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Systematics, biogeography and host plant associations of the *Pseudomyrmex viduus* group (Hymenoptera: Formicidae), *Triplaris*- and *Tachigali*-inhabiting ants

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The *Pseudomyrmex viduus* group is a Neotropical clade of arboreal ants containing 13 species, of which three are newly described here: ***P. insuavis***, ***P. ultrix***, and ***P. vitabilis***. Most species inhabit the domatia of specialized ant-plants. The ants keep brood and scale insects (Coccoidea) in the plant cavities, and defend their nest sites much more aggressively than do generalist species of *Pseudomyrmex* nesting in dead twigs. Five species are obligate associates of trees in the genus *Triplaris* (Polygonaceae) and five taxa are restricted to *Tachigali* (Fabaceae: Caesalpinioideae). One species, *P. viduus* (F. Smith), is much less host-specific, inhabiting *Cordia*, *Coussapoa*, *Ocotea*, *Pseudobombax*, *Pterocarpus*, *Sapium*, *Triplaris* and other myrmecophytes. Nothing is known about the biology of *P. vitabilis*, a close relative of *P. viduus*. The last member of the species group, *P. kuenckeli* (Emery), is a non-specialist but aggressive species that nests in dead branches of various plants. A cladistic analysis indicates that this aggressive behaviour evolved before obligate associations with specialized ant-plants, and that the *Triplaris* and *Tachigali* inhabitants each form their own clade. *P. viduus*, which is nested within the *Triplaris*-associated clade, suggests a possible model for host plant evolution in these ants wherein shifts from one ant-plant to another involve an intermediate phase of expanded host plant use. At least nine other *Pseudomyrmex* species, from two different species groups (not closely related to the *P. viduus* group), have evolved specialized associations with *Triplaris* or *Tachigali* including five new species: ***P. crudelis***, ***P. deminutus***, ***P. eculeus***, ***P. ferox*** and ***P. hospitalis***. Although the *P. viduus* group is centred in the Amazon basin, the geographic ranges of most species do not coincide with the Pleistocene forest refugia proposed by Haffer and others. A consideration of the phylogenetic relationships, distribution patterns, and host plant specificity of the ants indicates that much of the diversification of the *P. viduus* group occurred before the Pleistocene, and that the interactions with *Triplaris* and *Tachigali* plants are also of Tertiary origin.

ADDITIONAL KEY WORDS:—Neotropics – ant-plant mutualisms – myrmecophytes – Coccoidea – speciation – phylogeny – Amazonia – Hylaea – Pleistocene refugia.

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INTRODUCTION

Rivalling the New World acacia-ants (*Pseudomyrmex ferrugineus* group) in notoriety and ferocity, the *Triplaris*- and *Tachigali*-inhabiting ants of the *Pseudomyrmex viduus* group constitute an intriguing set of ant-plant specialists. Most of the species in this South American-based group are associated with a single plant genus, in whose domatia they keep brood and scale insects (Coccoidea). The species associated with *Triplaris* (Polygonaceae) occupy the hollow branches and trunk of the tree, while the *Tachigali* (Fabaceae: Caesalpinoideae) specialists inhabit swollen leaf petioles (Wheeler, 1942; Benson, 1985). One species, *P. viduus*, is more catholic in its choice of host plants (Ward, 1991), but it is also invariably associated with scale insects and live plant cavities. The workers of all species actively patrol their host plants, and they readily attack and sting intruders. Owing to their aggressive behaviour and painful stings the ants are well-known to the human inhabitants of Amazonia, often going by the indigenous name 'tachi' (Wheeler, 1921a, 1942; Kempf, 1961).

These ants have received less scrutiny from ecologists than have the acacia-ants, but they appear to exhibit equally strong, and apparently mutualistic, interactions with their myrmecophyte hosts. Early observations on the biology of the ants and their associated plants were contributed by Aublet (1775), Schomburgk (1838), Schimper (1888), Warming (1894), Forel (1904a), Spruce (1908), Ule (1906a,b, 1907, 1908), Wheeler (1913, 1921a, b, 1942), Bequaert (1922) and Bailey (1923). More recent studies include those of Schremmer (1984), Benson (1985), Jaffé, Lopez & Aragort (1986), Oliveira, Oliveira Filho & Cintra (1987), Davidson, Longino & Snelling (1988), Davidson, Snelling & Longino (1989), Verhaagh (1988), Davidson & McKey (1993), Fowler (1993), Fonseca (1993, 1994), Fonseca & Benson (1995) and Fonseca & Ganade (1996). The venom of one species, *Pseudomyrmex triplarinus*, has been characterized, and it shows some promise in the treatment of rheumatoid arthritis (Altman *et al.*, 1984; Schultz *et al.*, 1986; Hink, Pappas & Jaworski, 1994).

As is the case for most groups of ants, the early taxonomic work on the *Triplaris*- and *Tachigali*- inhabiting species is in the form of isolated descriptions of new taxa by F. Smith, Mayr, Emery, Forel and others, unaccompanied by keys or synoptic overviews. Wheeler (1921b, 1922, 1942) dealt with many of these *Pseudomyrmex* species, and added new taxa of his own. His 1942 paper is an excellent summary of the literature on these (and other Neotropical) plant-ants, but in retrospect he was not very discerning of species differences: all but one of the ten names that Wheeler proposed for ants in the *Pseudomyrmex viduus* group are now junior synonyms. Enzmann (1944) added to the taxonomic mayhem in *Pseudomyrmex* with a spurious classification of the genus and bogus descriptions of 'new' species and varieties that had already been described under the same (or similar) names by Wheeler (1942). Brown (1949) was able to neutralize some of the more egregious aspects of Enzmann's work by sinking the obvious junior synonyms. The first real progress in our understanding of *Triplaris*- and *Tachigali*-ants came with Kempf's (1961) paper, which stands out for its refreshing clarity. Kempf provided the first unambiguous definition of the *P. latinodus* group (now known as the *P. viduus* group, since *P. viduus* is the oldest available name—see Ward, 1989), summarized the composition of the group, and discussed some of the taxonomic problems requiring further investigation. Results presented in Ward (1989) gave additional taxonomic resolution and clarified the identities of several species.

The present contribution consists of a comprehensive species-level revision of the *Pseudomyrmex viduus* group, including keys to all three castes, a phylogenetic analysis, and a consideration of biogeographic patterns. Host plant associations and worker behaviour are traced on the phylogeny, providing insight into the evolution of these ant-plant interactions. In addition, other *Pseudomyrmex* species that have independently colonized *Triplaris* and *Tachigali*—mostly members of the *Pseudomyrmex sericeus* group—are described and keyed.

MATERIAL AND METHODS

Collections

Material was examined, or deposited, in the following collections. Abbreviations follow Arnett, Samuelson & Nishida (1993) for public institutions.

AMNH American Museum of Natural History, New York, NY, U.S.A.
BMNH Natural History Museum, London, U.K.
CASC California Academy of Sciences, San Francisco, CA, U.S.A.
CBFC Colección Boliviana de Fauna, La Paz, Bolivia
CELM Colección Entomologica 'Luis Maria Murillo', ICA, Bogotá, Colombia
CKIC Charles Kugler Collection, Radford, VA, U.S.A.
CPDC Jacques Delabie Collection, CEPEC/CEPLAC, Itabuna, Bahia, Brazil
CUIC Cornell University Insect Collection, Ithaca, NY, U.S.A.
EBCC Estación de Biologia Chamela, Jalisco, Mexico
FFIC Fernando Fernández Collection, Santa Fé de Bogotá, Colombia
GCSC Gordon C. Snelling Collection, Los Angeles, CA, U.S.A.

GCWC	G.C. & J. Wheeler Collection, Silver Springs, FL, U.S.A.
GHPC	G. H. Perrault Collection, Paris, France
ICCM	Carnegie Museum of Natural History, Pittsburg, PA, U.S.A.
IMLA	Instituto Miguel Lillo, Tucumán, Argentina
INBC	Instituto Nacional de Biodiversidad, San José, Costa Rica
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
ISNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
IZAV	Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela
JTLC	J.T. Longino Collection, Evergreen State College, Olympia, WA, U.S.A.
KSUC	Kansas State University Insect Collection, Manhattan, KS, U.S.A.
KWJC	Klaus W. Jaffé Collection, Caracas, Venezuela
LACM	Los Angeles County Museum of Natural History, Los Angeles, CA, U.S.A.
LMSG	Laboratoria voor Morfologie en Systematiek, Museum voor Dierkunde, Gent, Belgium
MCSN	Museo Civico di Storia Naturale, Genoa, Italy
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.
MECN	Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MPEG	Museu Paraense Emílio Goeldi, Belém, Brazil
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru
MZSP	Museu de Zoologia da Universidade de São Paulo, Brazil
NHMB	Naturhistorisches Museum, Basel, Switzerland
NHMV	Naturhistorisches Museum, Vienna, Austria
PSWC	P.S. Ward Collection, University of California at Davis, CA, U.S.A.
QCAZ	Universidad Católica del Ecuador, Quito, Ecuador
SMNK	Staatliches Museum für Naturkunde, Karlsruhe, Germany
UASC	Museo de Historia Natural 'Noel Kempff Mercado', Santa Cruz, Bolivia
UCDC	Bohart Museum of Entomology, University of California at Davis, CA, U.S.A.
UNCB	Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá, Colombia
USNM	National Museum of Natural History, Washington, DC, U.S.A.
WPMC	W.P. MacKay Collection, El Paso, TX, U.S.A.
WWBC	Woody W. Benson Collection, Campinas, Brazil

Metric measurements and indices

In the worker and queen castes of *Pseudomyrmex* there is not extensive development of integument sculpture or spinescence, nor is there extreme modification of body form. Accurate morphometric measurements are critical for capturing subtle differences in size and shape among taxa, and for revealing phylogenetically informative characters (see below). All metric measurements were taken at 50 × power with a Wild microscope, using an orthogonal pair of Nikon micrometers wired to a digital readout. The measurements were recorded to the nearest 0.001 mm, but most have been rounded to two decimal places for presentation here (except for a few very small structures). Additional details on measurement procedures for *Pseudomyrmex* are given in Ward (1985, 1989, 1993). The following measurements and indices were used in this study.

