65–1.00); (1) more elongate (>1.5 times as long as wide, such that OI 0.50–0.66 and OI2 0.50–0.64).

22. Worker, promesonotal connection (0) flexible; (1) rigidly fused.

23. Worker and queen, hind basitarsal sulcus (0) absent; (1) present.

24. Worker, queen and male, number of apical hind tibial spurs (0) 2; (1) 1.

25. Worker, queen and male, tarsal claws (0) with two teeth (apical and subapical or submedian); (1) simple.

26. Worker, queen and male, hind coxal cavities (0) open; (1) closed.

27. Worker and queen, opening of metapleural gland (0) not located immediately above the posteroventral margin of the metapleuron (separated by a distance greater than the diameter of the opening); (1) located immediately above the posteroventral margin of the metapleuron.

28. Worker and queen, opening of metapleural gland (0) directed laterally or ventrolaterally; (1) directed dorsally or posterodorsally.

29. Worker, queen and male, tergum of second abdominal segment (petiole) (0) with a lateral, dorsoventral carina or swelling located in front of the spiracle on anterior end of petiole, immediately behind the propodeal lobe; extending laterally as far as, or farther than, the propodeal lobe; (1) lacking such a carina or swelling.

30. Worker, queen and male, petiole (0) with laterotergite; (1) without laterotergite.

31. Worker, queen and male, posterior margin of petiolar sternite, in posterior view (0) semicircular, with flanking lobes; (1) broadly curved, without flanking sternal lobes.

32. Worker, queen and male, petiolar (second abdominal) tergum and sternum (0) not fully fused; (1) completely fused and incapable of independent movement.

33. Worker, queen and male, third abdominal tergum and sternum proper (0) not fully fused; (1) fully fused.

34. Worker, queen and male, third abdominal segment, presclerites (0) unfused; (1) fused, with presternite strongly protruding ven-

trally; (2) fused, with presternite not protruding ventrally.

35. Worker, queen and male, third abdominal segment (0) with presternite overlapped laterally by pretergite; (1) with presternite not overlapped laterally.

36. Worker, queen and male, fourth abdominal segment (0) without clearly differentiated presclerites; (1) with differentiated pretergite and presternite, forming a ball joint, not laterally fused; (2) with differentiated pretergite and presternite, forming a ball joint, fused laterally and tubulate.

37. Worker, presternite of abdominal segment IV (0) about one-half (40–60%) the total midline length of the sternum; (1) about 20–40% of the total length of the sternum; (2) much shorter than the total length of the sternum (5–20%).

38. Worker, presternite of abdominal segment IV (0) subequal to or longer than the pretergite, the latter not protruding downwards at their lateral juncture; (1) notably shorter than the pretergite, and the latter protruding downwards at their lateral juncture.

39. Worker, queen and male, stridulitrum on fourth abdominal pretergite (0) absent; (1) present.

40. Worker and queen, abdominal segment IV (0) without complete lateral fusion of the tergum and sternum; (1) with complete tergosternal fusion.

41. Worker and queen, sting apparatus, median connection of spiracular plate (0) sclerotized; (1) membranous.

42. Worker and queen, gonostylus (0) 2-segmented; (1) 1-segmented.

43. Male, sternum VIII, posterior margin (0) emarginate; (1) broadly convex.

44. Male, pygostyles (0) with a flexible, weakly sclerotized or membranous connection to the remnant of tergite X; (1) with a rigid, uninterrupted sclerotized connection; (2) missing.

45. Male, paramere, distal end, internal (mesial) face (0) with a considerable portion open or membranous distal to the base of the volsella; (1) more fully sclerotized distal to the volsella, membranous portion restricted to a subtriangular area or lacking.

46. Male, volsella (0) moderately well developed, usually with digitus and cuspis; (1) reduced to a small, setose, finger-like lobe

or fused to the lower, inner (mesial) wall of the paramere.

47. Male, aedeagus, external face (0) without cornuti; (1) with 6–8 cornuti.

48. Male, pupa, antennae (0) passing ventrally below the mandibles; (1) passing laterally on either side of the mandibles.

49. Worker, queen and male, pupa (0) enclosed in cocoon; (1) naked.

50. Worker, queen and male, larva (0) without trophothylax; (1) with trophothylax (food pocket).

Most of the foregoing characters are invariant (i.e. exhibit no more than one character state) within the pseudomyrmecine genera. For four characters which showed some variation, I made the following judgements about the generic ground-plan, based in part on a preliminary cladistic analysis of relationships among species and species groups within the subfamily (Ward, 1990):

2. Number of teeth on the masticatory margin of mandibles (workers and queens). There are 3–4 teeth in all *Tetraponera* known to me except three unrelated species: *T.tessmanni*, *T.rufonigra*, and an undescribed species from Madagascar, with 4–5, 5 and 6 teeth respectively. On the basis of numerous other characters (see Ward, 1990) these taxa do not appear to be basal in the genus; thus character state (0) (3–4 teeth) is considered the ground-plan for the genus.

8,9. Number of maxillary and labial palp segments. A palp formula of 6,4 is common in *Pseudomyrmex* and prevalent in *Tetraponera*. The species-level cladistic analysis (Ward, 1990) suggests that this is the plesiomorphic condition in both genera.

23. Hind basitarsal sulcus. This is present in workers and queens of nearly all *Tetraponera* (varying degrees of degeneration are seen) and its absence in three species (*T.bifoveolata*, *T.ophthalmica* and *T.tessmanni*) is presumed due to secondary loss.

When one of the other eight genera outside the Pseudomyrmecinae showed intrageneric variation in a character it was coded as having the character state unknown, except for characters

involving the number of antennal or palp segments. Here the maximum count known for the genus was used.

Subfamily Pseudomyrmecinae M. Smith

Pseudomyrmidae Forel, 1885: 37 (as tribe of subfamily Myrmicinae). Type genus: *Pseudomyrma* Guérin-Méneville, 1844: 427.

Pseudomyrminae Forel; Emery, 1899: 8 (raised to subfamily).

Leptaleinae Smith, 1951: 788. Type genus: *Leptalea* Erichson, 1839: 309.

Pseudomyrmecinae Smith, 1952: 98. Type genus: *Pseudomyrmex* Lund, 1831b: 106. Accepted subfamily name under Article 40b of ICZN, 1985.

Diagnosis, worker and queen

1. Mandibles rather short, with 0−3 and 3−10 teeth on the basal and masticatory margins, respectively.
2. Clypeus without a conspicuous posteromedial extension between the frontal carinae.
3. Antennae with 12 segments; reduced to 11 segments in one species.
4. Palp formula 6,4, with reductions to 5,4; 6,3; 5,3; 4,3; and 3,3.
5. Compound eyes relatively large (REL usually >0.25).
6. Median lobes of antennal sclerites visible in a full-face view of head (i.e. not overreached by frontal lobes) and partly covering the basal condyles of the antennae.
7. Scapes relatively short, less than three-quarters of head length (SL/HL 0.20−0.70).
8. Pronotum and mesonotum not fused with one another, freely articulating.
9. Propodeal spiracle located on upper third of propodeum and far forward.
10. Opening of metapleural gland directed laterally or ventrolaterally, and situated at the extreme posteroventral margin of the metapleuron.
11. Hind tibia with two apical spurs, the anterior one sometimes very reduced, but the posterior spur always well-developed and pectinate.
12. Hind coxal cavities closed.
13. Terga and sterna of abdominal segments II (petiole), III (postpetiole), and IV (first 'gastric' segment) not laterally fused; tergum overlapping sternum on segment IV.
14. Presternite of abdominal segment III overlapped laterally by the ventral margins of the pretergite, and not protruding mesoventrally below this.
15. Postpetiole distinctly developed.
16. Abdominal segment IV with differentiated presclerites, but these much narrower and shorter than the tergum and sternum proper: presternite notably shorter than the pretergite and the latter protruding ventrally at their lateral juncture.
17. Stridulitrum present on pretergite of abdominal segment IV.
18. Sting present and well developed.
19. Pupa naked.
20. Larva with trophothylax (food pocket).

Diagnosis, male

1. Mandibles short, with 0−1 and 2−18 teeth or denticles on the basal and masticatory margins respectively (proximal basal tooth lacking).
2. Antennae nearly always with 12 segments but with 13 segments in one species.
3. Palp formula: as in workers and queens.
4. Hind tibia with two apical spurs, the posterior spur pectinate.
5. Hind coxal cavities closed.
6−10. Structure of abdominal segments II, III and IV: as in workers and queens (13−17, above).
11. Volsella highly reduced: present as a small setose finger-like lobe (without differentiated digitus and cuspis) or fused to the inner wall of the paramere.
12. Pupa naked.
13. Larva with trophothylax (food pocket).

Extended description, worker

Typically monomorphic ants (marked polymorphism known in only two species of *Tetraponera*); varying considerably in size (HW 0.45−2.20 mm) and colour. Mandibles relatively short (MD3/HL 0.30−0.68); basal and masticatory margins usually distinct, with 0−3 and

3–10 teeth respectively (Figs 13–16). Venter of mandible typically with a ridge or escarpment preceding the masticatory and basal margins, although this can become quite reduced in some *Tetraponera* (e.g. Fig. 4). Trulleum and mandalus present. Palp formula 6,4; reduced to 5,4; 6,3; 5,3; 4,3; and 3,3 in various species. Anterior margin of clypeus with a weak to strongly developed median protrusion (median clypeal lobe) sometimes armed with teeth or lateral angles; posteromedial margin of clypeus more or less straight, not extending strongly backwards between the frontal carinae. Antennal sclerites inclined dorsomesially. Median lobes of antennal sclerites extending dorsolaterally and partly covering the basal condyles of the antennae, typically fusing anteriorly with the frontal carinae; frontal carinae not expanded laterally as frontal lobes, and as a result the median lobes of the antennal sclerites are visible in a full-face view of the head (e.g. Figs 7, 8). Antennae 12-segmented (reduced to 11 segments in *Myrcidris*), usually without a distinct funicular club. Scapes relatively short (SL/HL 0.20–0.70). Compound eyes typically large (REL 0.19–0.68, usually >0.25). Number of ocelli: 3; reduced to 2 or 0 in many *Tetraponera*. Head shape varying considerably, from broader than long to markedly elongate (CI 0.56–1.14).

Pronotum and mesonotum articulating flexibly, not fused. Metanotal groove usually impressed, becoming weak to obsolete in some species; in others a distinct metanotal (or mesoscutellar?) plate is also present. Propodeal spiracle conspicuous, circular to elongate, located far forward on the upper third of the propodeum. Spinescence lacking on mesosoma; basal face of propodeum typically rounding gently into the declivitous face, occasionally meeting at a sharp angle, very rarely forming pointed lateral corners. Metapleural gland well developed, the opening (meatus) large, directed laterally or ventrolaterally, and situated adjacent to the posteroventral margin of the metapleuron, immediately above the hind coxal insertion; anterior to the meatus is a longitudinal impression which continues to the anteroventral corner of the metapleuron and which is flanked dorsally by a carina of variable length. Hind coxal cavities closed (Fig. 5). Metasternal process weakly to moderately developed, consisting of a low rise or a pair of blunt triangular

points; the equivalent mesosternal process weakly to moderately incised medially, sometimes flanked by blunt triangular prominences. Propodeal lobes well developed; distance from posterior margin of hind coxal cavity to posteriormost extremity of the propodeal lobe exceeds the diameter of the cavity. Posterior metasternal margin with a medial, U-shaped excavation, which extends forward past the posterior margin of the hind coxal cavity. Petiole and postpetiole with well developed nodes, anterior peduncles variable in length. Distance between propodeal lobes exceeding the anterior width of the petiolar tergum. Posterior margin of petiolar sternum appearing semicircular in posterior view, with flanking lobes; in some species the semicircular margin has retreated internally (dorsomesially) and a new posterior extension of the sternum forms the posterior margin. Presternite of postpetiole (abdominal segment III) overlapped laterally by pretergite, not protruding ventrally; presternite often somewhat reduced in size and underlain by a forward-shifted anteroventral postpetiolar process (this occurs in association with the aforementioned reformation of the posterior margin of sternite II). Abdominal segment IV with differentiated presclerites, much shorter and narrower than the tergum and sternum proper; presclerite notably shorter than pretergite (Fig. 26), the latter protruding ventrally at their lateral juncture. Terga and sterna of abdominal segments II (petiole), III (postpetiole) and IV (first 'gastric' segment) not laterally fused, tergum IV conspicuously overlapping the corresponding sternum. Pretergite of abdominal segment IV with stridulatory file. Posterior margin of tergum VII (pygidium) simple, unarmed. Gonostylus 1-segmented. Sting present, well developed; sting shaft with 1–3 (usually 2) barbs; lancets barbed, with 5 teeth.

Tarsal claws with 2 teeth (apical, subapical), the subapical tooth occasionally reduced or absent; mid and hind tibiae each with 2 apical spurs, the posterior spur always (hind tibia) or nearly always (mid tibia) well developed and pectinate, the anterior spur smaller and sometimes very reduced in size. Mid and hind basitarsi often with a longitudinal sulcus, on the anterolateral face (Fig. 6) (but entirely absent in *Pseudomyrmex*). Standing pilosity varying widely: from abundant to very sparse. Appressed pubescence occurring in low to moderate

density on most of body (these hairs sometimes very small). Integument sculpture usually rather lightly impressed, never strongly rugose or costate.

Extended description, female

Similar to the worker in most features, except for the presence of wings and differences in mesosomal morphology. Ergatoid queens known in one *Tetraponera* species. Apicobasal area of mandible occasionally much broadened; juncture of basal and anterodorsal faces of mandible occasionally marked by sharp margination or carina; in some species mandible incised or geniculate basally such that the dorsal abductor swelling and immediately distal section of the mandible form an angle of 100° or less (in a frontal view of the head). Median clypeal lobe often more protuberant than that of worker, occasionally (e.g. *P.tachigaliae*) strikingly so. Ocelli always present. Mid and hind basitarsal sulci somewhat more prominent than in the worker. Forewing with one closed radial cell, and (typically) two cubital cells (reductions to one cubital cell occur). Hindwing with 8−18 hamuli; anal lobe lacking.