HW Head width: maximum width of head, including the eyes.

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 posterior margin (or, if the posterior margin is concave, from the midpoint of a line drawn across the margin) to the anterior extremity of the clypeal margin.

N1, N2, N3, N4, N5 A series of cumulative measurements taken during the measurement of HL, starting from the midpoint of a line drawn across the posterior margin of the head. N1: distance to the midpoint of a line drawn between the lateral ocelli; N2: distance to the middle of the median ocellus; N3: distance to a line drawn across the posterior margins of the compound eyes; N4: distance to a line drawn across the anterior margins of the compound eyes; N5: distance to a line drawn across the anterior margins of the antennal sclerites (toruli).

EL Eye length: length of compound eye, measured with the head in full face, dorsal view.

PFC Maximum frontal carinal distance: maximum distance between the frontal carinae, posterior to their fusion with, or approximation to, the antennal sclerites.

MFC Minimum frontal carinal distance: minimum distance between the frontal carinae, posterior to their fusion with, or approximation to, the antennal sclerites.

ASD Antennal sclerite distance: maximum distance between the lateral margins of the median lobes of the antennal sclerites, measured in full-face, dorsal view of the head.

ASM Antennal sclerite distance, inner margins: minimum distance between the inner margins of the antennal sclerites, measured in full-face, dorsal view of the head.

MD1, MD2, MD4, MD5, MD8, MD9 A series of mandibular measurements (see Ward, 1989, fig. 2). MD1: basal width of the mandible; MD2: width of mandible, taken parallel to MD1, at the level of the apicobasal tooth; MD4: distance along the basal margin of the mandible from the base to the mesial basal tooth; MD5: length of the basal margin; MD8: distance along the masticatory margin from the apex to the fourth tooth, counting from the apex; MD9: length of the masticatory margin.

EW Eye width: maximum width of compound eye, measured along its short axis in an oblique dorsolateral view of the head.

SL Scape length: length of the first antennal segment, excluding the radicle.

LF1 Length of first funicular segment: maximum measurable length of the first funicular segment (pedicel), including its basal articulation in workers and queens but excluding the basal articulation in males (where it is variably exposed).

LF2 Length of second funicular segment: maximum measurable length of the second funicular segment.

LF3	Length of third funicular segment: maximum measurable length of the third funicular segment.
WF2	Width of second funicular segment.
FL	Profemur length: length of the profemur, measured along its long axis in posterior view (see Ward, 1985, fig. 3).
FW	Profemur width: maximum measurable width of the profemur, measured from the same view as FL, at right angles to the line of measurement of FL.
DPL	Diagonal length of the propodeum: length of the propodeum, measured in lateral view along a diagonal line drawn from metanotal groove to the propodeal (often called 'metapleural') lobe (see Ward, 1985, fig. 2).
BF	Length of the dorsal (often called 'basal') face of the propodeum, measured in lateral view from the metanotal groove to the point on the surface of the propodeum which is maximally distant from the diagonal propodeal line.
DF	Length of the declivitous face of the propodeum, measured in lateral view from the propodeal lobe to the point on the surface of the propodeum which is maximally distant from the diagonal propodeal line.
MP	Depth of metanotal groove ('mesopropodeal impression'), measured in lateral view from the bottom of the metanotal groove to a line drawn across the dorsal surface of the mesonotum and propodeum.
PL	Petiole length: length of the petiole, measured in lateral view from the lateral flanges of the anterior peduncle to the posterior margin of the petiole (see Ward, 1985, fig. 4).
PND	Petiolar node distance: distance from the lateral flanges of the anterior petiolar peduncle to the maximum height of the node, measured from the same view as PL and along the same line of measurement (see Ward, 1985, fig. 4).
PH	Petiole height: maximum height of the petiole, measured in lateral view at right angles to PL, but excluding the anteroventral process.
PPL	Postpetiole length: length of the postpetiole, measured in lateral view, from the anterior peduncle of the postpetiole to the point of contact with the fourth abdominal tergum, excluding the pretergite (see Ward, 1985, fig. 4).
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: maximum width of the postpetiole, measured in dorsal view.
LHT	Length of the metatibia, excluding the proximomedial part of the articulation which is received into the distal end of the metafemur (see Ward, 1989, fig. 5).
CI	Cephalic index: HW/HL
OI	Ocular index: EW/EL
REL	Relative eye length: EL/HL
REL2	Relative eye length, using HW: EL/HW
VI	Vertex width index: VW/HW
FCI	Frontal carinal index: MFC/HW

FC12	Frontal carinal index, using ASD: MFC/ASD
ASI2	Antennal sclerite index, using ASM: ASM/ASD
SI	Scape index: SL/HW
SI2	Scape index, using EL: SL/EL
FLI	Funicular length index: (LF2 + LF3)/WF2
FI	Profemur 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
PLI2	Petiole length index, using PPL: PPL/PL
PWI	Petiole width index: DPW/PL
PWI2	Petiole width index, using PPW: DPW/PPW
PWI3	Petiole width index, using MPW: MPW/DPW
PWI4	Petiole width index, using LHT: DPW/LHT
PPWI	Postpetiole width index: PPW/PPL

Other conventions

The following setal counts are used:
MSC Mesosoma setal count: number of standing hairs, i.e. those forming an angle of 45° or more with the cuticular surface (Wilson, 1955), visible in outline on the dorsal surface of the mesosoma.
HTC Metatibial setal count: number of standing hairs visible in outline on the outer (extensor) surface of the metatibia, with the line of view orthogonal to the plane of tibial flexion. This count excludes small apical tufts of hair.

The *palp formula* is the number of maxillary palp segments followed by the number of labial palp segments. Descriptions of surface sculpture and integument reflectance apply to observations made under soft light, with an opaque (Mylar) filter placed between the specimen and the source of illumination. Terminology for sculpture largely follows Harris (1979).

The term ‘stat. nov.’ refers to a change in rank of a valid name (in all instances here, the elevation of an infraspecific name to species rank), while ‘stat. rev.’ signifies the revalidation of a name previously considered invalid.

In the lists of material examined, records are arranged alphabetically by country and by the principal administrative district within each country. For common species, only the localities and collectors are cited, with the source collections listed together at the beginning of each list. Clarifying comments about the collection site are added in square brackets where appropriate (e.g. Belém [as ‘Para’]). The expression ‘c.u.’ indicates collector unknown.

Species distributions (Figs 161–168) were plotted using a shareware mapping program (Versamap, Version 1.40), which required establishing the coordinates (latitude and longitude) of each collecting site. This was determined primarily from maps and gazetteers. The series of gazetteers produced by the United States Board on Geographic Names, now available online through the GEOnet Names Server (http://164.214.2.59/gns/html/index.html), was particularly useful. Several of the Ornithological Gazetteers of the Neotropics (Paynter, 1982, 1992, 1993, 1997; Paynter & Traylor, 1991; Stephens & Traylor, 1983, 1985) also proved to be helpful.

Some localities could not be found in any gazetteer nor on contemporary maps. Information on such difficult-to-locate sites was sought from colleagues and from geographical details in Chandless (1869), Coudreau (1901), Ferguson (1995), Hale (1912), MacCreagh (1926), Mann (1948), Noriega (1923), Oliveira (1928), Sampaio (1933), Silva (1991), Snethlage (1914), Stradelli (1901), Ule (1907), Urban (1906), and von Hagen (1937). In some cases—but too few!—latitude and longitude were given on the specimen label. The task of mapping species distributions would be considerably facilitated if field collectors were to treat such information as a standard part of their collection data.

In citations of the biological literature on the plant-ants and their associates, *Triplaris* nomenclature has been updated to agree with Brandbyge (1986, 1990); the genus *Tachigali* is considered to include *Sclerolobium*, reflecting recent opinion that these two genera are not distinct (Zarucchi & Herendeen, 1993, 1998; Pipoly, 1995; cf. Dwyer, 1954, 1957); and coccoid nomenclature follows Ben-Dov (1993, 1994) and Hodgson (1994).

Cladistic analysis

The set of characters listed below was developed for a species-level phylogenetic analysis of the *Pseudomyrmex viduus* group. The relative morphological homogeneity of the workers and queens necessitated the use of explicitly quantitative characters for these castes. Bivariate plots of morphometric measurements proved useful for revealing discrete clouds of points (Figs 105–152) which were then assigned to different character states. In contrast, for the male caste the genitalia were the principal source of character variation. In these ants the male genitalia provide a wealth of informative characters (numbers 49–72 below).