Extended description, male

Basal margin of mandibles typically devoid of teeth (proximal basal tooth always lacking; occasionally a mesial basal tooth present); masticatory margin with 2−18 teeth or denticles, when more than 6 in number those preceding preapical tooth usually rather indistinct. Ventral mandibular ridges less developed than in workers. Palp formula as in worker; in a few species where workers have a reduced palp formula, males may possess an additional maxillary palp segment (e.g. 4,3 in workers; 5,3 in some males of the same species). Second and third maxillary palp segments occasionally much elongated. Median clypeal lobe broadly rounded to medially angulate, rarely emarginate; upper surface non-truncate. Posterior margin of clypeus straight, not extending backwards between the antennal insertions. Frontal carinae usually absent, at best very weakly developed. Median lobes of antennal sclerites not prominently developed, but in some *Tetraponera* the antennal sclerites are produced anterodorsally and partly overhang the frontal

triangle. Antennae usually 12-segmented; 13-segmented in one species. Scapes not long, typically ≤length of first two funicular segments and less than one-sixth the length of the entire funiculus. First funicular segment one-quarter or more the length of the second. Compound eyes and ocelli prominent. Notauli absent; in some *Tetraponera* mesonotum centrally constricted, with resulting broad transverse or arched-transverse furrows. Parapsidal lines present, usually well developed and extending about half the length of the mesonotum. Hind coxal cavities closed. Petiole and postpetiole distinct, as in worker, but tending to be more slender. Tergosternal structure of petiole, postpetiole and fourth abdominal (first gastric) segment as in worker. Stridulitrum present on fourth abdominal pretergite. Subgenital plate (sternite IX) variable in shape but never furcate. Cerci (pygostyles) present. Paramere narrowing apically, typically complex in shape with a series of lobes and impressions (e.g. Figs 24, 25); in contrast, volsella highly reduced: a small, setose, finger-like lobe, sometimes fused to the inner wall of the paramere and very inconspicuous. Aedeagus variable in shape, with or without marginal teeth. Tarsal claws and tibial spurs as in worker. Mid and hind basitarsal sulci always lacking. Wing venation as in queen.

Discussion

Synapomorphies supporting the monophyly of the subfamily Pseudomyrmecinae include:
1. Worker, queen, male: larva with a trophothylax (food pocket) on the ventral surface of the thorax (for a more extensive description of pseudomyrmecine larvae see Wheeler & Wheeler, 1956, 1973, 1976).
2. Worker, queen: posteromedial margin of clypeus more or less straight, not extending posteriorly between the frontal carinae.
3. Male: volsella highly reduced.
4. Worker, queen: opening of metapleural gland located at extreme posteroventral margin of metapleuron, immediately above the hind coxal insertion.
5. Worker, queen: scapes short (SL/HL ≤0.70).

The last two conditions are seen in some other ants: the opening of the metapleural gland tends to be in an extreme posteroventral position in Cerapachyinae; and short scapes appear

in various ponerines, cerapachyines, and army ants (Dorylinae and Ecitoninae).

Other features of the Pseudomyrmecinae which are possibly derived within the 'poneroid complex' (*sensu* Taylor, 1978) but are probably not autapomorphies for the subfamily (see Cladistic analysis, below), include the following:

1. Worker and queen: mandibles short, with 10 or fewer teeth on the masticatory margin.
2. Male: scape length more than one-third the combined length of the first two funicular segments (SL/(LF1 + LF2) 0.40−0.90).
3. Male: first funicular segment one quarter or more the length of the second funicular segment.
4. Worker, queen, male: hind coxal cavities closed.
5. Worker, queen, male: postpetiole distinctly developed.
6. Worker, queen, male: presclerites of abdominal segment IV much shorter in length than the total length of the segment (presternite 5−20% of the midline length of the entire sternum).
7. Worker, queen, male: presternite of abdominal segment IV notably shorter in length than the pretergite, the latter produced ventrally at their lateral juncture.
8. Worker, queen, male: pupa naked (cocoon lost).

Many of the remaining features of the Pseudomyrmecinae are symplesiomorphies, either within the 'poneroid complex' (e.g. differentiated presclerites and dorsal stridulitrum of abdominal segment IV; perhaps also the stereotyped dorsal carrying posture of workers, see Duelli (1977)) or within the family Formicidae (large eyes; palp formula of 6,4; exposed median lobes of antennal sclerites; flexible promesonotal articulation; pectinate tibial spurs; lack of tergosternal fusion of abdominal segments II, III and IV; presence of sting), reflecting the rather generalized morphology of these ants.

Among ants whose workers can be said to have a distinct postpetiole (Pseudomyrmecinae; Myrmeciinae; Myrmicinae; Leptanillinae; some Dorylinae, Ecitoninae, Cerapachyinae and Ponerinae), those of the Pseudomyrmecinae can be distinguished from all except the Myrmicinae and Ponerinae by the presence of a dorsal stridulitrum on abdominal segment IV;

from the Ponerinae by the short mandibles (MD3/HL <0.70), straight posteromedial margin of the clypeus, position of the metapleural gland opening, and unfused terga and sterna of abdominal segments III and IV; and from the Myrmicinae by various traits including the straight posteromedial margin of the clypeus, flexible promesonotal connection, two hindtibial spurs (anterior spur may be quite small), position of the metapleural gland opening, and unfused petiolar tergum and sternum.

Relationships among pseudomyrmecines and other ants in the 'poneroid complex' are explored further below, under 'Cladistic analysis'.

Redefinition of genera

The two principal pseudomyrmecine genera, *Pseudomyrmex* Lund and *Tetraponera* F. Smith, have a tangled nomenclatural history. Most *Pseudomyrmex* species were described under the genus name *Pseudomyrma* Guérin-Méneville, until Smith (1952) pointed out the priority of Lund's name. Many *Tetraponera* were originally described in the genus *Sima* Roger, partly because of confusion over the type-species of these two genera. For a discussion and justification of the synonymy of *Sima* under *Tetraponera* see Donisthorpe (1916).

The arguments have thus revolved around the validity of names, rather than the validity of these taxa as monophyletic groups. In practice, New World pseudomyrmecines have been placed in the genus *Pseudomyrmex*, while most Old World species have been assigned to *Tetraponera*, without the differences between these two genera being critically assessed. In fact the distinctions cited by Wheeler (1922c) and Emery (1921) in the shape of the clypeus are not diagnostic.

Complicating the situation is the description of two additional genera of specialist plant-inhabiting ants from Africa. *Pachysima* Emery, containing two species usually associated with *Barteria* (*P.aethiops*, *P.latifrons*), was originally described as a subgenus of *Sima* [=*Tetraponera*] (Emery, 1912) but was later raised to genus by Wheeler (1919). *Viticicola* Wheeler (1919) was established for a distinctive *Vitex*-inhabiting

species (*V.tessmanni*), originally described in *Sima*. These genera were recognized by Bolton (1973) and Wheeler & Wheeler (1985), but Brown (1973) provisionally synonymized them under *Tetraponera* without any explicit argumentation; his decision was subsequently adopted by Snelling (1981) and Hölldobler & Wilson (1990).

Critical re-examination of the pseudomyrmecine genera, based on a study of more than 200 nominal species and using an expanded set of morphological traits, supports the monophyly of both *Pseudomyrmex* and *Tetraponera*, but only if the latter genus includes *Pachysima* and *Viticicola*. The major differences between *Pseudomyrmex* and *Tetraponera* (s.l.) are outlined in Table 1.

The two species of *Pachysima* share all of the traits of *Tetraponera*. The *Viticicola* species (*V.tessmanni*) possesses most of these, but its worker and queen have slightly aberrant mandibular dentition (4−5 teeth on the masticatory margin) and they lack a hind basitarsal sulcus. There are, however, a few other *Tetraponera* which are exceptional in this regard, e.g. *T.rufonigra* has 5 mandibular teeth,

Table 1. Major diagnostic differences between *Pseudomyrmex* and *Tetraponera* (s.l.). Putative synapomorphies are in bold type.

Character	Caste(s) w=worker q=queen m=male	*Pseudomyrmex*	*Tetraponera*
Mandible, proximal basal tooth	w,q	Present	**Absent**
Mandible, median no. teeth on masticatory margin	w,q	5−10	**3−4 (exceptionally 5−6)**
Ditto	m	**6−18 (if 6, then HW < 0.98)**	2−6 (if 6, then HW > 1.00)
Mandible, basal margin, length in relation to masticatory margin	m	**One-half or less**	Two-thirds or more
Mandible, ventral ridges	w,q	**Trenchant escarpment behind masticatory margin, terminating at apicobasal tooth**	Non-trenchant ridge or weak rise, continuous and broadly rounded behind the masticatory and basal margins
Median clypeal lobe, upper (anterodorsal) surface	w,q	**Discontinuous and at least partially truncate**	Continuous, broadly convex, non-truncate
Compound eye	w	**Elongate (>1.5 times as long as wide)**	Less elongate (≤1.5 times times as long as wide)
Median lobe of antennal sclerite, lateral expansion	w	**Slight to moderate (ASI 0.40−0.74)**	Strong (ASI 0.75−1.00)
Hind basitarsal sulcus	w,q	**Absent**	Present (exceptionally absent)
Sting apparatus, median connection of spiracular plate	w,q	Sclerotized	**Membranous**
Pupa, antennae	m	**Passing ventrally below the mandibles**	Passing laterally on either side of the mandibles

and the hind basitarsal sulcus is absent in *T.ophthalmica* and *T.bifoveolata*. A preliminary analysis of relationships among pseudomyrmecine species and species groups (Ward, 1990) shows *V.tessmanni* nested well within the genus *Tetraponera*. Thus its exceptional character states are most parsimoniously interpreted as derived conditions within *Tetraponera*. The same is true of those features originally used to set off *Pachysima* (larval exudatoria) and *Viticicola* (larval morphology; reduced palp formula) from *Tetraponera*. I could find no synapomorphies supporting the genus *Tetraponera* if *Pachysima* and *Viticicola* are excluded from it.

Synonymy of these two genera under *Tetraponera* is here advocated not because *Pachysima* and *Viticicola* are insufficiently distinct (they are both specialized plant-ants and possess a number of unique traits, especially as larvae) but because recognition of them as distinct genera would render *Tetraponera* paraphyletic. Similarly, the justification for retaining *Pseudomyrmex* and *Tetraponera* as valid genera is *not* that there are a considerable number of characters which exhibit distinct differences between them, but that the derived (apomorphic) conditions of these characters are apportioned among *both* genera. Synapomorphies for *Pseudomyrmex* include the long masticatory margin of the male mandible (with 6 or more teeth), truncate median clypeal lobe (workers, queens), elongate compound eye (workers), loss of hind basitarsal sulcus (workers, queens), and ventral repositioning of the antennae in the male pupa (Figs 19, 20). *Tetraponera* exhibits fewer derived features, of which the following may be mentioned (all worker- and queen-based): mandible lacking proximal basal tooth; masticatory margin of mandible with 3–4 (exceptionally 5–6) teeth; and median connection of spiracular plate (of sting apparatus) membranous.

This reduces the number of valid described genera in the subfamily to two. Moreover they continue to be biogeographically distinct, with all Old World species belonging to *Tetraponera*. There is, however, an undescribed pseudomyrmecine species, known only from the Amazon Basin, which I believe represents a third genus (described below as *Myrcidris* gen.n.). This possesses a mix of the traits of *Pseudomyrmex* and *Tetraponera*; for example,

the workers possess a proximal tooth on the basal margin of the mandibles and well developed basitarsal sulci. Moreover, among the differences between *Myrcidris* on the one hand and *Pseudomyrmex* and *Tetraponera* on the other, are two apparently derived traits shared by the last two genera: reduction in the number of male antennal segments from 13 to 12, and increased sclerotization of the inner (mesial) wall of the distal end of the paramere. Hence the new genus would appear to be a sister group to all other extant pseudomyrmecines. (See also Cladistic analysis, below.)

Key to genera: workers and queens

1. (a) Antennae 12-segmented; hind basitarsal sulcus variable, always absent in New World species 2

   (b) Antennae 11-segmented; hind basitarsal sulcus well developed (Fig. 6) (Brazil) ....
   .... *Myrcidris*

2. (a) Mandibles with proximal tooth on the basal margin (Figs 2, 15, 16); eyes elongate, width two-thirds or less than length (OI 0.50–0.66, OI2 0.50–0.64); hind basitarsal sulcus lacking (Fig. 12) (southern Nearctic, Neotropical) ...
   .... *Pseudomyrmex*

   (b) Mandibles without proximal tooth on the basal margin (Figs 3, 4, 13, 14); eyes less elongate, width two-thirds or more than length (OI 0.67–0.95, OI2 0.65–1.00); hind basitarsal sulcus usually present (Fig. 11) (Paleotropical) .... *Tetraponera*

Key to genera: males

1. (a) Antennae 13-segmented; posterior margin of sternum VIII broadly convex; external face of aedeagus with cornuti (Brazil) ..... *Myrcidris*

   (b) Antennae 12-segmented; posterior margin of sternum VIII emarginate; external face of aedeagus lacking cornuti 2

2. (a) Mandibles with 6–18 teeth or denticles on masticatory margin, those preceeding the preapical tooth often quite small and abraded; the minimum number of teeth (6) seen only in species which are small in size (HW <0.98); basal margin of mandibles one half or less the length of the masticatory margin (MD5/MD9 ≤0.55), the two converging angularly at the

apicobasal tooth or corner (New World) . . . . .
. . . . *Pseudomyrmex*

(b) Mandibles usually with 2–5 teeth on masticatory margin, typically subequal in size; rarely with 6 teeth, in which case HW ≥1.00; basal margin of mandibles two-thirds or more the length of the masticatory margin (MD5/MD9≥0.65), the juncture between the two angulate *or* rounded (Old World) . . . .
. . . . *Tetraponera*

Myrcidris Ward gen.n.
(Figs 1, 6, 21–25, 29–32)

Type species: *Myrcidris epicharis* Ward sp.n.

Diagnosis, worker. Monomorphic, and relatively small in size (HW 0.49–0.61 in the only known species). Mandibles with distinct basal and masticatory margins, the former shorter than the latter (MD5/MD9 ≈ 0.75); both underlain ventrally by ridge lines which meet angularly at the apicobasal tooth (Fig. 1); basal margin with a single, rather weak, proximal tooth; masticatory margin with four evenly spaced teeth, increasing in size towards the apex. Palp formula: 5,3. Distal margin of labrum with a broad v-shaped cleft; labrum without prominent teeth or protuberances. Median clypeal lobe broadly rounded anteriorly; upper surface continuous, non-truncate and with several finely attenuate, apically bent setae, directed anteriorly (Fig. 29). Number of antennal segments: 11 (with partial fusion of the second and third funicular segments in the only known species); scapes short (SI ≈ 0.42); funiculus swollen apically as an indistinctly 4-segmented club. Median lobes of antennal sclerites rather well developed laterally (Fig. 29) (ASI ≈ 0.90). Frontal carinae relatively well separated (MFC twice or more the basal scape width). Compound eyes with long axis directed anterolaterally, not exceptionally elongate (OI2 ≈ 0.70). Ocelli (3) present but very small. Metanotal groove distinctly impressed; basal face of propodeum slightly shorter than, and rounding gently into, declivitous face (Fig. 30). Propodeal spiracle elliptical. Two tarsal claws; mid and hind tibiae both with a well-developed pair of apical spurs; mid and hind basitarsal sulci present, well-developed (Fig. 6). Petiole relatively short and high

(PLI ≈ 0.76), with short, broadly attached anterior peduncle. Median connection of spiracular plate (of sting apparatus) sclerotized.

Diagnosis, queen. Deciduously winged; agreeing with most of the foregoing worker traits, except median clypeal lobe more protuberant; head and petiole more elongate. Forewing with two cubital cells.

Diagnosis, male. Masticatory margin of mandibles with 3 teeth. Palp formula: 5,3. Median clypeal lobe broadly convex anteriorly, adorned with several fine, apically bent setae. Antennae 13-segmented, with a short scape (subequal in length to second funicular segment). Notauli absent; parapsidal lines lightly impressed. Basitarsal sulci lacking. Claws and tibial spurs as in the worker. Posterior margin of sternum VIII slightly convex; posterior margin of sternum IX (subgenital plate) broadly rounded; tergum VIII (pygidium) apicomedially constricted and emarginate. Pygostyles with a rigid, sclerotized connection to remnants of terga IX and X. Parameres narrowing apically, but with a distinct posterodorsal lobe, and a mesial dorsoventral lobe on the inner surface (Figs 24, 25). Internal face of paramere predominantly membranous (unsclerotized) distal to the volsella and proximal to the mesial dorsoventral lobe. Volsella reduced to a small, setose, finger-like lobe. External face of inner valve (aedeagus) adorned with cornuti; internal face with flat plate-like surface separated from dorsal margin by a membranous groove. Antennae in the pupal stage lying ventrally below the mandibles.

Discussion

The unique features of workers and queens of *Myrcidris* are the 11-segmented antennae, single proximal tooth (and no others) on the basal margin of the mandibles, the particular configuration of ventral mandibular ridges (Fig. 1), and the presence of fine, attenuate, apically bent setae on the upper medial surface of the clypeus. Also characteristic are the four teeth on the masticatory margin of the mandibles; non-truncate upper surface of the median clypeal lobe; laterally extended median lobes of the antennal sclerites; and well-developed mid and hind basitarsal sulci.

Distinguishing features of males are the 13-segmented antennae; apically bent clypeal

mdvl

pdl

mdi

24

25

23

0.5mm

22

21
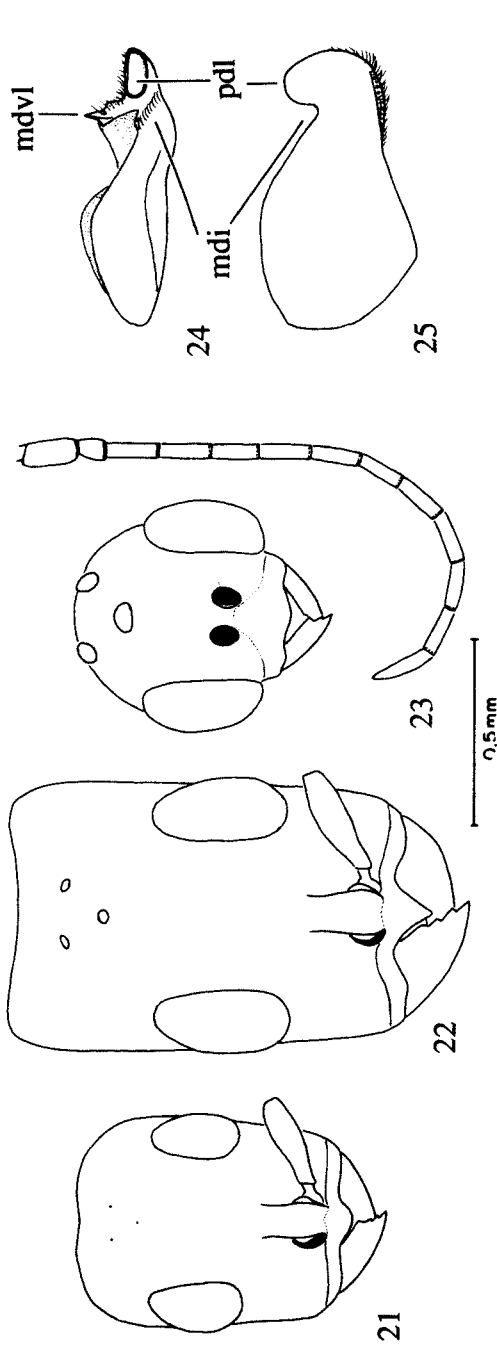
Figs 21–25. *Myrcidris epicharis*. 21, worker, frontal view of head, pilosity and antennae (except left scape) not shown; 22, queen, same; 23, male, same, with right antenna depicted separately; 24, 25, male, left paramere, dorsal and lateral views, respectively, caudal end to right. mdi = mediodorsal impression, mdvl = mesial dorsoventral lobe, pdl = posterodorsal lobe.

28

0.5mm

27

26
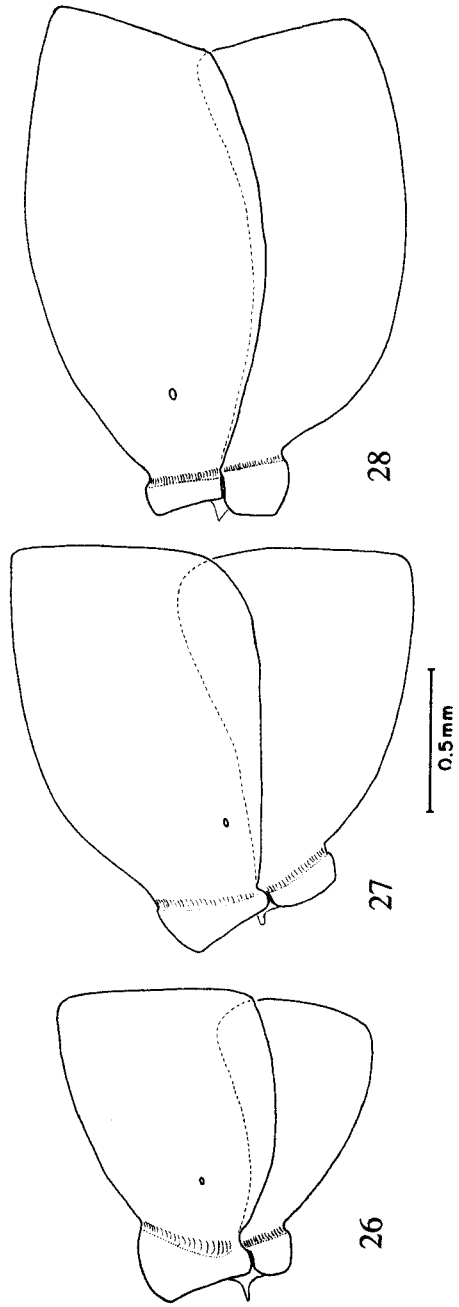
Figs 26–28. Lateral view, from left side, of fourth abdominal (first gastric) tergum and sternum. 26, *Tetraponera grandidieri*, male; 27, *Pogonomyrmex subdentatus*, male; 28, *Eciton burchelli*, worker.
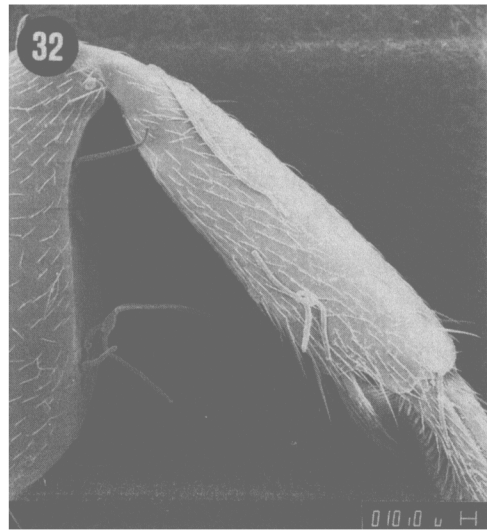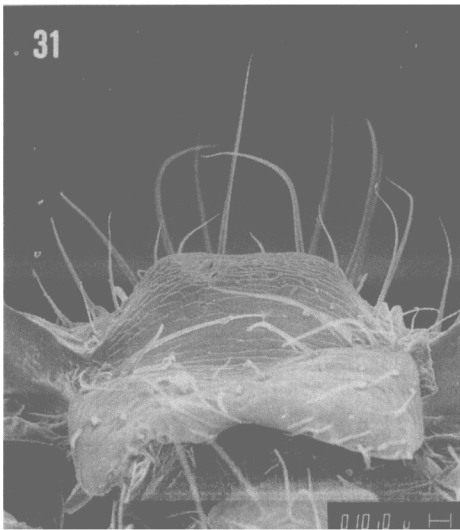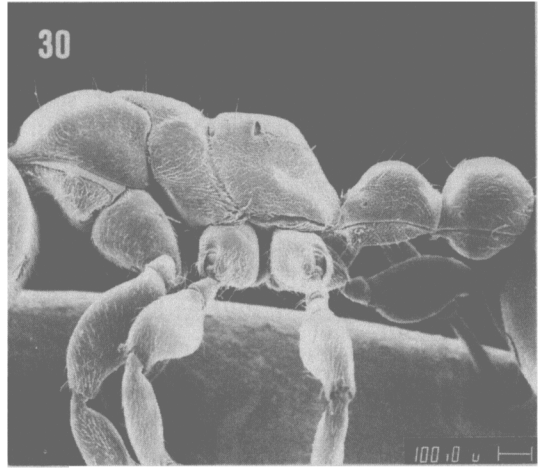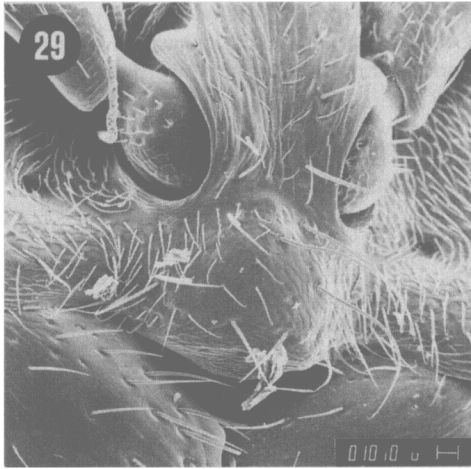
Figs 29–32. *Myrcidris epicharis*, worker. 29, oblique anterodorsal view of frontoclypeal complex; 30, lateral view of mesosoma, petiole, and postpetiole; 31, anterior view of median clypeal lobe; 32, anterior view of left hind tibia.

setae; convex posterior margin of sternum VIII; sclerotized attachment of the pygostyles to tergum X; membranous internal face of the paramere behind the mesial dorsoventral lobe; and presence of cornuti on the external face of the inner valve (aedeagus).

Myrcidris is known only from a single species, inhabiting live swollen stems of a rainforest ant-plant, *Myrcia* sp. (Myrtaceae), in Amazonas, Brazil. The relationship of *Myrcidris* to the other two pseudomyrmecine genera is discussed below (under Cladistic analysis).

Myrcidris epicharis Ward sp.n.
(Figs 1–6, 21–25, 29–32)

Holotype worker. BRAZIL, Amazonas: Faz. Esteio, 80 km NNE Manaus, 80 m, 2°25′S, 59°46′W, 15.ix.1987, ex live terminal stem of *Myrcia* sp. (Myrtaceae), in INPA/WWF rain-forest reserve (no. 1101) (*P. S. Ward acc. no. 9146*) (INPA) HW 0.58, HL 0.75, EL 0.27, PL 0.29, PH 0.23.

Paratypes. Same locality and date as holotype, P. S. Ward acc. nos. 9143–9148: series of

workers, queens, and males, from different individual trees of *Myrcia* sp.; BRAZIL, Amazonas: Res. Campina, near Manaus, 29.vii.1979 ex '*Siparuna*' [= *Myrcia* sp.], (*W. W. Benson acc. no. 26F*) workers; Res. Campina, km 44, BR-174, near Manaus 27.viii.1979 ex '*Siparuna*' [= *Myrcia* sp.] (*W. W. Benson acc. no. 50F*) workers; E.E.S.T., km. 44.5, BR-174, near Manaus, 30.vii.1981, ex 7 m '*Siparuna*' [= *Myrcia* sp.], (*W. W. Benson acc. no. 370F*) workers and queens; Reserva 1101, km 27, ZF-3, near Manaus 10.viii.1981 (*W. W. Benson*) 1 worker. Paratypes deposited in ANIC, BMNH, INPA, IZAV, JTLC, LACM, MCSN, MCZC, MHNG, MJPL, MNCR, MZSP, NHMB, PSWC, UCDC, UNCB, USNM, and WWBC.

Worker measurements (n = 14). HL 0.65–0.79, HW 0.49–0.61, MFC 0.082–0.102, CI 0.75–0.79, OI 0.67–0.74, REL 0.33–0.37, REL2 0.43–0.48, OOI 0.34–0.64, VI 0.76–0.86, FCI 0.156–0.182, SI 0.40–0.46, SI2 0.85–1.07, FI 0.45–0.50, PDI 0.78–0.93, MPI 0.039–0.075, NI 0.52–0.58, PLI 0.72–0.84, PWI 0.61–0.74, PWI3 0.56–0.65, PPWI 1.32–1.63.

Queen measurements (n = 6). HL 1.03–1.11, HW 0.68–0.73, MFC 0.119–0.131, CI 0.62–0.68, OI 0.69–0.75, REL 0.32–0.35, REL2 0.50–0.53, OOI 0.87–1.38, VI 0.93–0.98, FCI 0.164–0.191, SI 0.41–0.44, SI2 0.79–0.86, FI 0.48–0.51, NI 0.63–0.67, PLI 0.60–0.65, PWI 0.58–0.66, PWI3 0.67–0.75, PPWI 1.35–1.45.

Worker diagnosis. A small species (HW 0.49–0.61) with head notably longer than broad (Fig. 21); sides of head broadly convex, rounding into the occipital margin which is flat to weakly concave medially; frontal carinae separated by about maximum scape width; scapes bent proximally and enlarged distally, very short, subequal to or less than eye length; first funicular segment exceeding in length the next three segments combined; second and third funicular segments much broader than long (FLI 0.77–1.16), sometimes partly fused; the three ocelli very weak, usually reduced to slight pin-prick impressions; pronotum laterally rounded; fore-femur moderately swollen; propodeal spiracles laterally protuberant in dorsal view; petiole longer than high or wide, with a conspicuous anteroventral tooth and with a rather broad anterior peduncle; postpetiole markedly broader than long.