1. Worker, median number of teeth on masticatory margin of mandibles (0) 3, (1) 5, (2) 6–8.
2. Worker, queen and male, palp formula (0) 6,4, (1) 5,3, (2) 4,3.
3. Worker, median clypeal lobe, anterolateral corners (0) rounded, (1) angulate.
4. Worker, minimum distance between frontal carinae (MFC) relative to HW (0) small, (1) larger, lying in upper region in plot of MFC on HW (Fig. 105).
5. Worker and queen, frontal carinae, maximum separation posterior to the median lobes of the antennal sclerites (0) small, worker PFC ≤ 0.075, (1) larger, worker PFC ≥ 0.075, and lying in the upper region in plots of PFC on HW and LHT (Fig. 106).
6. Worker and queen, PFC relative to ASM, (0) small, (1) larger, lying in upper region in Figures 107, 137.
7. Worker and queen, ASD (0) relatively large in relation to HW, worker and queen ASD/HW >0.12, (1) smaller, worker and queen ASD/HW ≤ 0.12.
8. Worker, scape length, relative to HW (0) large, lying in upper region in Figure 108, (1) intermediate, (2) small, lying in lowermost region in Figure 108.
9. Queen, scape length, relative to HW (0) large, lying in upper region in Figure 139, (1) smaller, lying in lowermost region in Figure 139.
10. Worker, scape length (SL) relative to HL and DPL (0) large, (1) smaller, lying in the lower region of points in Figure 109.
11. Queen, scape length, relative to HL (0) large, SL/HL ≥ 0.41, (1) intermediate, SL/HL 0.36–0.41, (2) small, SL/HL 0.28–0.35; see also Figure 138.

12. Worker, scape length, relative to profemur length (FL) (0) large, (1) smaller, lying in the lower region of Figure 110.
13. Queen, scape length, relative to profemur length (FL) (0) large, (1) intermediate, (2) small, lying in the lower region of Figure 140.
14. Worker, first three funicular segments (0) long, (1) shorter, (2) shortest, lying in lowermost region in Figure 111.
15. Queen, first three funicular segments (0) long, (1) of intermediate length, (2) shorter, (3) shortest, lying in lowermost region in Figure 141.
16. Worker, funiculus (0) moderately expanded apically (apical antennomere <1.7 times the width of first funicular segment), (1) strongly enlarged apically, maximum width of apical antennomere 1.7–2.0 times the width of the first funicular segment.
17. Worker and queen, eye length (EL), relative to HL (0) large, worker REL >0.50, queen REL >0.52 (1) smaller, worker REL ≤ 0.48, queen REL ≤ 0.50.
18. Queen, eye length (EL), relative to HW (0) large, REL2 >0.54 (1) smaller, REL2 <0.54.
19. Worker and queen, eye width, relative to HW and LHT (0) larger (1) smaller, lying in the lower region of points in Figures 112, 142.
20. Queen, eye width, relative to HL (0) large, EW/HL ≥ 0.28 (1) medium, EW/HL 0.20–0.27, (2) small, EW/HL ≤ 0.21 and lying in the lowest righthand region of points in Figure 143.
21. Worker, width of head at level of the lateral ocelli (=VW) relative to maximum head width (=HW) (0) large, VI usually >0.74 (1) smaller, VI usually <0.75, and lying in the lower region of points in Figure 113.
22. Queen, width of head at level of the lateral ocelli (=VW) relative to maximum head width (=HW) (0) large, VI >0.75 (1) smaller, VI <0.70.
23. Worker, queen, NI (= distance from posterior margin of head to midpoint of line drawn across the lateral ocelli), relative to HL and N5 (= distance from posterior margin of head to midpoint of line drawn across the anterior margins of the antennal sclerites; see above for further explanation of N1, N2, N3, etc.) (0) larger, worker N1/N5 >0.14, worker N1/HL >0.13, (1) smaller, worker N1/N5 <0.14, worker N1/HL <0.13, and lying in lower region in a plot of N1 against either N5 or HL (Fig. 114).
24. Worker, queen, N3 (= distance from posterior margin of head to midpoint of line drawn across the posterior margins of the eyes), relative to HL and N5 (0) smaller, worker N3/N5 <0.24, queen N3/N5 <0.25, (1) larger, worker N3/N5 >0.24, queen N3/N5 >0.26; see also Figures 115, 144.
25. Worker, head (0) elongate, CI <0.80, (1) broader, CI 0.80–1.05, (2) very broad, CI >1.05; see also Figure 116.
26. Queen, head (0) small, HW <1.00, very elongate, CI 0.50–0.69, (1) medium-large, HW >1.00, moderately elongate, CI 0.70–0.89, (2) large, HW >1.40, moderately broad, CI 0.90–0.99, (3) of medium size, HW 1.20–1.40, but very broad, CI >1.05; see also Figure 145.
27. Worker, profemur (0) broad in relation to HW, lying in upper left region in Fig. 117, (1) of moderate width, (2) slender, in lower right region in Figure 117.
28. Queen, profemur width relative to HW (0) large, (1) medium, (2) small, lying in the lower and rightmost region in Figure 146.
29. Queen, profemur length relative to HL (0) long, FL/HL >0.76 (1) medium, FL/HL 0.56–0.75, (2) short, FL/HL ≤ 0.60 and lying in lower righthand region in Figure 147.

30. Worker, length of metatibia (LHT) relative to HL (0) long, LHT/HL $\geq$0.78, (1) shorter, LHT/HL usually <0.78, and lying in lower region in Figure 118.
31. Worker, mesopropodeal impression (0) very shallow, (1) moderately impressed.
32. Worker, DPL relative to LHT (0) large, (1) intermediate, (2) small (see Fig. 119).
33. Worker, dorsal face of propodeum (=BF), relative to HW and LHT, (0) long, (1) of moderate length, (2) short (see Fig. 120).
34. Worker, declivitous face of propodeum (=DF), relative to HW, (0) of moderate length, (1) short (see Fig. 121).
35. Worker and queen, PL relative to HL (0) large, worker PL/HL >0.58, queen PL/HL >0.60, (1) smaller, worker PL/HL <0.54, queen PL/HL <0.60; see also Figure 122.
36. Worker and queen, PL relative to HW and LHT (0) large, worker PL/LHT $\geq$0.68, (1) intermediate, worker PL/LHT 0.48–0.68, (2) small, worker PL/LHT 0.36–0.42; see also Figures 123, 148.
37. Worker and queen, petiole, minimum anterior width (=MPW) relative to HW (0) small, (1) intermediate, (2) large, lying in upper region in plot of MPW with HW (Fig. 124).
38. Queen, petiole, minimum anterior width (=MPW) relative to LHT (0) small, MPW/LHT $\approx$ 0.12, (1) intermediate, MPW/LHT 0.16–0.24, (2) large, MPW/LHT $\geq$0.25, and lying in upper region in a bivariate plot of the two measurements (Fig. 149).
39. Worker, petiole, MPW relative to DPL (0) smaller, MPW/DPL $\leq$0.18, (1) larger, MPW/DPL >0.18, and lying in upper region in Figure 125.
40. Worker, maximum petiolar width (=DPW) relative to HW (0) small, DPW/HW $\leq$0.33, (1) larger, DPW/HW >0.33, and lying in the upper region in Figure 126.
41. Queen, maximum petiolar width (=DPW) relative to HW and LHT (0) small, PW14 <0.44, (1) larger, PWI4 0.45–0.67, (2) very large, PWI4 >0.68, and lying in the upper region in Figure 150.
42. Worker, DPW relative to DPL (0) small, (1) intermediate, (2) large; see Figure 127.
43. Worker, postpetiole, PPW relative to DPL (0) small, (1) larger; see Figure 128.
44. Worker and queen, punctate sculpture on posterior third of head dorsum (0) moderately dense, uniformly dispersed, the punctures mostly 0.005–0.020 mm in diameter and subcontiguous or separated by one to several diameters (1) sparser, of less uniform density, most punctures small (0.005–0.015 mm diameter) and separated by many diameters, leaving extensive smooth interspaces, (2) very fine, most punctures <0.010 mm in diameter, uniformly and sparsely dispersed.
45. Queen, sculpture on head venter (0) densely and uniformly punctate or puncticulate throughout, (1) densely punctate on anterior half, becoming sparsely punctate posteriorly.
46. Worker, standing pilosity on side of head as seen in frontal view (0) sparse or absent (1) common and conspicuous, and occurring both above and below compound eye.
47. Worker, standing pilosity on mesosoma (0) sparse, lying in lower part of bivariate plots of MSC on LHT and MSC on HW, (1) commoner, lying in upper part of same plots (Figs 129, 130).
48. Worker and queen, standing pilosity on external face of metatibia (0) absent or

very sparse, worker HTC 0–2, (1) common, worker HTC 4–22, usually >6, (2) abundant, worker HTC >24.

49. Male, hypopygium (sternite IX), posterior margin (0) with slight to moderate concavity (Figs 89–92), (1) with deep (longer than wide), semicircular concavity (Figs 93, 94).

50. Male, paramere, posteromesial surface (0) without subcircular or elongate concavity, (1) with such a concavity but the margins not continuously carinate, (2) with such a concavity, the margins more or less continuously carinate (Figs 69–74).

51. Male, paramere, posteromesial surface (0) without smooth, lamellate dorsal and posterior margins, (1) with continuous, smooth, lamellate dorsal and posterior margins (part of the posteromesial concavity), moderately developed (Fig. 72), (2) with same margins, well developed (Figs. 69–71).

52. Male, paramere, posteromesial concavity (or equivalent region in outgroup taxa lacking the concavity) (0) with at least some standing pilosity, (1) without standing pilosity.

53. Male, paramere, posteromesial concavity, if present (0) subcircular or subquadrate (Figs 72–74, 81–84), (1) elongate (Figs 69, 70), (2) very elongate (Fig. 71).

54. Male, paramere, posteromesial concavity, if present (0) directed ventromesially (Figs 86–88), (1) directed mesially (Fig. 85), (2) directed dorsomesially (Figs 75–80).

55. Male, paramere, posteromesial concavity, if present (0) with its ventral margin situated dorsal to the ventral margin of the paramere (Figs 69–74), (1) with ventral margin confluent with that of paramere, as seen in mesial view (Figs 81–84).