Outer surface of mandibles smooth and shiny, becoming striato-punctate towards the masticatory margin. Head smooth and shiny on upper half, with widely scattered punctulae, becoming sublucid and much more densely punctulate anteromedially; opaque and densely coriarious-punctulate between the frontal carinae. Mesosoma dorsum smooth and shiny with scattered punctulae, laterally sublucid and imbricate-coriarious except for smooth areas on the propleuron and upper half of mesopleuron. Petiole, postpetiole and fourth abdominal (first gastric) tergite sublucid, covered with fine piligerous punctures. Appressed pubescence moderately dense on most of body except the smooth shiny areas on the head and mesosoma. Fine standing pilosity moderately common on scapes, gula, mesosoma dorsum (9–15 hairs), petiole and postpetiole; absent or very sparse on gastric terga (excluding posterior margins), external face of mid- and hind-tibiae, sides of head (frontal view) and upper half of head (except for 1 pair of supraocular setae). Orange-brown, with weakly infuscated bands on posterior margins of gastric terga; head a little darker than mesosoma; appendages paler luteous, mandibles darker, ferrugineous brown.

Queen diagnosis. Head elongate (CI ≈ 0.65), subrectangular, with parallel sides and a concave occipital margin (Fig. 22); median clypeal lobe subtriangular and protuberant; scape and funiculus similar to that of worker; ocelli (3) well developed; petiole more slender than that of worker (compare PLI and PWI values), with a larger anteroventral process, body sculpture paralleling that of worker; standing pilosity more common, especially on gaster and upper half of head. Dark castaneous brown, antennae, tibiae, and tarsi a contrasting luteous brown, femora intermediate.

Male diagnosis. Small (HW ≈ 0.60), with prominent compound eyes and ocelli (Fig. 23); first funicular segment about one half the length of the second and succeeding segments which are subequal in length and do not become shorter distally; forefemur not swollen; petiole slender, lacking a distinct anteroventral tooth. Body more extensively smooth and shiny than in the worker; appressed pubescence and decumbent to suberect pilosity common. Dark brown, with contrasting paler appendages. See also generic diagnosis.

Discussion

This species was originally discovered by Woody Benson, and is referred to as a 'small timid *Pseudomyrmex*' living in '*Siparuna*' in his review (Benson, 1985) of Amazonian ant-plants. It is known from only a few sites in lowland rainforest north of Manaus.

M.epicharis bears some resemblance to the *Tachigali*-inhabiting species (*Pseudomyrmex concolor* complex) in the *Pseudomyrmex viduus* group. I assume the resemblance reflects a combination of convergent similarity (both being specialist plant-ants) and symplesiomorphy (the *Pseudomyrmex viduus* group being close to the inferred ground plan of the genus). It is interesting that the workers of both are frequently attacked by an external fungus (?Laboulbeniaceae) (see Figs 8, 32).

Pseudomyrmex Lund

Pseudomyrme Lund, 1831a: 137. Vernacular.

Pseudomyrmex Lund, 1831b: 106. Type species: *Formica gracilis* Fabricius (designated by Smith, 1952: 98).

Leptalea Erichson, 1839: 309. Type species: *Formica gracilis* Fabricius (designated by Wheeler, 1911: 166). Synonymy by Smith, 1952: 98.

Pseudomyrma Guérin-Méneville, 1844: 427. Type species: *Formica gracilis* (designated by Wheeler, 1911: 171). Synonymy (under *Leptalea* Erichson) by Smith, 1951: 788.

Myrmex Guérin-Méneville, 1844: 427. Preoccupied. Type species: *Myrmex perboscii* Guérin-Méneville (by monotypy). Synonymy (under *Pseudomyrma* Guérin-Méneville) by F. Smith, 1858: 153.

Ornatinoda Enzmann, 1945: 61. Type species: *Pseudomyrma tenuis* (Fabricius) (original designation) **Syn.n.**

Clavanoda Enzmann, 1945: 61. Type species: *Pseudomyrma gracilis* (Fabricius) (original designation) **Syn.n.**

Triangulinoda Enzmann, 1945: 61. Type species: *Pseudomyrma spinicola* Emery (original designation) **Syn.n.**

Apedunculata Enzmann, 1945: 62. Type species: *Pseudomyrma sericea* Mayr (original designation) **Syn.n.**

Latinoda Enzmann, 1945: 62. Type species: *Pseudomyrma latinoda* Mayr (original designation) **Syn.n.**

'*Formica*' (in part): Fabricius, 1804: 405.

'*Myrmica*' (in part): Weddell, 1849: 263; Spinola, 1851: 241.

'*Tetraponera*' (in part): F. Smith, 1852: 45.

'*Ponera*' (in part): Buckley, 1867: 172.

The names which Enzmann used for different 'branches' of *Pseudomyrmex* have not been included in previous lists of the subgeneric and generic names of ants (e.g. Brown, 1973; Snelling, 1981) but it was pointed out to me by Barry Bolton (pers. comm.) that they must be considered subgeneric names, under Articles 10e and 13b of the ICZN (1985). Consonant with Enzmann's other contributions, these groupings are entirely artificial, if not fanciful, and have no taxonomic merit.

Diagnosis, worker. Monomorphic, varying greatly in size (worker HW 0.45−2.86). Basal and masticatory margins of mandibles distinct, the former bearing a proximal tooth and 1 (rarely 2) mesial tooth (teeth); masticatory margin with 5−10 teeth or denticles (Figs 2, 15, 16). Venter of mandible with a sharp ridge or escarpment, preceding the masticatory margin, which terminates at the apico-basal tooth; corresponding ridge behind basal margin weak or absent (Fig. 2). Palp formula: 6,4; with reductions to 6,3; 5,4; 5,3; and 4,3. Distal margin of labrum with a broad, v-shaped cleft; labrum without prominent teeth or protuberances. Upper (anterodorsal) surface of median clypeal lobe discontinuous and (at least laterally) truncate. Antennae 12-segmented. Median lobes of antennal sclerites slightly to moderately expanded laterally, the basal condyles of the antennae correspondingly exposed (Fig. 8) (ASI 0.40−0.74). Frontal carinae often rather closely contiguous, but not always so (FCI 0.01−0.13). Compound eyes relatively large, and elongate (OI2 <0.65). Ocelli (3) always present. Metanotal groove varying from distinctly impressed to entirely absent. Petiolar node varying in shape, distinct anterior peduncle present or absent. Mid and hind basitarsal sulcus always absent (Fig. 12). Median connection of spiracular plates (of sting apparatus) sclerotized.

Diagnosis, queen. Deciduously winged, agreeing with most worker characters, except for caste-specific differences in mesosomal morphology. Mandibles and median clypeal lobe occasionally modified from the condition

seen in worker. Forewing with two cubital cells.

Diagnosis, male. Basal and masticatory margins of mandibles distinct, former one-half or less the length of the latter; basal margin lacking teeth entirely; masticatory margin with 6–18 teeth or denticles, those preceding the preapical tooth often quite small in size. Palp formula and labrum as in workers. Anterior margin of median clypeal lobe varying from broadly convex to medially angulate; upper (antero-dorsal) surface non-truncate. Antennae 12-segmented. Median lobes of antennal sclerites little developed; frontal carinae absent or obsolete. Antennal sclerites often (but not always) remote from the posteromedial margin of the clypeus (i.e. separated by notably more than the maximum diameter of the antennal fossa). Paramere usually with posterodorsal lobe and mesial dorsoventral lobe, and frequently other adornments. Internal face of inner valve (aedeagus) typically with a flat, plate-like structure separated from the dorsal margin by a membranous groove or strip. Wing venation generally as in queen; some males of *P. viduus* group exhibit intra- and inter-individual variation in the number of cubital cells (1–2). Male pupa with unique antennal configuration: the antennae pass ventrally over the mandibles (Figs 19, 20), and are frequently (but not in the *P. gracilis* group, *P. sericeus* group, and a few other species) curled in a semi-circular position.

Discussion

Pseudomyrmex is the largest genus in its subfamily, with more than 150 valid specific and infraspecific names. It ranges from southern United States (as far north as 40°N on the east and west coasts) to south-central Chile and Argentina (34°S). Nesting habits vary widely, with the majority of the species nesting non-specifically in dead hollow twigs of various plants, but with a substantial minority being obligate inhabitants of specialized ant-plants such as *Triplaris*, *Tachigali* and swollen-thorn *Acacia* (review in Ward, 1990).

Tetraponera F. Smith

Tetraponera F. Smith, 1852: 44. Type species: *Tetraponera atrata* F. Smith = *Eciton nigrum* Jerdon (designated by Wheeler, 1911: 173).

Sima Roger, 1863a: 178. Type species: *Pseudomyrma? allaborans* Walker (designated by Bingham, 1903: 107). Synonymy by F. Smith, 1877: 68; see also Donisthorpe, 1916.

Pachysima Emery, 1912: 97. Type species: *Tetraponera aethiops* F. Smith (original designation). **Syn.n.** (conditional synonymy by Brown, 1973: 183).

Viticicola Wheeler, 1919: 130. Type species: *Sima tessmanni* Stitz (original designation). **Syn.n.** (conditional synonymy by Brown, 1973: 185).

Sima Emery (nec Roger), 1921: 23. Type species: *Eciton rufonigrum* Jerdon (original designation). **Syn.n.**

Parasima Donisthorpe, 1947: 592. Replacement name, now unnecessary, for *Sima* Emery (nec Roger). **Syn.n.** (conditional synonymy by Brown, 1973: 183).

'*Eciton*' (in part): Jerdon, 1851: 111, 112.

'*Pseudomyrma*' (in part): F. Smith, 1855: 168; F. Smith, 1858: 159, 160; F. Smith, 1859: 145; F. Smith, 1860a: 106; F. Smith, 1863: 20; F. Smith, 1877: 60.

'*Cerapachys*' (in part): Motschoulsky, 1863: 21, 22.

Diagnosis, worker. Monomorphic or (rarely) polymorphic, variable in size (worker HW 0.42–2.25). Basal and masticatory margins of mandibles usually distinct, occasionally meeting at a rather oblique angle; basal margin with 0–2 teeth, proximal tooth always lacking; masticatory margin with 3–6 teeth, usually 3 or 4, subequal in size (Figs 3, 4, 13, 14). Venter of mandible with a single ridge or weak rise, which is continuous and broadly rounded behind the masticatory and basal margins (sometimes this ridge is very reduced) (Figs 3, 4). Palp formula: 6,4 in all species, except *T. tessmanni* where reduced to (4p3,3). Distal margin of labrum usually with a narrow, notch-like cleft; prominent teeth or protuberances sometimes present on the labrum. Anterodorsal surface of median clypeal lobe continuous, non-truncate; anterior margin often toothed or crenulate. Antennae 12-segmented. Median lobes of antennal sclerites rather strongly expanded laterally, covering most of the basal condyles of the antennae (Fig. 7) (ASI 0.75–1.00). Frontal carinae separated by more than basal scape width (FCI 0.08–0.25). Compound eyes relatively large, width two-thirds or more the length. Number of ocelli: 3, with reductions to 2 and (commonly) 0.

Metanotal groove usually distinctly impressed, sometimes preceded by a distinct, flattened, metanotal (or mesoscutellar?) plate. Hind basitarsal sulcus (Fig. 11) nearly always present, becoming rather reduced in some species and absent in three. Mid basitarsal sulcus less frequently developed. Mid and hind tarsi each with a pair of apical spurs, the anterior spur sometimes very reduced, the posterior spur pectinate. Median connection of spiracular plates (of sting apparatus) membranous.

Diagnosis, queen. Deciduously winged (ergatogynes known in one species). Similar in most respects to workers; mandibles often modified, e.g. with a much expanded apicobasal area or basally geniculate. Genal pit often present, just above mandibular insertions. Ocelli (3) always present. Mid and hind basitarsal sulci more prominent than in workers. Forewing typically with two cubital cells; reductions to one cell occur.

Diagnosis, male. Basal margin of mandibles two-thirds or more the length of the masticatory margin, the two often meeting at a rounded corner rather than a sharp apico-basal angle; basal margin with 0, rarely 1, teeth; masticatory margin with 2–6 teeth, generally subequal in size (6 teeth occurring only in larger species, with HW ≥1.00). Palp formula and labrum as in workers. Anterior margin of clypeus straight to broadly convex, rarely emarginate; clypeal lobe sometimes dorsomedially protuberant. Antennal sclerites often projecting anterodorsally over the frontal triangle; antennal insertions situated relatively close to the posterior margin of the clypeus (separated by less than the maximum diameter of the antennal fossa). Tibial spurs as in workers. Volsella a small, setose, finger-like lobe; in some species even further reduced and fused to the inner wall of the paramere (where it is quite inconspicuous). Internal face of inner valve (aedeagus) lacking a differentiated, plate-like structure which is separated from the dorsal margin. Wing venation as in queen. Antennae in pupa passing laterally on either side of the mandibles (Figs 17, 18).

Discussion

Widespread in the Old World tropics, *Tetraponera* contains approximately 110 nominal taxa, occurring in Africa, Madagascar, India, south-east Asia and Australia. Five species have been described from Baltic amber, and one from Oligocene deposits in France.

Although less diverse than its New World counterpart, *Tetraponera* is nevertheless a conspicuous element of the ant fauna in some regions, especially Madagascar. Most species are unspecialized twig-nesters; a few have become obligately associated with ant-plants (*Barteria*, whistling-thorn *Acacia*, and several others; see Ward, 1990).

Excluded from Pseudomyrmecinae

Ponerinae, *incertae sedis*,
Condylodon Lund, 1831a: 131. Type species: *Condylodon audouini* Lund (by monotypy).

This inadequately described taxon appears in a paper by Lund (1831a) on Brazilian ants. No type material is known to exist. *Condylodon* was synonymized under *Pseudomyrma* (=*Pseudomyrmex*) by Dalle Torre (1893), an action which was followed by most subsequent authors (e.g. Wheeler, 1911; Donisthorpe, 1943; Brown, 1973; Snelling, 1981; Hölldobler & Wilson, 1990; and, with a query, Kempf, 1972). However, upon reading the original description and adjacent text, I find no compelling reasons to accept this synonymy. After discussing two ants of the subfamily Ponerinae (an *Odontomachus* and a *Pachydondyla* species), Lund (1831a) describes *Condylodon* as similar to a ponerine ant with respect to the constriction between the second and third metasomal ('abdominal') segments, as well as the presence of a sting, but differing by other (unspecified) characters. Lund then lists *C.audouini* as the sole species, of which he found a single individual on leaves. We are given no further description of *Condylodon*, but the following paragraph reads (p. 132): '*Next* come the ants with the pedicel of the abdomen formed of two nodes...' (emphasis mine). Lund proceeds to discuss several myrmicine ants, and finishes (p. 137) by describing *Pseudomyrmex*, using the vernacular name, Pseudomyrme, suggested to him by Latreille. It is clear from the text that Lund was impressed by the distinctness and conspicuousness of these ants (*Pseudomyrmex*). He mentions, in particular, their large, elongated eyes, two-noded pedicel, and sting.

Given the entire context of Lund's description of *Condylodon*, it seems highly unlikely that *Condylon* is a pseudomyrmecine. Emery's (1921: 28) assessment of *Condylodon* as a ponerine ant is most reasonable considering the available evidence. Beyond that, its identity remains obscure although *Ectatomma* comes to mind as a possibility.

Cladistic analysis

Generic relationships within the Pseudomyrmecinae

Given only three genera, all arguably mono-phyletic, in the subfamily Pseudomyrmecinae, one might expect the resolution of generic re-lationships to be straightforward. A difficulty arises, however, with the choice of an outgroup. Previous higher-level taxonomic studies within the Formicidae have not clearly identified a sister-group to the Pseudomyrmecinae. The pseudomyrmecines can be assigned to the 'poneroid complex' (*sensu* Taylor, 1978), on the basis of possessing differentiated presclerites on abdominal segment IV and a dorsal stridulitrum on the pretergite of the same. About six or seven other subfamilies belong in this group (the stridulitrum must be presumed lost in some of these). A dataset on morpho-logical variation among the pseudomyrmecine genera was therefore expanded to include seven other genera from the 'poneroid complex'. The

morphologically primitive ant, *Nothomyrmecia*, not typically considered a part of the 'poneroid complex', was also added and served as an outgroup for the expanded set of taxa. The dataset (Table 2) was analysed using Hennig86 and PAUP, with the same results: a single most parsimonious tree of length 99 steps (consistency index 0.586) (Fig. 33).

This tree depicts *Myrcidris* as the sister-group to the other two genera of Pseudomyrmecinae. Monophyly of (*Pseudomyrmex* + *Tetraponera*) is supported by two synapomorphies: reduction in male antennal segment number from 13 to 12; and increased sclerotization of the inner (mesial) wall of the paramere, distal to the volsella.

This conclusion is tempered, however, by the fact that there is almost equal support for an alternative arrangement: (*Tetraponera* + (*Pseudomyrmex* + *Myrcidris*)). This requires only one additional step; it would, of course, imply convergence of the afore-mentioned male characters in *Pseudomyrmex* and *Tetraponera*, but other characters, e.g. the proximal tooth on the basal margin of the mandible in workers and queens, become putative synapomorphies of *Pseudomyrmex* and *Myrcidris*. While the more parsimonious interpretation is to be pre-ferred, additional character state information is desirable.

If *Myrcidris* is indeed positioned basally in the subfamily, this has interesting biogeographic implications. The two species-rich genera, *Pseudomyrmex* and *Tetraponera*, divide cleanly

Table 2. Character state data used in cladistic analysis of pseudomyrmecine genera and representative genera from other subfamilies. Characters 6, 34 and 36 were treated as unordered. A "?" signifies inapplicable or unknown.

	1	11	21	31	41
Nothomyrmecia	1210?20000	0001000000	0010000011	0000001??0	0100100?00
Myrmecia	??101?000?	0001000000	0010000000	0000021000	000000?000
Myrcidris	0000100110	1001101101	0010011011	0000012110	0111011011
Pseudomyrmex	0101010001	1000011101	1000011011	0000012110	0100110111
Tetraponera	1000121000	1001011101	0010011011	0000012110	1100110011
Myrmica	1101120000	0101000211	0101110111	1100112110	1000000010
Pogonomyrmex	1100120210	0101000211	0101110111	1100112110	1100000010
Cerapachys	1201120210	0?11001201	010??1100?	101102?000	0?02000000
Ambylopone	??101?0110	0001001101	0000110100	1012020001	000?100000
Paraponera	0210110111	0101000000	0110000001	1112020011	0000100?00
Ectatomma	1211110110	0101000000	0101000101	1112020011	0000000?00

33

Length: 99
C. I.: 0.586

Nothomyrmecia
Myrcidris
Pseudomyrmex
Tetraponera
Myrmica
Pogonomyrmex
Myrmecia
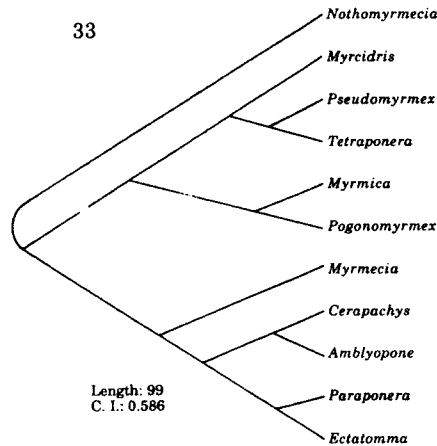Cerapachys
Amblyopone
Paraponera
Ectatomma

Fig. 33. Most parsimo: .ious (minimum-length) tree obtained in a cladistic analysis of ten 'poneroid' genera, with *Nothomyrmecia* as outgroup. C.I. is the consistency index (in the sense of Kluge & Farris, 1969).
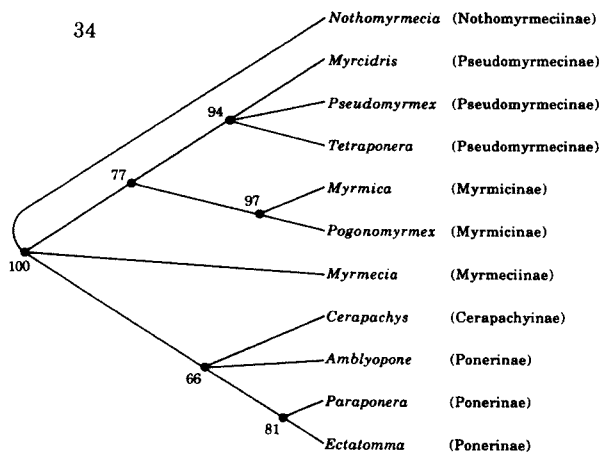
34

Nothomyrmecia	(Nothomyrmeciinae)
Myrcidris	(Pseudomyrmecinae)
Pseudomyrmex	(Pseudomyrmecinae)
Tetraponera	(Pseudomyrmecinae)
Myrmica	(Myrmicinae)
Pogonomyrmex	(Myrmicinae)
Myrmecia	(Myrmeciinae)
Cerapachys	(Cerapachyinae)
Amblyopone	(Ponerinae)
Paraponera	(Ponerinae)
Ectatomma	(Ponerinae)

94
77
97
100
66
81

Fig. 34. Majority rule consensus tree of 100 bootstrapped replicates of the original data set. The number at each node indicates the number of times that the group subtending the node appeared (in 100 replicates).

on geographical grounds: the former is confined to the New World, while *Tetraponera* has a Palaeotropical distribution, with the more generalized species found, for the most part, in Africa and Madagascar. If the origin of these two genera dates to the rift between South America and Africa, *Myrcidris* demonstrates that this occurred *after* there had been some initial diversification in the subfamily.

Obligate (usually mutualistic) associations with domatia-bearing plants have arisen re-

peatedly in the Pseudomyrmecinae (Ward, 1990). Presence of this trait in *Myrcidris*, in the primitive *Pseudomyrmex viduus* group, and in other species groups in both *Pseudomyrmex* and *Tetraponera*, indicates a long history in the subfamily of mutually beneficial relations with plants. It seems most likely that generalized arboreal nesting habits are part of the ground-plan for the subfamily, but some lineages must have specialized as plant-ants quite early on in the Tertiary.

Relationship of Pseudomyrmecinae to other formicids

There has not been a clear consensus on the phylogenetic affinities of the Pseudomyrmecinae. Emery (1899, 1921), Forel (1885, 1893) and Wheeler (1920) treated them as a tribe or subfamily, within or related to, the Myrmicinae on the basis of the common possession of a postpetiole. Brown (1950) suggested that the Pseudomyrmecinae were allied to the Myrmeciinae (including *Nothomyrmecia*) within his 'myrmecioid complex' which also included Dolichoderinae and Formicinae. He discounted a close relationship to the Myrmicinae, and considered the latter to be a derived group within the 'poneroid complex', composed of four other subfamilies: Ponerinae, Cerapachyinae, Dorylinae and Leptanillinae. A similar scheme was presented by Wilson *et al.* (1967) and Wilson (1971). Taylor (1978) proposed a different arrangement in which the Myrmeciinae (excluding *Nothomyrmecia*) and Pseudomyrmecinae were considered to be basal lineages in the 'poneroid complex'. The erstwhile 'myrmecioid complex', bereft of *Myrmecia* but still including *Nothomyrmecia*, was renamed the 'formicoid complex'. Taylor (1978) gave no synapomorphies for the latter group, but the 'poneroid complex' was defined by a 'tubulate' fourth abdominal segment bearing a dorsal stridulatory organ.

Finally in the first explicit, multi-character cladistic analysis of the Formicidae, Baroni Urbani (1989) presented a cladogram in which the Pseudomyrmecinae and Myrmicinae were sister groups nested within the following larger complex of 'poneroid' subfamilies: (((Dorylinae + Leptanillinae) + Ecitoninae) + (Myrmeciinae + (Ponerinae + (Myrmicinae + Pseudomyrmecinae)))). The characters apparently uniting the Pseudomyrmecinae and Myrmicinae were stereotyped carrying behaviour (see also Duelli, 1977) and naked pupae. However, there are some ambiguities in the coding of character states − compare Fig. 1 and Table 1 in Baroni Urbani (1989) − and Baroni Urbani's (1989) dataset (Table 1) is consistent with a large number of other equally parsimonious trees, not all of which place the Pseudomyrmecinae and Myrmicinae together.

The present study represents an attempt to reassess the phylogenetic relationships between the Pseudomyrmecinae and other poneroid taxa, using an expanded set of morphological characters and including a more detailed character analysis of abdominal segments II−IV. The numerical cladistic analysis is restricted to six subfamilies, represented by exemplar genera; three other subfamilies (Dorylinae, Ecitoninae and Leptanillinae) are not included. Genera were chosen which were thought to be most likely to portray the ground-plan characteristics of their subfamily, although as the character state information accumulated it became obvious that even putatively 'primitive' genera like *Amblyopone* in fact possess a mix of derived and ancestral features. Nevertheless, a preliminary survey of other genera, including representatives from the Dorylinae, Ecitoninae, and 'formicoid' subfamilies (see 'Materials and Methods'), suggests that the major conclusions (below) are valid for the subfamilies concerned, not just the genera included directly in the numerical cladistic analysis.

The most parsimonious interpretation of the character state information (Table 2) is that, among the eleven taxa being considered, the three pseudomyrmecine genera (*Myrcidris* + (*Pseudomyrmex* + *Tetraponera*)) are a sister group of the two myrmicine genera (*Pogonomyrmex* + *Myrmica*) (Fig. 33). This larger group is in turn a sister group of (*Myrmecia* + ((*Cerapachys* + *Amblyopone*) + (*Ectatomma* + *Paraponera*))). The evidence supporting some of these components is rather weak. The sister-group relationship between *Cerapachys* and *Amblyopone* may be a spurious one, and could be attributed to their convergent possession of reduced features; but it also reflects the paucity of synapomorphies for the Ponerinae, in which *Amblyopone* is typically included.

To assess the relative support for different branches of the cladogram, the tree estimate was bootstrapped, i.e. the characters were randomly sampled with replacement, using the BOOT algorithm of PHYLIP. Fig. 34 depicts the majority rule consensus tree (Margush & McMorris, 1981) from 100 bootstrapped replicates; this shows those groups which appeared in more than 50% of the replicates. Using this as a (very liberal) guide to confidence limits, the following conclusions emerge from the cladistic analysis: The Pseudomyrmecinae and Myrmicinae are sister groups; together

they are part of an unresolved trichotomy in the poneroid complex involving (Pseudomyrmecinae + Myrmicinae), Myrmeciinae, and (Cerapachyinae + Ponerinae).

Evidence for the monophyly of the Pseudomyrmecinae is quite strong and includes the five characters mentioned previously (under the subfamily diagnosis), plus the proximal basal tooth on the mandible of workers and queens which must be presumed secondarily lost in *Tetraponera*. Among the apparent synapomorphies of the Myrmicinae are laterally expanded frontal carinae of the worker; male scape length more than one-fifth the total length of the funiculus; fused promesonotum of the worker; loss of one hindtibial spur; dorsally or posterodorsally directed metapleural gland opening; fusion of petiolar tergum and sternum; and the ventral position of the lateral margins of presternite III. The conclusion that the Pseudomyrmecinae and the Myrmicinae (as represented by *Pogonomyrmex* and *Myrmica*) form a monophyletic group is supported by the following derived characters (w = worker; q = queen, m = male):

1. Masticatory margin of mandibles with ≤10 teeth (w, q).
2. Mandibles relatively short; MD3/HL <0.70 (w).
3. Scape more than one-third the length of first two funicular segments (m).
4. First funicular segment one-quarter or more the length of the second (m).
5. Hind coxal cavities closed (w, q, m).
6. Abdominal segment IV with differentiated but unfused presclerites (w, q, m).
7. Presternite IV much shorter than (about 5–20% of) the total length of the sternum (w, q, m).
8. Presternite IV shorter than pretergite IV, the latter protruding downward laterally (w, q, m) (Figs 26, 27).
9. Pupa naked (w, q, m).

Note that the character 'postpetiole' does not appear in the above list. There are more fundamental similarities between the two subfamilies than the formation of a second node-like segment on the metasoma. In particular, the configuration of the pretergite and presternite of abdominal segment IV appears to be unique to the Pseudomyrmecinae and Myrmicinae; it is not seen in other poneroids which have devel-

oped a distinct postpetiole, for example *Eciton* (compare Figs 26–28). In some myrmicines pretergite IV has become shorter than presternite IV, in association with the loss of a dorsal stridulitrum, but this is clearly a secondarily derived condition within the subfamily. The other characters listed above (1–7 and 9) have arisen, presumably convergently, in some other poneroids, particularly Cerapachyinae and army ants (Ecitoninae and Dorylinae). There are also several symplesiomorphous characters which, while not providing evidence of a close relationship between the two subfamilies, preclude the Myrmicinae from being derived within the group of (Ponerinae + Cerapachyinae). The most important of these are the unfused conditions of both the tergum and sternum proper of abdominal segment III and the presclerites of the same segment.