56. Male, paramere, posteromesial concavity, if present (0) with straight or gradually curved posterior margin, as seen in posterior view, (1) with strongly incised posterior margin, as seen in posterior view (Figs 79, 80).

57. Male, paramere, posterodorsal extremity, in lateral view (0) rounded (e.g. Fig. 81), (1) angulate (Figs 82–84).

58. Male, paramere, posterodorsal surface (0) without a deep, transverse impression, (1) with a deep, cylindrical, transverse impression (Figs 83, 84).

59. Male, paramere, mediodorsal lobe, more or less confluent with the upper extremity of the mesial dorsoventral lobe (0) absent, (1) present, small, acute (Fig. 81), (2) present, well developed, subconical (Figs 82–84).

60. Male, paramere, dorsal surface, anterior to the mediodorsal lobe (or upper extremity of the mesial dorsoventral lobe) (0) without a large lamellate lobe, (1) with such a lobe (Fig. 81).

61. Male, paramere, mesial dorsoventral lobe, as seen in posterior view, (0) upper half without a rounded, keel-like mesial protrusion, (1) with such a mesial protrusion (Figs 87, 88).

62. Male, paramere, mesial dorsoventral lobe, as seen in posterior view, (0) without prominent, acute, subtriangular mesial protrusion, (1) with such a mesial protrusion (Figs 79, 80).

63. Male, paramere, outer margin in dorsal view (0) gradually rounded, (1) subangulate (Figs 83, 84).

64. Male, paramere, orientation of mesial dorsoventral lobe (and usually also the posterior margin of paramere), as seen in mesial view (0) posterodorsal to anteroventral (Figs 81–84), (1) vertical (Figs 69–72), (2) anterodorsal to posteroventral (Figs 73, 74).

65. Male, paramere, mesial face, acute posterior extension of membranous tissue (0) close to the ventral margin, (1) distant from ventral margin (Figs 69–74).

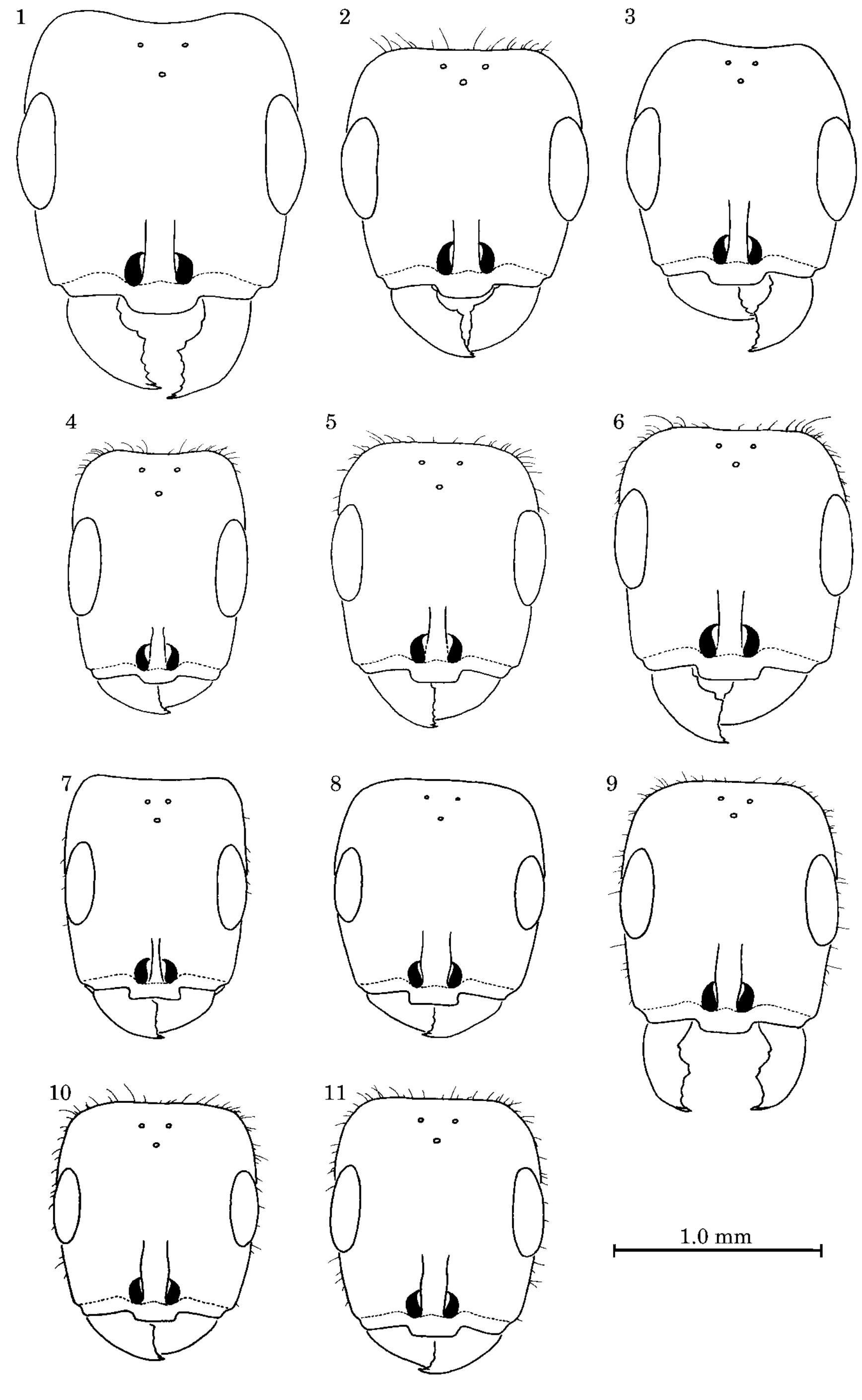
66. Male, aedeagus, posterior margin (0) not evenly curved, lamellate and directed posterolaterally, (1) of such a form (Figs 95–100).
67. Male, aedeagus, posteroventral tooth on posterior margin (0) well developed (Figs 99, 100, 104), (1) small (Figs 95, 96, 98), (2) absent.
68. Male, aedeagus, second large tooth dorsal to posteroventral tooth on posterior margin (0) absent, (1) present (Fig. 104).
69. Male, aedeagus, row of well developed teeth on posterior margin (0) absent, (1) present (Figs 101–103).
70. Male, aedeagus, lamellate posterodorsal lobe (0) well developed (Figs 95–98, 104), (1) weakly developed (Figs 99, 100), (2) absent.
71. Male, aedeagus, anterodorsal margin with thin, transluscent lamella (0) absent, (1) present (Fig. 101–103).
72. Male, aedeagus, external face, upwardly curved carina arising anteroventrally (0) absent, (1) present, reverse C-shaped (as in Fig. 104, or a weaker version of same, e.g. Fig. 103), (2) present, J-shaped, well developed, extending to near the dorsal margin (Figs 99, 100), (3) present, J-shaped, less well developed, not extending to near dorsal margin (Figs 95–98).

The dataset was analysed using Steve Farris' Hennig86 parsimony program (version 1.5). Bootstrap values were calculated with Mark Siddall's Random Cladistics program, using 1000 bootstrap replicates. The outgroups were *Pseudomyrmex gracilis* and *P. termitarius*, two morphologicaly generalized and ecologically unspecialized *Pseudomyrmex* species, and *Tetraponera natalensis*. *Tetraponera* is the sister genus of *Pseudomyrmex* (Ward, 1990). Characters were not explicitly polarized. Rather, *T. natalensis* was used to root the tree, with *P. gracilis* and *P. termitarius* being allowed to influence character state reconstructions closer to the ingroup. The ingroup was not constrained to be monophyletic. All multi-state characters were treated as ordered, in the sequence given above, except for characters 26, 44 and 72, which were considered unordered (non-additive). (A separate analysis in which all characters were coded as non-additive gave very similar results.)