Similarities between the Pseudomyrmecinae and the Myrmeciinae reflect retained primitive features (large eyes; exposed median lobes of antennal sclerites; flexible articulation of the promesonotum; unfused sclerites of abdominal segments II–IV; well developed sting; etc.). I could find no derived characters which would support a sister-group relationship between these two subfamilies.

The position of the Myrmeciinae remains problematic, but the monophyly of a group including the Cerapachyinae, Ecitoninae, Dorylinae and Ponerinae is indicated by the following synapomorphies: (i) fusion, in both sexes, of the presclerites of abdominal segment III; (ii) complete lateral fusion, in workers, of the tergum and sternum proper of the same segment. The Leptanillinae also exhibit these traits (B. Bolton, pers. comm.).

Finally, during the course of this study, which included cursory examination of representatives from the other extant subfamilies of ants, it became apparent that *Nothomyrmecia* probably belongs at the base of the 'poneroid complex', rather than with the 'formicoid' group (Dolichoderinae, Aneuretinae, Formicinae). *Nothomyrmecia* shows incipient differentiation of presclerites on abdominal segment IV. This is particularly evident in the male where there is a slight but definite impression separating these differentiated anterior regions from the remainder of the tergum and sternum. The impression continues across the entire plate, becoming obsolete only at the lateral margins. In addition,
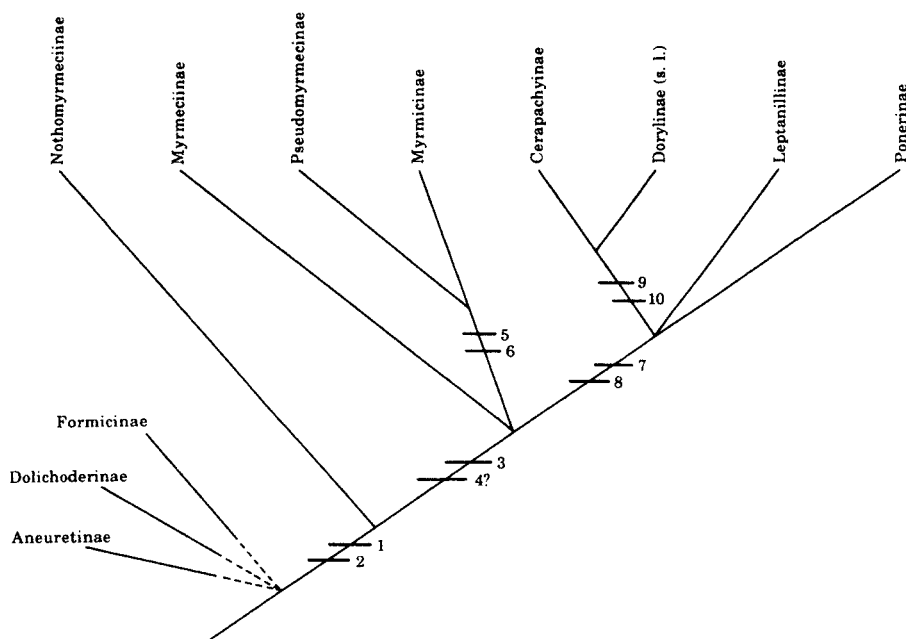
Fig. 35. Proposed (partially resolved) phylogeny of the extant subfamilies in the 'poneroid complex' of ants. The Ecitoninae are included in the Dorylinae. The subfamilies are assumed to be monophyletic but this needs confirmation for the Ponerinae, for which only one autapomorphy (tergosternal fusion of abdominal segment IV) is known. Derived conditions shared by two or more subfamilies are (w = worker, q = queen, m = male): (1) longitudinal sulcus on mid- and hind-basitarsi (w, q; rarely m; secondarily lost in higher poneroids); (2) incipient differentiation of presclerites on abdominal segment IV (w, q, m); (3) sharply differentiated presclerites on abdominal segment IV, forming a ball joint (w, q; usually m); (4) dorsal stridulitrum on pretergite IV (w, q, m; may have arisen twice within the poneroid complex); (5) pupa naked (w, q, m); (6) presclerites IV very short, presternite shorter than pretergite, which protrudes ventrolaterally (w, q, m); (7) fusion of presclerites of abdominal segment III (w, q, m); (8) fusion of tergum and sternum proper of abdominal segment III (w); (9) furcate subgenital plate (m); (10) ventrally protruding presternite III (w). Relationships among the 'formicoid' subfamilies (Formicinae, Dolichoderinae, Aneuretinae) are uncertain (but see Lutz, 1986).

workers of *Nothomyrmecia* possess a longitudinal sulcus on the hind and mid basitarsi, a trait shared with the Myrmeciinae, Pseudomyrmecinae, and at least one ponerine genus: *Paraponera*. This character must be presumed lost in other, more derived poneroid groups.

The conclusions of this study are summarized in Fig. 35, which provides a partially resolved phylogeny of the 'poneroid complex'. This should be treated as a working hypothesis — the most parsimonious interpretation of the data at hand, but one certainly subject to revision as additional character state information accumulates. When uncertainties are resolved, the phylogenetic tree of the ants may be more pectinate than in previous schemes depicting two major clades.

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Appendix

Synonymic list of species in the subfamily Pseudomyrmecinae

Taxa examined during the present study are marked with an asterisk (*). A 't' next to an available name signifies that the holotype, lectotype or syntype(s) was(were) examined. Country of type locality is given for each available name, as is the original reference for all previously established synonymy. Detailed species-level studies currently underway indicate the existence of considerable additional synonymy, particularly among infraspecific names. The latter are here listed as binomina, with their current nominal combination (cnc) given in parentheses. New generic combinations (all in *Tetraponera*) are indicated by **comb.n.** Fossil taxa and unavailable names are listed separately at the end of each genus.

Myrcidris Ward

*,t *epicharis* Ward, sp.n. (Brazil)

Pseudomyrmex Lund

*,t *acaciarum* (Wheeler, 1942: 176) (Panama) (cnc: *sericeus acaciarum*)
  t   = *acaciorum* (Enzmann, 1945: 90) (Panama) (Brown, 1949: 43)

*,t *acanthobius* (Emery, 1896b: 628) (Paraguay)
*,t *adustus* (Borgmeier, 1929: 198) (Brazil)
*,t *alustratus* Ward, 1989: 409 (Peru)
*,t *alfari* (Forel, 1906: 228) (Costa Rica)
*,t *alternans* (Santschi, 1936a: 197) (French Guiana)
*,t *alvarengai* Kempf, 1961: 372 (Brazil)
  antiguanus (Enzmann, 1945: 78) (Guatemala)
*,t *apache* Creighton, 1952: 134 (United States)
*,t *argentinus* (Santschi, 1934: 27) (Argentina) (cnc: *gracilis argentinus*)
*,t *atrinodus* (Santschi, 1934: 26) (Brazil) (cnc: *gracilis atrinodus*)
*,t *atripes* (F. Smith, 1860b: 70) (Brazil)
  t   = *kitschelti* (Forel, 1911b: 279) (Colombia) (Kempf, 1967: 2)
*,t *atrox* (Forel, 1912c: 24) (Panama) (cnc: *spinicola atrox*)
*,t *beccarii* (Menozzi, 1935: 192) (Guyana)
*,t *belgranoi* (Santschi, 1916: 372) (Argentina) (cnc: *solisi belgranoi*)
*,t *bicinctus* (Santschi, 1922a: 347) (Costa Rica) (cnc: *nigrocinctus bicinctus*)
*,t *bicolor* (Guérin, 1844: 427) (Colombia) (cnc: *gracilis bicolor*)
*,t *boopis* (Roger, 1863b: 25) (Panama) (replacement name)
  t   = *modestus* (F. Smith 1862: 32) (Panama) (preoccupied)
  t   = *excavatus* (Mayr, 1870: 410) (Colombia) (Kempf, 1967: 2)
  t   = *flaviventris* (Emery, 1896a: 2) (Panama) (Kempf, 1960: 22)
  t   = *fusciceps* (Santschi, 1931: 271) (Panama) (Kempf, 1960: 22)
    = *guatemalensis* (Enzmann, 1945: 92) (Guatemala) (Kempf, 1960: 22).
*,t *browni* Kempf, 1967: 3 (Panama)
*,t *brunneus* (F. Smith, 1877: 630) (Mexico)
  t   = *nigritus* (Enzmann, 1945: 82) (Mexico) (Ward, 1985: 231)
  brunnipes (Enzmann, 1945: 79) (Guatemala) (cnc: *antiguanus brunnipes*)
*,t *caeciliae* (Forel, 1913b: 214) (Guatemala)
*,t *canescens* (F. Smith, 1877: 66) (Brazil)
*,t *castus* (Wheeler, 1942: 173) (Peru) (cnc: *pictus castus*)
*,t *championi* (Forel, 1899a: 96) (Mexico)
  t   = *leonhardi* (Stitz, 1937: 132 (Kempf, 1961: 391)
*,t *cladoicus* (F. Smith, 1858: 157) (Brazil)

*,t *cocae* (Santschi, 1922b: 243) (Argentina)
(cnc: *acanthobius cocae*)
colei (Enzmann, 1945: 83) (Peru)

*,t *concolor* (F. Smith, 1860b: 70) (Brazil)

t   = *penetrator* (F. Smith, 1877: 66) (Brazil)
(Kempf, 1967: 5)

t   = *latinodus* (Mayr, 1877: 877) (Brazil)
(Ward, 1989: 435)

t   = *damnosus* (Wheeler, 1921b: 139)
(Guyana) (Kempf, 1961: 406)

*,t *cordiae* (Forel, 1904d: 690) (Peru) (cnc:
sericeus cordiae)

*,t *cordobensis* (Forel, 1914b: 265) (Argentina)
(cnc: *triplarinus cordobensis*)

*,t *coronatus* (Wheeler, 1942: 167) (Guyana)

t   = *coronatus* (Enzmann, 1945: 88)
(Guyana) (Brown, 1949: 42)

costaricensis (Enzmann, 1945: 96) (Costa
Rica) (cnc: *voytowskii costaricensis*)

*,t *cretus* Ward, 1989: 412 (Costa Rica)

*,t *cubaensis* (Forel, 1901a: 342) (Cuba)

*,t *curacaensis* (Forel, 1912c: 23) (Curaçao)

*,t *dendroicus* (Forel, 1904b: 40) (Brazil)

t   = *emarginatus* (Forel, 1904d: 684)
(Brazil) (Ward, 1989: 436)

*,t *denticollis* (Emery, 1890: 66) (Paraguay)

*,t *depressus* (Forel, 1906: 225) (Colombia)

*   *dimidiatus* (Roger, 1863a: 177) (Colombia)
(cnc: *gracilis dimidiatus*)

*,t *distinctus* (F. Smith, 1877: 63) (Mexico)

t   = *pulchellus* (Forel, 1899a: 94) (Mexico)
(Kempf, 1967: 5)

*,t *duckei* (Forel, 1906: 227) (Brazil)

*,t *eduardi* (Forel, 1912c: 29) (Jamaica)

*,t *ejectus* (F. Smith, 1858: 157) (unknown)
= *lincecumii* (Buckley, 1867: 172) (United
States) (Ward, 1989: 436)

*,t *elongatulus* (Dalle Torre, 1892: 89)
(Mexico) (replacement name)

t   = *elongatus* (F. Smith, 1877: 66) (Mexico)
(preoccupied)

t   = *decipiens* (Forel, 1899a: 95) (Mexico)
(Kempf 1967: 6)

*,t *elongatus* (Mayr, 1870: 413) (Colombia)

t   = *alliodorae* (Wheeler, 1942: 157)
(Panama) (Ward, 1989: 419)

t   = *allidorus* (Enzmann, 1945: 77)
(Panama) (Brown, 1949: 42)

t   = *tandem* (Forel, 1906: 228) (Costa Rica)
(Creighton 1955: 18)

*,t *endophytus* (Forel, 1912c: 22) (Brazil)

*,t *ethicus* (Forel, 1911b: 280) (Brazil)

*,t *euryblemma* (Forel, 1899a: 90) (Costa Rica)

t   = *kurokii* (Forel, 1906: 226) (Colombia)
(Ward, 1989: 437)

*,t *excisus* (Mayr, 1870: 410) (Colombia)

*,t *faber* (F. Smith, 1858: 157) (Brazil)

t   = *perforator* (F. Smith, 1860b: 69)
(Brazil) (Perrault, 1987: 382)

*,t *ferrugineus* (F. Smith, 1877: 64) (Mexico)

t   = *fulvescens* (Emery, 1890: 64) (Guate-
mala) (Ward, 1989: 437)

t   = *canescens* (Wasmann, 1915: 321)
(Mexico) (preoccupied) (Ward, 1989: 437)

t   = *wasmanni* (Wheeler, 1921a: 92)
(Mexico) (replacement name)

t   = *bequaerti* (Wheeler, 1942: 164)
(Honduras) (Ward, 1989: 437)

t   = *saffordi* (Wheeler, 1942: 162) (Mexico)
(Ward, 1989: 437)

t   = *vesanus* (Wheeler, 1942: 163) (Mexico)
(Ward, 1989: 437)

t   = *bequaerti* (Enzmann, 1945: 80)
(Honduras) (Brown, 1949: 42)

t   = *honduranus* (Enzmann, 1945: 87)
(Honduras) (Ward, 1989: 437)

*,t *fervidus* (F. Smith, 1877: 65) (Mexico)

*,t *fiebrigi* (Forel, 1908b: 383) (Paraguay)

*,t *filiformis* (Fabricius, 1804: 405) (Guyana)

t   = *cephalicus* (F. Smith, 1855: 168)
(Brazil) (Roger, 1862: 289)

t   = *biconvexus* (Forel, 1899a: 95) (Costa
Rica, Guatemala) (Wheeler, 1919: 128)

t   = *longiceps* (Forel, 1906: 229) (Colombia)
(Ward, 1989: 438)

longiceps (Stitz, 1933: 69) (Venezuela)
(preoccupied) (Ward, 1989: 438)

*,t *flavicornis* (F. Smith, 1877: 67) (Nicaragua)

t   = *belti* (Emery, 1890: 63) (Costa Rica)
(Ward, 1989: 438)

t   = *obnubilus* (Menozzi, 1927: 273) (Costa
Rica) (Ward, 1989: 438)

t   = *fellosus* (Wheeler, 1942: 160)
(Nicaragua) (Ward, 1989: 439)

*,t *flavidulus* (F. Smith, 1858: 157) (Brazil)

*,t *fortis* (Forel, 1899a: 89) (Mexico) (cnc:
sericeus fortis)

*,t *fuscatus* (Emery, 1896b: 629) (Paraguay)
(cnc: *acanthobius fuscatus*)

*,t *gaigei* (Forel, 1914a: 615) (Colombia) (cnc:
spinicola gaigei)

*,t *gebelli* (Forel, 1899b: 303) (Colombia)

*,t *gibbinotus* (Forel, 1908b: 384) (Brazil)

*,t *glabriventris* (Santschi, 1922a: 345) (Bolivia)
(cnc: *gracilis glabriventris*)

*,t *godmani* (Forel, 1899a: 95) (Panama)

t   = *semotus* Kempf, 1960b: 392 (Brazil)
(Kempf, 1967: 6)

*,t *goeldii* (Forel, 1912c: 28) (Brazil)

*,t *gracilis* (Fabricius, 1804: 405) (Guyana)

t   = *variabilis* (F. Smith, 1877: 62)
(Barbados) (Ward, 1989: 439)

t   = *longinodus* (Enzmann, 1945: 87) (Peru)
(Brown, 1949: 43)

*,t *haytianus* (Forel, 1901a: 342) (Haiti)

t   = *affinis* (Wheeler, 1936: 196) (Haiti)
(Kempf, 1961: 393)

t   = *torquatus* (Wheeler, 1936: 196) (Haiti)
(Kempf, 1961: 393)

*,t *heterogynus* (Wheeler & Mann, 1942a: 172)
(Bolivia) (cnc: *pictus heterogynus*)

*,t *holmgreni* (Wheeler, 1925: 11) (Peru)

*,t *huberi* (Santschi, 1922a: 346) (Brazil) (cnc:
sericeus huberi)

*,t *humboldi* (Enzmann, 1945: 75) (Bolivia)
(cnc: *pictus humboldi*)

*,t *incurrens* (Forel, 1912c: 21) (Brazil)

*,t *infernalis* (Wheeler, 1942: 180) (Panama)
(cnc: *spinicola infernalis*)

t   = *infernalis* (Enzmann, 1945: 91)
(Panama) (Brown, 1949: 43)

*,t *ita* (Forel, 1906: 230) (cnc: *sericeus ita*)

*,t *kuenckeli* (Emery, 1890: 62) (Costa Rica)

t   = *dichrous* (Forel, 1904b: 41) (Colombia)
(Kempf, 1961: 402)

t   = *bierigi* (Santschi, 1932: 412) (Panama)
(Kempf, 1961: 402)

    = *crenulatus* (Enzmann, 1945: 84)
(Mexico) (Kempf, 1961: 402)

*,t *laevifrons* Ward, 1989: 440 (Brazil) (re-
placement name)

t   = *laeviceps* (F. Smith, 1877: 63) (Brazil)
(preoccupied)

*,t *laevigatus* (F. Smith, 1877: 62) (Brazil)

*,t *landolti* (Forel, 1912c: 26) (Colombia) (cnc:
pallens landolti)

*,t *leptosus* Ward, 1985: 233 (United States)

*,t *levivertex* (Forel, 1906: 227) (Colombia)
(cnc: *flavidulus levivertex*)

lisus (Enzmann, 1945: 90) (Peru) (cnc:
sericeus lisus)

*,t *lizeri* (Santschi, 1922a: 346) (Bolivia) (cnc:
flavidulus lizeri)

*,t *longior* (Forel, 1904d: 690) (Peru) (cnc:
sericeus longior)

*,t *longus* (Forel, 1912c: 24) (Brazil) (cnc:
elongatulus longus)

*   *lynceus* (Spinola, 1851: 241) (Chile)

*,t *maculatus* (F. Smith, 1855: 158) (Brazil)

t   = *laticeps* (Forel, 1906: 229) (Trinidad)
(Kempf, 1958: 454)

t   = *wagneri* (Santschi, 1922a: 347)
(Argentina) (Kempf: 1958: 454)

*,t *major* (Forel, 1899a: 91) (Mexico) (cnc:
gracilis major)

*,t *malignus* (Wheeler, 1921b: 143) (Guyana)

t   = *cholericus* (Wheeler, 1921b: 146)
(Guyana) (Ward, 1989: 440)

t   = *crucians* (Wheeler, 1921b: 147)
(Guyana) (Ward, 1989: 440)

t   = *auripes* (Wheeler, 1922a: 5) (Trinidad)
(Ward, 1989: 440)

mandibularis (Spinola, 1853: 680 (Brazil)

*   *mexicanus* (Roger, 1863: 178) (Mexico)

*,t *monochrous* (Dalle Torre, 1892: 89) (Brazil)
(replacement name)

t   = *unicolor* (F. Smith, 1877: 68) (Brazil)
(preoccupied)

*,t *niger* (Donisthorpe, 1940: 39) (Guyana)

*,t *nigrescens* (Forel, 1904b: 308) (Brazil)

*,t *nigrocinctus* (Emery, 1890: 64) (Costa Rica)

*,t *nigropilosus* (Emery, 1890: 62) (Costa Rica)

*,t *oculatus* (F. Smith, 1855: 159) (Brazil)

t   = *advena* (F. Smith, 1855: 157) (Brazil)
(Forel, 1911: 277)

t   = *dolichopsis* (Forel, 1899a: 87) (Costa
Rica) (Kempf, 1961: 375)

t   = *implicatus* (Forel, 1911b: 277) (Brazil)
(Kempf, 1961: 375)

t   = *altinodus* (Mann, 1916: 427) (Brazil)
(Ward, 1989: 422)

    = *tuberculatus* (Enzmann, 1945: 98)
(Peru) (Ward, 1989: 422)

t   = *wessoni* (Enzmann, 1945: 97) (Peru)
(Ward, 1989: 422)

*,t *oki* (Forel, 1906: 225) (Colombia)

opacior (Forel, 1904c: 170) (Cuba)

*,t *osurus* (Forel, 1911b: 279) (Costa Rica)

    = *insularis* (Enzmann, 1945: 88)
(Panama) (Ward, 1989: 441)

*,t *pallens* (Mayr, 1870: 411) (Colombia)

*,t *pallidus* (F. Smith, 1855: 160) (United
States)

*,t *pazosi* (Santschi, 1909: 309) (Cuba)

t   = *jaumei* (Aguayo, 1932: 217) (Cuba)
(Ward, 1989: 441)

*,t *peltatus* (Menozzi, 1927: 273) (Costa Rica)

*,t *peperi* (Forel, 1913b: 213) (Guatemala)

t   = *convarians* (Forel, 1913b: 214)
(Guatemala) (Ward, 1989: 452)

t   = *saffordi* (Enzmann, 1945: 89) (Mexico)
(Ward, 1989: 452)

*   *perboscii* (Guérin, 1844: 428) (Mexico)
  t   = *testaceus* (F. Smith, 1852: 45) (Peru)
       (Ward, 1989: 442)
  t   = *simoides* (Forel, 1911b: 281) (Brazil)
       (Ward, 1989: 442)
  t   = *ictericus* (Wheeler, 1922a: 4) (Trinidad)
       (Ward, 1989: 442)
*,t *peruvianus* (Wheeler, 1925: 11) (Peru)
*,t *phyllophilus* (F. Smith, 1858: 156) (Brazil)
  t   = *muticus* (Mayr, 1887: 627) (Brazil)
       (Kempf, 1967: 8)
*,t *pictus* (Stitz, 1913: 209) (Brazil)
*,t *pilosulus* (F. Smith, 1877: 157) (Barbados)
*,t *pisinnus* Ward, 1989: 425 (Brazil)
*,t *pupa* (Forel, 1911b: 274) (Brazil)
*,t *rochai* (Forel, 1912c: 27) (Brazil)
*,t *rubiginosus* (Stitz, 1913: 211) (Brazil) (cnc:
       sericeus rubiginosus)
*,t *rufiventris* (Forel, 1911b: 275) (Paraguay)
*,t *rufomedius* (F. Smith, 1877: 66) (Guate-
       mala)
  t   = *stolli* (Forel, 1912c: 20) (Guatemala)
       (Ward, 1989: 443)
*,t *rurrenabaquensis* (Wheeler & Mann, 1942b:
       188) (Bolivia) (cnc: *triplarinus rurrena-
       baquensis*)
*,t *salvini* (Forel, 1899a: 94) (Mexico)
       santschii (Enzmann, 1945: 89) (Peru)
*,t *scelerosus* (Wheeler, 1942: 181) (Nicaragua)
       (cnc: *spinicola sclelerosus*)
  t   = *scelerosus* (Enzmann, 1945: 91)
       (Nicaragua) (Brown, 1949: 43)
*,t *schuppi* (Forel, 1901c: 298) (Brazil)
  t   = *confusior* (Forel, 1901c: 299) (Brazil)
       (Kempf, 1961: 380)
  t   = *geraensis* (Forel, 1912c: 23) (Brazil)
       (Kempf, 1961: 380)
*,t *seminole* Ward, 1985: 237 (United States)
*,t *sericatus* (F. Smith, 1855: 159) (Brazil) (cnc:
       gracilis sericatus)
*,t *sericeus* (Mayr, 1870: 412) (Colombia)
*,t *simplex* (F. Smith, 1877: 64) (Brazil)
  t   = *delicatulus* (Forel, 1899a: 93) (Jamaica)
       (Ward, 1985: 238)
  t   = *capperi* (Forel, 1899a: 93) (Jamaica)
       (Ward, 1985: 238)
  t   = *panamensis* (Forel, 1899a: 93) (Gua-
       temala) (Ward, 1985: 238)
*,t *simulans* Kempf, 1958: 459 (Panama)
*,t *solisi* (Santschi, 1916: 371) (Argentina)
*,t *spiculus* Ward, 1989: 430 (Costa Rica)
*,t *spinicola* (Emery, 1890: 64) (Costa Rica)
*,t *squamiferus* (Emery, 1890: 60) (Brazil)

*,t *subater* (Wheeler & Mann, 1914: 19) (Haiti)
*,t *subtilissimus* (Emery, 1890: 65) (Costa Rica)
*,t *symbioticus* (Forel, 1904b: 38) (Colombia)
       (cnc: *triplarinus symbioticus*)
*,t *tachigaliae* (Forel, 1904d: 686) (Peru)
  t   = *bradleyi* (Wheeler, 1942: 169) (Peru)
       (Ward, 1989: 444)
  t   = *bradleyi* (Enzmann, 1945: 82) (Peru)
       (Brown, 1949: 43)
*,t *tenuis* (Fabricius, 1804: 405) (Guyana)
  t   = *lignisecus* (F. Smith, 1858: 158) (Brazil)
       (Roger, 1862: 289)
  t   = *rufus* (F. Smith, 1877: 64) (Brazil)
       (Kempf, 1960a: 27)
  t   = *pittieri* (Forel, 1906: 230) (Costa Rica)
       (Kempf, 1960a: 27)
       = *paraensis* (Forel, 1912c: 19) (Brazil)
       (Kempf, 1960a: 27)
  t   = *andinus* (Enzmann, 1945: 92) (Peru)
       (Kempf, 1960a: 27)
*,t *tenuissimus* (Emery, 1905: 119) (Brazil)
  t   = *culmicola* (Forel, 1912c: 27) (Trinidad)
       (Ward, 1989: 432)
*,t *terminalis* (F. Smith, 1877: 64) (Brazil)
*,t *termitarius* (F. Smith, 1855: 158) (Brazil)
  t   = *nigriceps* (F. Smith, 1855: 159) (Brazil)
       (Perrault, 1987: 384)
  t   = *elegans* (F. Smith, 1855: 159) (Brazil)
       (Kempf, 1960a: 8)
  t   = *infuscus* (Forel, 1908b: 382) (Brazil)
       (Kempf, 1960a: 8)
  t   = *breviceps* (Forel, 1912c: 20) (Trinidad)
       (Kempf, 1960a: 8)
       thoracius (Norton, 1871: 8) (Mexico)
*,t *triplaridis* (Forel, 1904d: 684) (Brazil)
  t   = *boxi* (Wheeler, 1942: 184) (Guyana)
       (Ward, 1989: 444)
  t   = *boxi* (Enzmann, 1945: 94) (Guyana)
       (Brown, 1949: 43)
*   *triplarinus* (Weddell, 1849: 263) (Brazil,
       Bolivia, Peru)
  t   = *arborissanctae* (Emery, 1894: 147)
       (Bolivia) (Wheeler, 1942: 186)
  t   = *ecuadorianus* (Enzmann, 1945: 79)
       (Ecuador) (Brown, 1949: 44)
*,t *unicolor* (F. Smith, 1855: 158) (Brazil)
  t   = *mutilloides* (Emery, 1890: 61) (Brazil)
       (Kempf, 1958: 439)
  t   = *anceps* (Santschi, 1925: 222) (Brazil)
       (Kempf, 1958: 439)
       = *ater* (Stitz, 1933: 69) (Brazil) (Kempf,
       1969: 276)
*,t *urbanus* (F. Smith, 1877: 65) (Brazil)

t   = *chodati* (Forel, 1920: 201) (Paraguay) (Ward, 1989: 427)

t   = *ogloblini* (Santschi, 1936b: 402) (Argentina) (Ward, 1989: 427)

velifer (Stitz, 1933: 68) (Guatemala) (cnc: *gracilis velifer*)

*,t *veneficus* (Wheeler, 1942: 162) (Mexico)

t   = *veneficus* (Enzmann, 1945: 81) (Mexico) (Brown, 1949: 42)

*,t *venustus* (F. Smith, 1858: 158) (Brazil)

t   = *agilis* (F. Smith, 1860b: 70) (Brazil) (Kempf, 1967: 10)

t   = *sedulus* (F. Smith, 1877: 67) (Brazil) (Kempf, 1967: 10)

t   = *carapunus* (Mann, 1916: 428) (Brazil) (Kempf, 1958: 446)

     = *peruvianus* (Enzmann, 1945: 86) (Peru) (Kempf, 1958: 446)

*,t *viduus* (F. Smith, 1858: 158) (Brazil)

t   = *caroli* (Forel, 1899a: 89) (Costa Rica) (Ward, 1989: 445)

t   = *sapii* (Forel, 1904d: 688) (Brazil) (Ward, 1989: 445)

t   = *ulei* (Forel, 1904d: 689) (Brazil) (Ward, 1989: 445)

t   = *baileyi* (Wheeler, 1942: 185) (Guyana) (Ward, 1989: 445)

     = *tigrinus* (Wheeler, 1942: 186) (Guyana) (Ward, 1989: 445)

t   = *biolleyi* (Enzmann, 1945: 93) (Guyana) (Brown, 1949: 43)

t   = *trigonus* (Enzmann, 1945: 94) (Guyana) (Brown, 1949: 43)

*,t *villosus* Ward, 1989: 434 (Brazil)

*,t *vinneni* (Forel, 1906: 230) (Brazil) (cnc: *sericeus vinneni*)