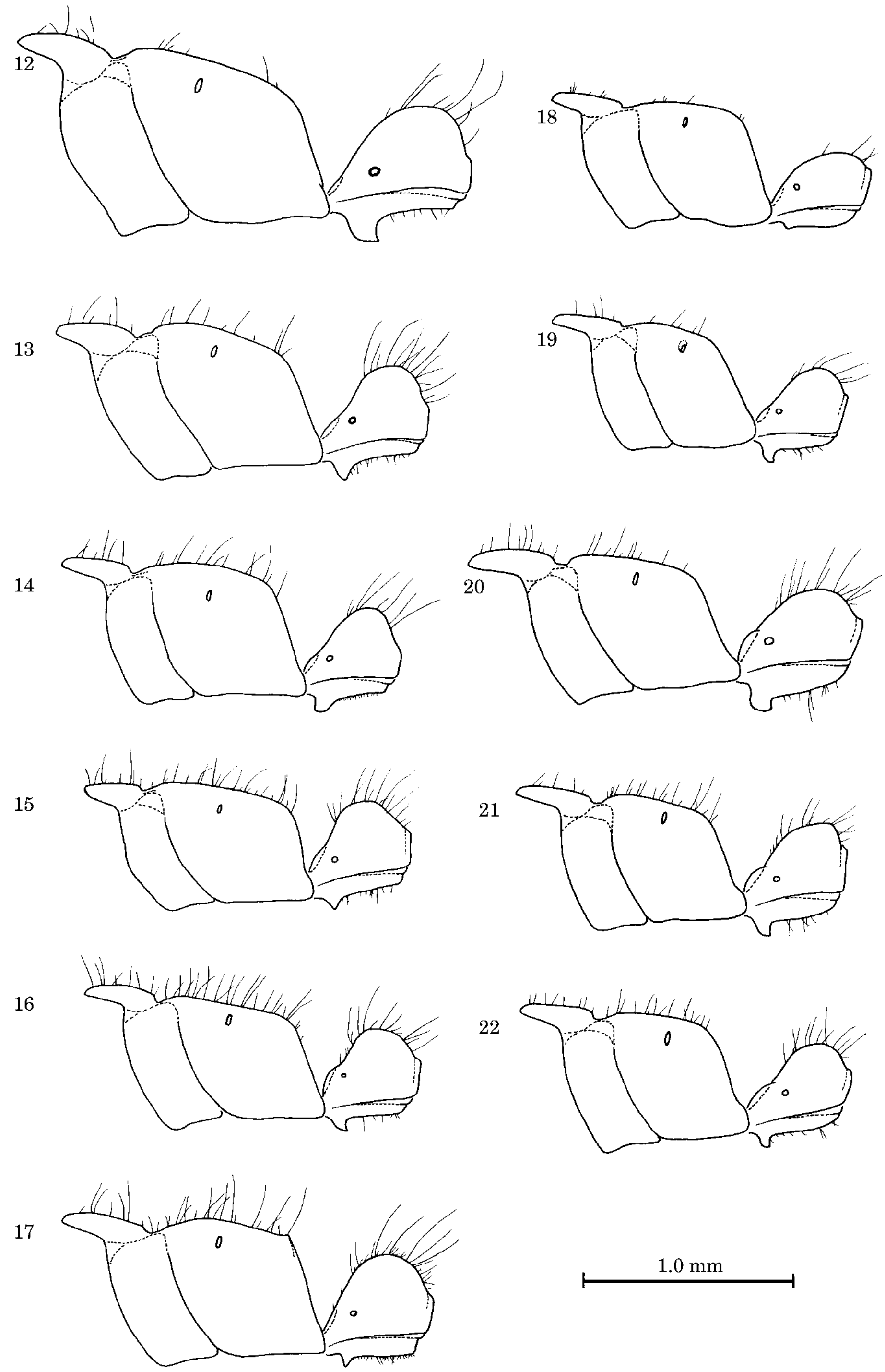
PSEUDOMYRMEX VIDUUS GROUP

Introduction

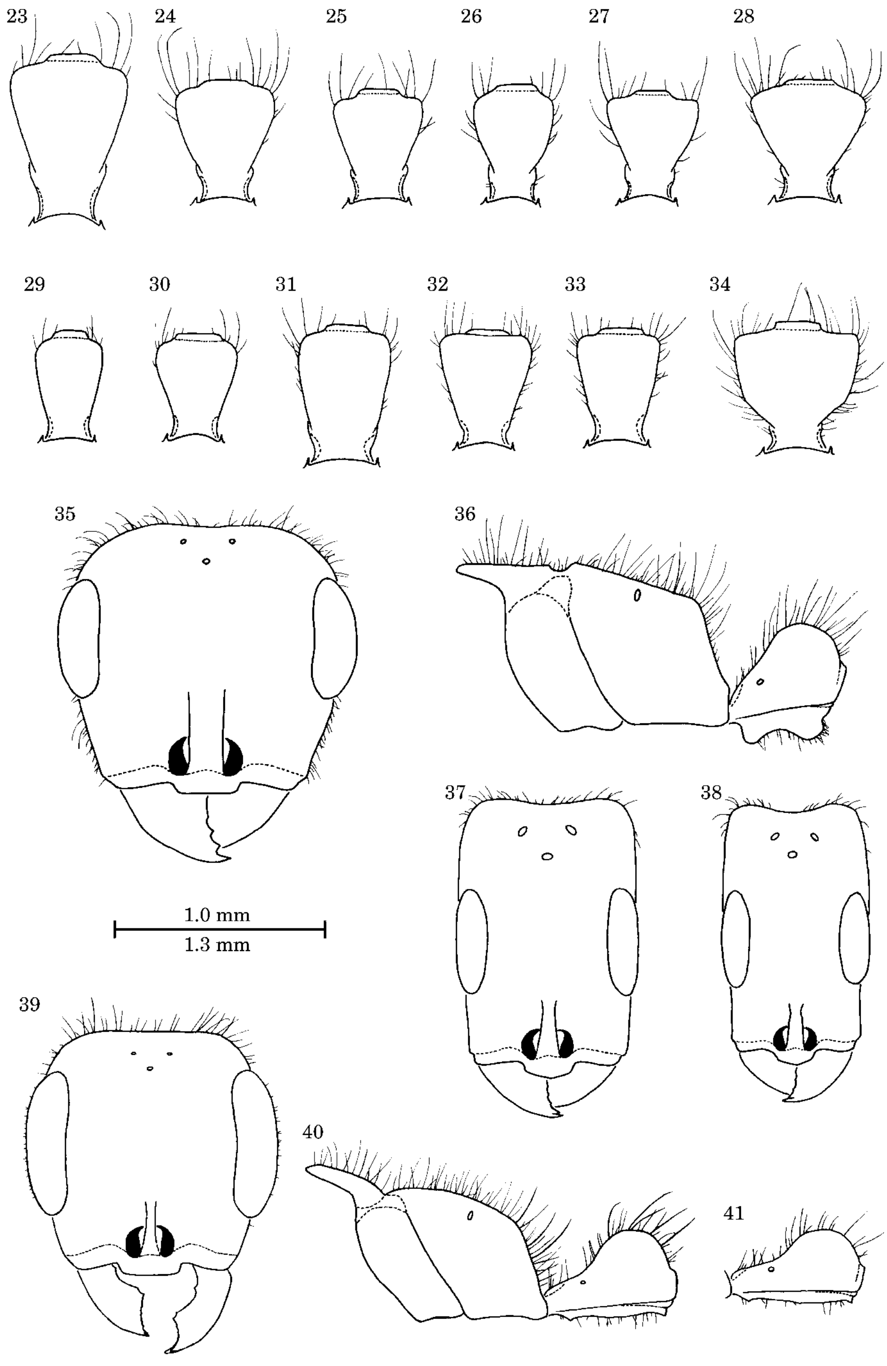
Worker, diagnosis. Medium to large sized species (HW 0.74–1.51, HL 0.91–1.55, LHT 0.57–1.36). Head varying from rather elongate to notably broader than long (CI 0.70–1.16), with relatively short eyes (REL 0.32–0.48, REL2 0.35–0.57) (Figs 1–11, 35). External and basal margins of mandible subparallel, MD1/MD2 about 1.00 (except in *P. kuenckeli*, where MD1/MD2 approximately 0.84); mesial tooth on basal margin closer to apicobasal angle than to proximal tooth, MD4/MD5 about 0.65–0.80. Masticatory margin of mandible with 5–7 teeth, MD8/MD9 approximately 0.60–0.82. Palp formula 6,4, with reductions to 5,3 and 4,3. Anterior margin of median clypeal lobe usually broadly rounded, but becoming laterally angulate in some species. Frontal carinae generally well separated (FCI 0.027–0.170, AS12 0.55–0.87), fusing anterolaterally with antennal sclerites. First funicular segment 1.6–2.6 times longer than broad; funicular segments 2 and 3 varying from markedly broader than long to slightly longer than broad (LF2/WF2 0.43–1.39; FLI 0.97–2.49); funicular segments 4–10 consistently broader than long in all species except *P.*



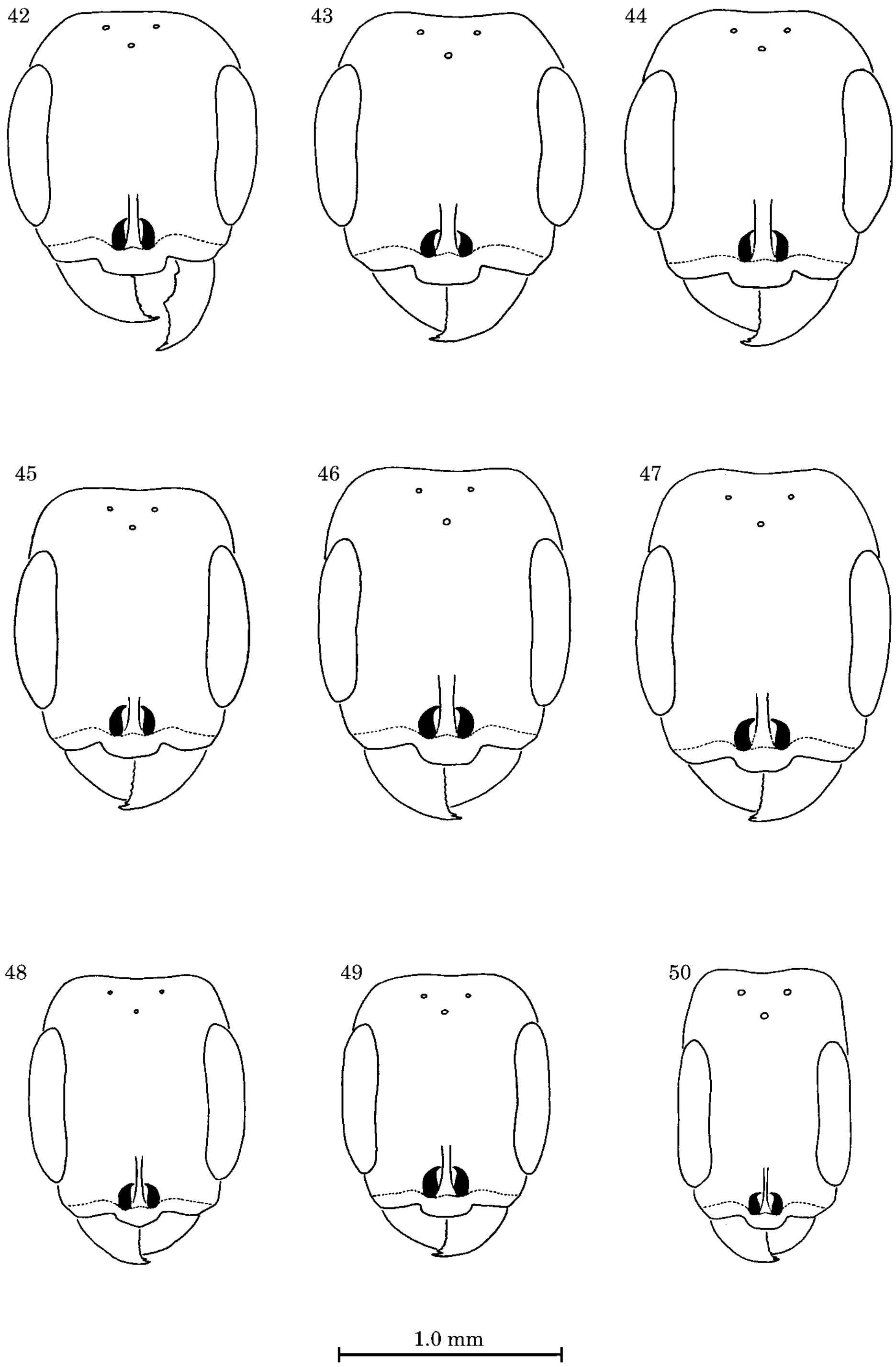
Figures 1–11. *Pseudomyrmex viduus* group, workers, full-face (dorsal) view of head, with pilosity shown in outline (omitted from mandibles and clypeus). 1, *P. dendroicus* (Ecuador); 2, *P. triplarinus* (Bolivia); 3, *P. mordax* (Colombia); 4, *P. viduus* (Brazil); 5, *P. triplaridis* (Brazil); 6, *P. ultrix* (Ecuador, holotype); 7, *P. tachigaliae* (Peru); 8, *P. malignus* (Venezuela); 9, *P. concolor* (Brazil); 10, *P. insuavis* (Colombia, holotype); 11, *P. penetrator* (Brazil).