*,t *virgo* (Santschi, 1922a: 345) (Brazil) (cnc: *acanthobius virgo*)

*,t *vistanus* (Enzmann, 1945: 84) (Peru) (cnc: *colei vistanus*)

*,t *volatilis* (F. Smith, 1877: 65) (Mexico)

voytowskii (Enzmann, 1945: 95) (Peru)

*,t *weberi* (Enzmann, 1945: 96) (Guatemala)

wheeleri (Enzmann, 1945: 99) (Peru)

fossil taxa

*,t *extinctus* (Carpenter, 1930: 29) (United States: Florissant shales)

unavailable names

affinis (Wheeler & Mann, 1914: 18) (unavailable infrasubspecific name)

     = *affinis* (Wheeler, 1936)

     = jr. syn. of *haytianus* (Forel, 1901) (Kempf, 1961: 393)

guayaquilensis (Forel, 1907: 7) (unavailable infrasubspecific name)

limae (Enzmann, 1945: 7) (unavailable infrasubspecific name)

loewensohni (Forel, 1918: 719) (unavailable infrasubspecific replacement name)

     = *panamensis* (Forel, 1912c: 22) (unavailable infrasubspecific name; also preoccupied)

paulinus (Forel, 1911a: 305) (unavailable infrasubspecific name)

     = *phyllophilus* (F. Smith, 1858) (Gallardo, 1932: 58)

torquatus (Wheeler & Mann, 1914: 18) (unavailable infrasubspecific name)

     = *torquatus* (Wheeler, 1936)

     = jr. syn. of *haytianus* (Forel, 1901a) (Kempf, 1961: 393)

vittatus (Forel, 1912c: 26) (unavailable infrasubspecific name)

     = *simplex* (F. Smith, 1877) (Ward, 1985: 238)

Tetraponera F. Smith

*,t *aethiops* F. Smith, 1877: 71 ('S. Africa')

t   = *spininoda* (André, 1892: 51) (Gabon) (Emery, 1912: 97)

*,t *aitkenii* (Forel, 1902: 245) (India)

*,t *allaborans* (Walker, 1859: 375) (Sri Lanka)

t   = *compressa* (Roger, 1863a: 179) (Sri Lanka) (F. Smith, 1877: 69)

t   = *femoralis* (Motschoulsky, 1863: 21) (Sri Lanka) (Dalle Torre, 1893: 53).

t   = *ceylonica* (Motschoulsky, 1863: 22) (Sri Lanka) (Dalle Torre, 1893: 53)

t   = *subtilis* (Emery, 1889: 500) (Burma) (Dalle Torre, 1893: 53)

*,t *ambigua* (Emery, 1895a: 23) (South Africa)

*,t *andrei* (Mayr, 1895: 144) (Mozambique)

*,t *angolensis* Santschi, 1930: 61 (Angola) (cnc: *ophthalmica angolensis*)

*,t *angusta* (Arnold, 1949: 266) (Zimbabwe) **comb.n.**

angusticeps (Karawajew, 1933: 266) (Indonesia) (cnc: *bidentata angusticeps*)

*,t *anthracina* (Santschi, 1910a: 355) (Congo)

*,t *arrogans* (Santschi, 1911b: 117) (Madagascar)

atra Donisthorpe, 1948: 493 (Indonesia)

*,t *attenuata* F. Smith, 1877: 71 (Malaysia)

t   =   *tenuissima*   (Emery,   1901a: 675)
(Indonesia) (Forel, 1912a: 54)
  bidentata (Karawajew, 1933: 264) (In-
  donesia)
*,t *bifoveolata* (Mayr, 1895: 146) (Mozam-
  bique, Tanzania)
*,t *binghami* (Forel, 1902: 243) (Burma, India)
  biozellata (Karawajew, 1931: 42) (Kenya)
  (cnc: *mocquerysi biozellata*) **comb.n.**
*,t *birmana* (Forel, 1902: 245) (Burma)
*,t *braunsi* (Forel, 1913a: 112) (South Africa)
*,t *brevicornis* (Emery, 1901a: 675) (Philip-
  pines)
*,t *caffra* (Santschi, 1914b: 15) (South Africa)
  (cnc: *natalensis caffra*)
  capensis (F. Smith, 1858: 160) (South
  Africa)
*,t *carbonaria* (F. Smith, 1863: 20) (Indonesia)
*,t *ceylonensis* (Forel, 1909: 394) (Sri Lanka)
  (cnc: *rufonigra ceylonensis*)
*,t *claveaui* (Santschi, 1913: 304) (Senegal)
*,t *clypeata* (Emery, 1886: 361) (South Africa)
*,t *continua* (Forel, 1908a: 138) (Ethiopia)
  (cnc: *penzigi continua*)
*,t *crassiuscula* (Emery, 1901a: 677) (In-
  donesia) (cnc: *allaborans crassiuscula*)
*,t *cuitensis* (Forel, 1911c: 368) (Angola) (cnc:
  natalensis cuitensis)
*,t *demens* (Santschi, 1911a: 282) (Madagascar)
  dentifera   (Karawajew,   1933:   266)
  (Indonesia)
*,t *deplanata* (Forel, 1904a: 375) (Madagascar)
  (cnc: *sahlbergi deplanata*)
*,t *diana* (Santschi, 1911b: 119) (Madagascar)
*,t *difficilis* (Emery, 1901a: 677) (Indonesia)
  dilatata (Karawajew, 1933: 267) (Indonesia)
*,t *dimidiata* (Forel, 1895: 487) (Madagascar)
  (cnc: *hysterica dimidiata*)
*,t *durbanensis* (Forel, 1914b: 218) (South
  Africa) (cnc: *braunsi durbanensis*)
*,t *elongata* (Stitz, 1911: 378) (Uganda) (cnc:
  mocquerysi elongata)
*,t *emacerata* (Santschi, 1910b: 352) (Kenya)
*,t *emeryi* (Forel, 1911c: 367) (South Africa)
*,t *encephala* (Santschi, 1919: 84) (Senegal)
*,t *erythraea* (Emery, 1895a: 23) (Yemen D.R.)
  (cnc: *ambigua erythraea*)
*,t *exasciata* (Forel, 1892: 261) (Madagascar)
*,t *fergusoni* (Forel, 1902: 248) (India) (cnc:
  nigra fergusoni)
*,t *fictrix* (Forel, 1897: 198) (Madagascar)
*,t *flexuosa* (Santschi, 1911b: 120) (Mada-
  gascar)
*,t *fulva* (Viehmeyer, 1916: 117) (Singapore)

*,t *gerdae* (Stitz, 1911: 381) (Tanzania)
*,t *grandidieri* (Forel, 1891: 203) (Madagascar)
*,t *hildebrandti* (Forel, 1891: 204) (Madagascar)
  (cnc: *grandidieri hildebrandti*)
*,t *humerosa* (Emery, 1901a: 674) ('N.
  Guinea')
*,t *hysterica* (Forel, 1892: 258) (Madagascar)
*,t *illota* (Santschi, 1914a: 334) (Nigeria) (cnc:
  triangularis illota)
*,t *inflata* (Emery, 1900: 273) (Madagascar)
  (cnc: *hysterica inflata*)
*,t *insularis* (Emery, 1901b: 113) (Sri Lanka)
  (cnc: *nigra insularis*)
*,t *kimberleyensis* (Forel, 1915: 37) (Australia)
  (cnc: *punctulata kimberleyensis*)
*,t *krama* (Forel, 1912b: 105) (Indonesia) (cnc:
  nigra krama)
*,t *laeviceps* (F. Smith, 1859: 145) (Indonesia)
*,t *latifrons* (Emery, 1912: 98) (Gabon)
  ledouxi Terron, 1969: 629 (Cameroon)
*,t *lemoulti* (Santschi, 1920: 375) (Central
  African Republic)
*,t *lepida* Wheeler, 1922b: 106 (Zaire) (cnc:
  mocquerysi lepida)
*,t *liengmei* (Forel, 1894: 88) (Mozambique)
*,t *lindgreeni* (Forel, 1902: 245) (India) (cnc:
  binghami lindgreeni)
*,t *longiceps* (Forel, 1902: 247) (India) (cnc:
  difficilis longiceps)
*,t *longinoda* (Forel, 1909: 394) (Sri Lanka)
  (cnc: *allaborans longinoda*)
*,t *longula* (Emery, 1895b: 340) (Madagascar)
  (cnc: *sahlbergi longula*)
*,t *lutea* (Stitz, 1911: 381) (Zaire) (cnc:
  mocquerysi lutea)
*,t *maculifrons* (Santschi, 1912: 62) (Djibouti)
  (cnc: *bifoveolata maculifrons*)
*,t *maffini* Donisthorpe, 1947: 591 (Indonesia)
*,t *mandibularis* (Emery, 1895b: 340) (Mada-
  gascar)
  mayri (Forel, 1901b: 53) (Cameroon)
  minuta (Jerdon, 1851: 112) (India)
*,t *mocquerysi* (André, 1890: 319) (Sierra
  Leone)
*,t *modesta* (F. Smith, 1860a: 106) (Indonesia)
  monardi (Santschi, 1937b: 218) (Angola)
  comb.n.
*,t *morondaviensis* (Forel, 1891: 206) (Mada-
  gascar) (cnc: *sahlbergi morondaviensis*)
*,t *nasuta* Bernard, 1952: 22 (Guinea)
*,t *natalensis* (F. Smith, 1858: 160) (South
  Africa)
*,t *nebulosa* (Forel, 1903: 404) (India) (cnc:
  siggi nebulosa)

*,t *nicobarensis* (Forel, 1903: 402) (India)

* *nigra* (Jerdon, 1851: 112) (India)
   = *atrata* F. Smith, 1852: 44 (India) (Dalle Torre, 1893: 54)

*,t *nitens* (Stitz, 1925: 117) (Philippines)

*,t *nitida* (F. Smith, 1860a: 106) (Indonesia)

*,t *oberbecki* (Forel, 1911d: 275) (Zaire) (cnc: *emacerata oberbecki*)

*,t *obscurata* (Emery, 1895a: 22) (South Africa) (cnc: *natalensis obscurata*)

*,t *odiosa* (Forel, 1916: 403) (Zaire) (cnc: *emacerata odiosa*)

*,t *ophthalmica* (Emery, 1912: 98) (Cameroon)

*,t *penzigi* (Mayr, 1907: 10) (Tanzania)

*,t *perlonga* Santschi, 1928: 60 (Madagascar)

*,t *petiolata* F. Smith, 1877: 70 (Sri Lanka)

*,t *pilosa* (F. Smith, 1858: 160) ('Borneo')
   platynota (Karawajew, 1933: 269 (Indonesia)

*,t *plicatidens* (Santschi, 1926: 26) (Madagascar) **comb.n.**
   poultoni Donisthorpe, 1931: 497 (Uganda)

*,t *praestigiatrix* Santschi, 1937a: 50 (Tanzania) (cnc: *penzigi praestigiatrix*)

*,t *prelli* (Forel, 1911c: 365) (Tanzania)

* *punctulata* F. Smith, 1877: 72 (Australia)

*,t *rakotonis* (Forel, 1891: 206) (Madagascar)

*,t *rhodesiana* (Forel, 1913a: 112) (Zimbabwe) (cnc: *ambigua rhodesiana*)
   rufipes (Jerdon, 1851: 112) (India)

* *rufonigra* (Jerdon, 1851: 111) (India)

*,t *sahlbergi* (Forel, 1887: 386) (Madagascar)

*,t *schulthessi* (Santschi, 1915: 249) (Mozambique)

*,t *scotti* Donisthorpe, 1931: 498 (Ethiopia)

*,t *setifera* (Viehmeyer, 1916: 119) (Singapore) (cnc: *siggi setifera*)

*,t *siggi* (Forel, 1902: 246) (Thailand)

*,t *spuria* (Forel, 1897: 199) (Madagascar) (cnc: *sahlbergi spuria*)

*,t *stipitum* (Forel, 1912a: 54) (Singapore)

*,t *sumatrensis* (Emery, 1901a: 676) (Indonesia) (cnc: *allaborans sumatrensis*)

*,t *syriaca* (Wheeler & Mann, 1916: 167) (Egypt) (cnc: *bifoveolata syriaca*)

*,t *tenebrosa* Santschi, 1928: 61 (Zaire) (cnc: *ophthalmica tenebrosa*)

*,t *tessmanni* (Stitz, 1910: 131) (Equatorial Guinea)
   t   = *castanea* (Wheeler, 1922b: 112) (Zaire) (Brown, 1950: 248)

*,t *testaceonigra* (Forel, 1903: 402) (India) (cnc: *rufonigra testaceonigra*)

*,t *thagatensis* (Forel, 1902: 249) (Burma)

*,t *triangularis* (Stitz, 1910: 131) (Equatorial Guinea)

*,t *unidens* Santschi, 1928: 60 (Zaire) (cnc: *ophthalmica unidens*)

*,t *usambarensis* (Forel, 1911c: 367) (Tanzania) (cnc: *natalensis usambarensis*)

*,t *variegata* (Forel, 1895: 487) (Madagascar) (cnc: *grandidieri variegata*)

*,t *yeensis* (Forel, 1902: 248) (Burma) (cnc: *rufonigra yeensis*)

*,t *zavattarii* (Menozzi, 1939: 99) (Ethiopia) **comb.n.**

fossil taxa

   angustata (Mayr, 1868: 102) (Baltic amber) **comb.n.**
   klebsi (Wheeler, 1915: 41) (Baltic amber) **comb.n.**
   lacrimarum (Wheeler, 1915: 44) (Baltic amber) **comb.n.**
   ocellata (Mayr, 1868: 101) (Baltic amber) **comb.n.**
   oligocenica (Theobald, 1937: 127) (France) **comb.n.**
   simplex (Mayr, 1868: 102) (Baltic amber) **comb.n.**

unavailable names

bulawayana (Forel, 1913a: 112) (unavailable infrasubspecific name)

equidentata (Arnold, 1916: 184) (unavailable infrasubspecific name)

occidentalis (Stitz, 1916: 336) (unavailable infrasubspecific name)

quaniama (Santschi, 1937b: 218) (unavailable infrasubspecific name)

umbrata (Santschi, 1929: 98) (unavailable infra-subspecific name)

Excluded from *Tetraponera*

1. *Sima andamanensis* Forel (1903: 403), based on a male described from the Andaman Islands, India, is a member of the myrmicine genus *Paratopula* (Bolton, 1988).

2. *Sima aethiops* subsp. *grisea* Forel (1910: 5), based on males described from Botswana, is a junior synonym of *Platythyrea lamellosa* Roger (Forel, 1913c; Wheeler, 1922d).