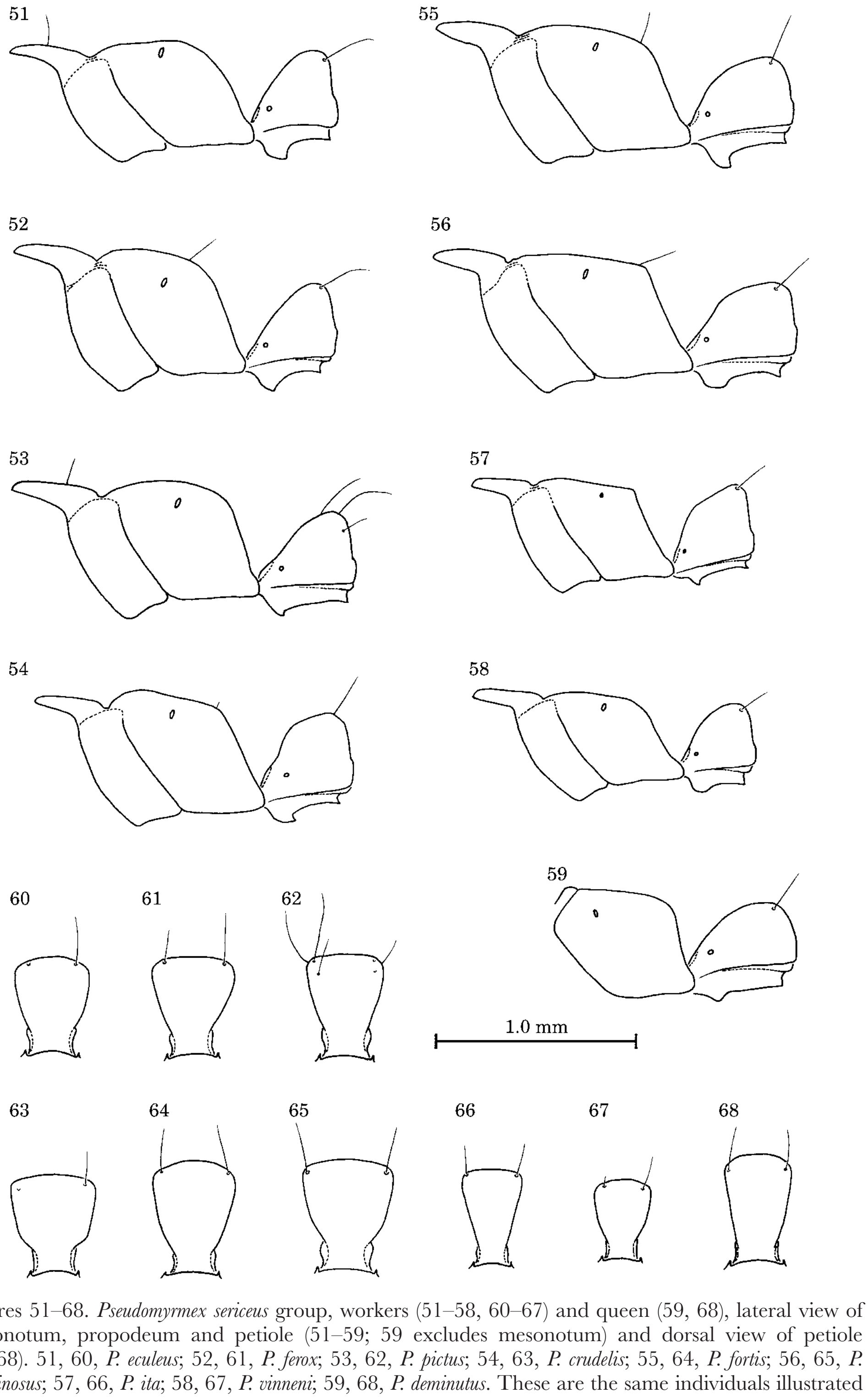
Figures 12–22. *Pseudomyrmex viduus* group, workers, lateral view of mesonotum, propodeum and petiole. Pilosity shown in outline only. 12, *P. dendroicus*; 13, *P. triplarinus*; 14, *P. mordax*; 15, *P. viduus*; 16, *P. triplaridis*; 17, *P. ultrix*; 18, *P. tachigaliae*; 19, *P. malignus*; 20, *P. concolor*; 21, *P. insuavis*; 22, *P. penetrator*. These are the same individuals illustrated in Figs 1–11.



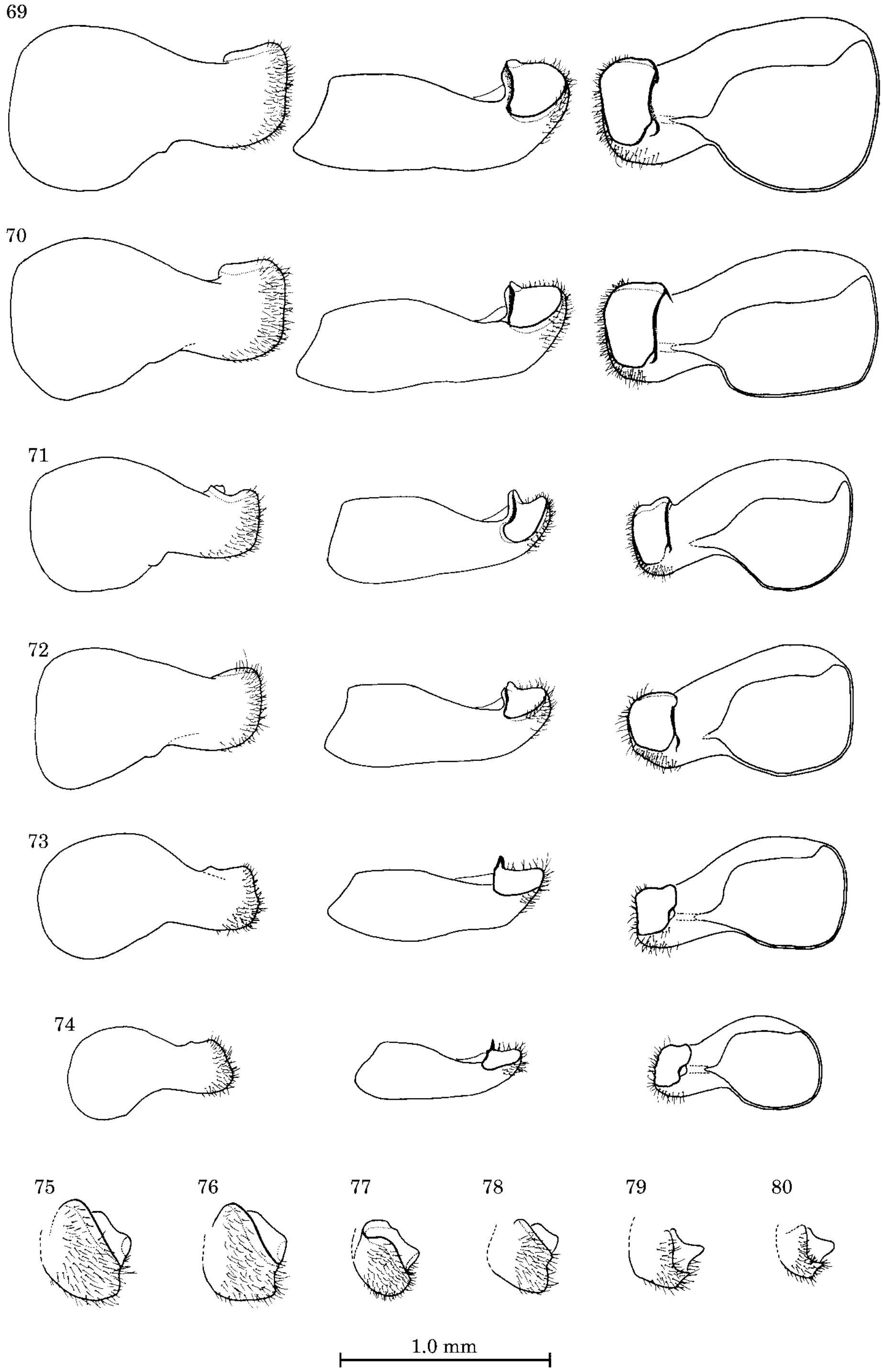
Figures 23–41. *Pseudomyrmex* workers (23–36, 39–41) and queens (37, 38), dorsal view view of petiole (23–34), full-face view of head (35, 37–39), lateral view of mesonotum, propodeum and petiole (36, 40), lateral view of petiole (41). Pilosity shown in outline only. Figs 23–33 depict the same individuals shown in Figs 1–11. 23, *P. dendroicus*; 24, *P. triplarinus*; 25, *P. mordax*; 26, *P. viduus*; 27, *P. triplaridis*; 28, *P. ultrix*; 29, *P. tachigaliae*; 30, *P. malignus*; 31, *P. concolor*; 32, *P. insuavis*; 33, *P. penetrator*; 34–36, *P. kuenckeli* (Costa Rica); 37, *P. viduus* (Brazil); 38, *P. vitabilis* (Colombia, holotype); 39–40, *P. hospitalis* (Peru, holotype), 41, *P. gracilis* (Peru). Scale bar = 1.00 mm for Figs 23–38 and 1.30 mm for Figs 39–41.



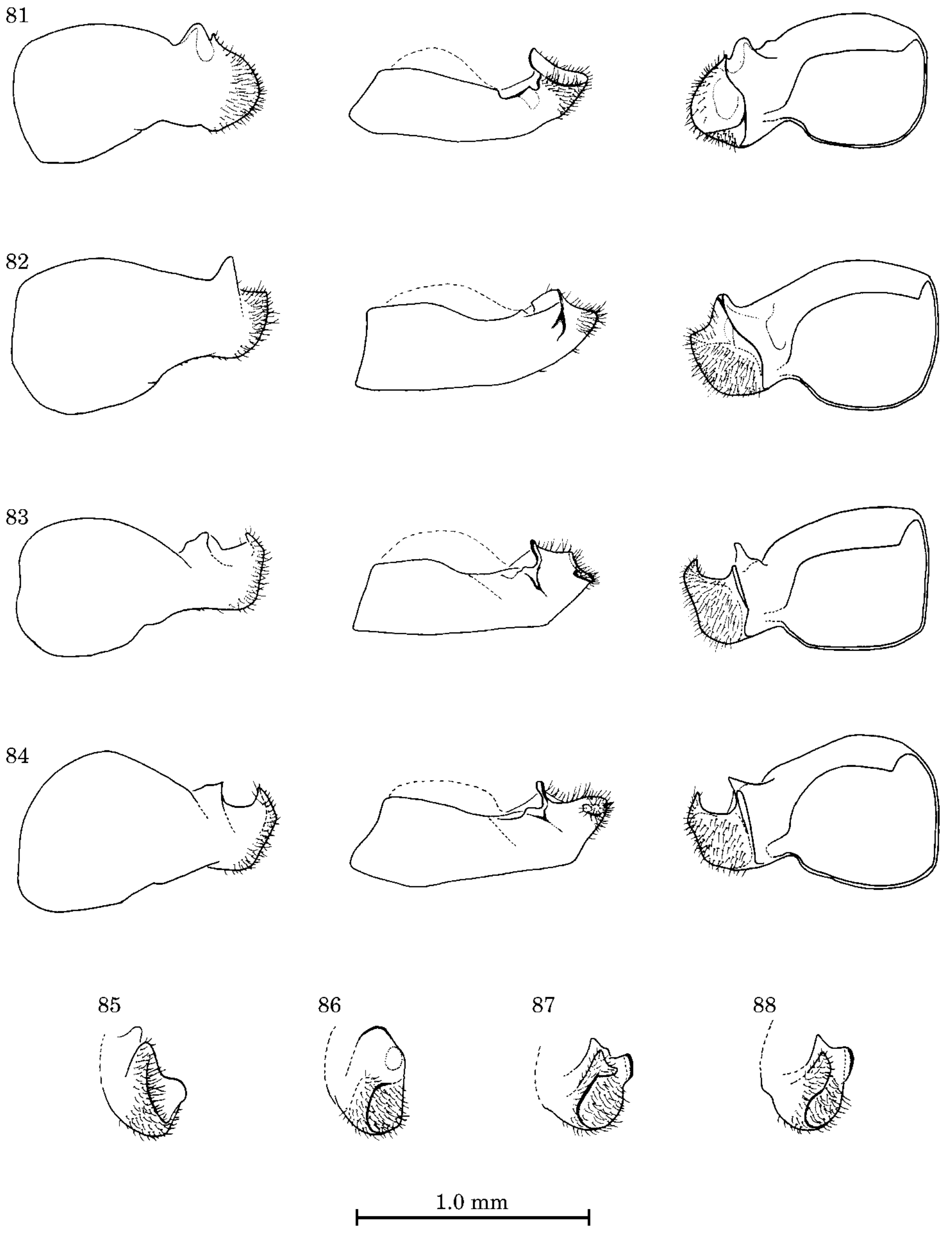
Figures 42–50. *Pseudomyrmex sericeus* group, workers (42–49) and queen (50), full-face view of head. 42, *P. eculeus* (Ecuador, holotype); 43, *P. ferox* (Peru, holotype); 44, *P. pictus* (Brazil); 45, *P. crudelis* (Peru, holotype); 46, *P. fortis* (Guatemala); 47, *P. rubiginosus* (Brazil); 48, *P. ita* (Costa Rica); 49, *P. vinneni* (Brazil); 50, *P. deminutus* (Brazil, holotype).



Figures 51–68. *Pseudomyrmex sericeus* group, workers (51–58, 60–67) and queen (59, 68), lateral view of mesonotum, propodeum and petiole (51–59; 59 excludes mesonotum) and dorsal view of petiole (60–68). 51, 60, *P. eculeus*; 52, 61, *P. ferox*; 53, 62, *P. pictus*; 54, 63, *P. crudelis*; 55, 64, *P. fortis*; 56, 65, *P. rubiginosus*; 57, 66, *P. ita*; 58, 67, *P. vinneni*; 59, 68, *P. deminutus*. These are the same individuals illustrated in Figs 42–50.

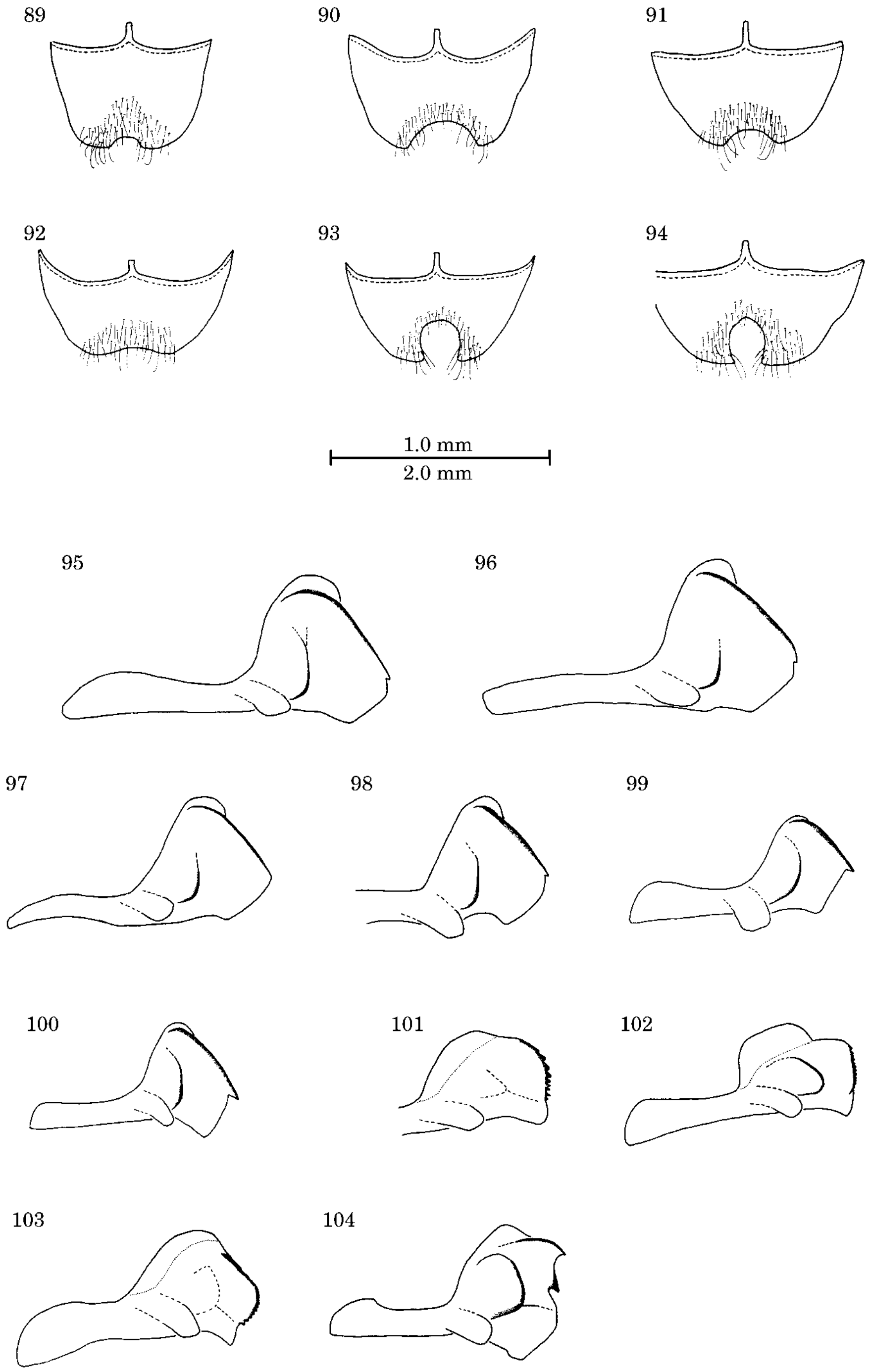


Figures 69–80. *Pseudomyrmex viduus* group, male genitalia, left parameres. 69–74: lateral (left), dorsal (center) and mesial (right) views; 75–80: posterior view. 69, 75, *P. dendroicus* (Ecuador); 70, 76, *P. triplarinus* (Brazil); 71, 77, *P. mordax* (Colombia); 72, 78, *P. ultrix* (Ecuador); 73, 79, *P. triplaridis* (Brazil); 74, 80, *P. viduus* (Brazil).



Figures 81–88. *Pseudomyrmex viduus* group, male genitalia, left parameres. 81–84: lateral (left), dorsal (center) and mesial (right) views; 85–88: posterior view. 81, 85, *P. kuenckeli* (Bolivia); 82, 86, *P. tachigaliae* (Brazil); 83, 87, *P. malignus* (Brazil); 84, 88, *P. concolor* (Brazil).

kuenckeli. Profemur relatively slender (FI 0.31–0.49). Pronotum laterally rounded (submarginate in *P. kuenckeli*). Metanotal groove usually well marked (exception: *P. kuenckeli*) (MPI 0.011–0.092). Basal and declivitous faces of propodeum moderately well differentiated and subequal in length (PDI 0.83–1.51), in profile the juncture between the two varying from rounded to subangulate (Figs 12–22, 36). Petiole



Figures 89–104. *Pseudomyrmex viduus* group, male terminalia. 89–94: hypopygium (sternite IX); 95–104: aedeagus, left lateral view. 89, *P. kuenckeli* (Bolivia); 90, *P. mordax* (Colombia); 91, *P. triplaridis* (Brazil); 92, *P. tachigaliae* (Brazil); 93, *P. malignus* (Brazil); 94, *P. concolor* (Brazil); 95, *P. dendroicus* (Peru); 96, *P. triplarinus* (Brazil); 97, *P. mordax* (Colombia); 98, *P. ultrix* (Ecuador); 99, *P. triplaridis* (Brazil); 100, *P. viduus* (Brazil); 101, *P. malignus* (Brazil); 102, *P. concolor* (Brazil). 103, *P. tachigaliae* (Brazil); 104, *P. kuenckeli* (Bolivia). Scale bar = 1 mm for Figs 89–94 and 2 mm for Figs 95–104.

relatively short (PL/HL 0.35–0.49), high (PLI 0.70–1.28), and broad (PWI 0.71–1.40), anteroventral tooth usually present and well developed, sometimes conspicuously recurved. Minimum (anterior) petiolar width rather large, so that in dorsal view the articulation of the petiole with the propodeum is broad (MPW/PL 0.34–0.58, MPW/DPL 0.19–0.29). Postpetiole notably broader than long (PPWI 1.29–1.90). Body sculpture varying from smooth and shining with scattered punctulae to densely corarious-imbricate and opaque. Dorsum of head usually with smooth, shiny interspaces; punctulae separated by more than their diameters on at least some upper parts of the head (*P. tachigaliae* has exceptionally dense sculpture). Standing pilosity usually common to abundant, present on the scapes, head, entire mesosoma dorsum, petiole, postpetiole, gaster, and extensor faces of tibiae. Ten or more standing hairs visible in outline on the mesosoma dorsum, except *P. tachigaliae* where there may be as few as six (this species also exceptional in lacking standing pilosity on the external faces of the tibiae). Appressed pubescence moderately dense on most of body, ranging from sparse to dense on abdominal tergite IV. Colour varying from light yellow- or orange-brown to dark brown, and including various bicoloured combinations.

Queen, diagnosis. Similar to worker except for caste-specific differences. Larger in size (HW 0.71–2.01, HL 1.18–2.26, LHT 0.76–1.60), head more elongate (CI 0.56–1.08). Ocular indices differing slightly: REL 0.32–0.48, REL2 0.35–0.57. Mandibles tending to be more modified than those of workers, with basal incisions, dorsal ridges, and reductions in dentition seen in various species. Palp formula as in worker. Median clypeal lobe narrower and usually more protruding, anterior margin convex or straight, laterally rounded or subangulate. Petiole and postpetiole generally more slender (PL/HL 0.35–0.58, PLI 0.54–1.28, PWI 0.61–1.31, PPWI 1.21–1.95). Forewing with 1 or 2 cubital cells.

Male, diagnosis. Of medium size (HW 0.90–1.33, LHT 0.89–1.45; $n = 53$), head usually as broad as, or broader than, long but occasionally more elongate (CI 0.85–1.19). Masticatory margin of mandible with 6–9 teeth, often small or obsolete. Palp formula as in female. Dorsal surface of clypeus slightly to strongly convex; median clypeal lobe small, with convex anterior margin. Eye moderately large (REL 0.44–0.56, REL2 0.43–0.61). Scape of typical length for the genus (SI 0.20–0.30, SI2 0.40–0.60); length of second funicular segment varying from about two-thirds of scape length to slightly longer than the scape (LF2/SL 0.64–1.18). Profemur, petiole and postpetiole more slender than in worker (PLI 0.51–1.04, PWI 0.45–1.01). Posterolateral corners of sternites IV–VIII not notably protruding ventrally. Hypopygium (sternite IX) with a posteromedial concavity, varying from slight to pronounced (Figs 89–94). Pygidium (tergum VIII) posteromedially constricted, its margin somewhat thickened, directed posteroventrally, and straight or (more often) emarginate; in one species (*P. tachigaliae*) posteromedial margin of pygidium furnished with a prominent spine. Paramere as in Figures 69–88, appearing somewhat truncated distally in lateral view. Posteromesial face of paramere with a saucer-shaped concavity, variously modified in different species. Aedeagus as in Figures 95–104, posterior margin entire or furnished with a set of small teeth (two large teeth in *P. kuenckeli*); portions of the dorsal margin lamellate, either in the form of a thin posterodorsal lobe or an anterodorsal keel.

Comments. Workers and queens of the *P. viduus* group can be distinguished from all other *Pseudomyrmex* by their possession of the following combination of traits: eyes relatively short (worker REL 0.32–0.48, queen REL 0.33–0.50); standing pilosity common on mesosoma dorsum and external faces of tibiae (secondarily reduced in *P. tachigaliae*); petiole broad posteriorly (worker PWI 0.71–1.40, queen PWI 0.61–1.31) and anteriorly (worker MPW/PL 0.34–0.58, queen MPW/PL 0.32–0.65, queen MPW/LHT 0.25–0.38); and head densely punctulate with conspicuous shiny interspaces. In most species the frontal carinae are well separated and the worker metanotal groove is conspicuously impressed. Among the eight other major species groups of *Pseudomyrmex* (diagnosed in Ward, 1989), the *P. tenuis* group, *P. sericeus* group, *P. oculatus* group and *P. subtilissimus* group can be distinguished by their more elongate eyes and general scarcity of tibial pilosity. The species in the *P. gracilis* group have longer eyes, a laterally submarginate worker pronotum, and more teeth (7–10) on the masticatory margin of the mandibles. In the *P. pallens* and *P. pallidus* groups worker eye length overlaps with that of the *P. viduus* group but standing pilosity is absent from the external faces of the tibiae and usually sparse on the mesosoma dorsum, and the petiole is more slender. Among the remaining species of *Pseudomyrmex* not assigned to a species group, those most likely to be confused with the *P. viduus* group are *P. duckei* (Forel), *P. filiformis* (Fabricius), *P. depressus* (Forel), *P. fervidus* (F. Smith) and *P. perbosci* (Guérin). The workers of these species have more slender and/or anteriorly constricted petioles, and those of the first two species have longer eyes (REL >0.48). In addition, *P. depressus* and *P. duckei* have more closely contiguous frontal carinae (worker FCI ≈ 0.025), and *P. filiformis* and *P. perbosci* lack standing pilosity on the external faces of the tibiae.

Distribution. The *Pseudomyrmex viduus* group as a whole is distributed throughout most of the Neotropics, from Mexico (and possibly also Cuba; see discussion under *P. viduus*) to Argentina, Bolivia and southern Brazil (Fig. 161). Most species are confined to mainland South America, however, and species richness is highest in the Amazon basin and adjacent foothills.

Synonymic list of species

P. concolor (F. Smith, 1860) Colombia, Venezuela, Guyana, Brazil
 = *P. latinodus* (Mayr, 1878) (synonymy by Ward, 1989)
 = *P. endophytus* (Forel, 1912) **syn. nov.**
 = *P. damnosus* (Wheeler, 1921b) (synonymy, under *latinodus*, by Kempf, 1961)
P. dendroicus (Forel, 1904a) Colombia, Venezuela, Ecuador, Peru, Brazil, Bolivia
 = *P. emarginatus* (Forel, 1904c) (synonymy by Ward, 1989)
***P. insuavis* sp. nov.** Colombia
P. kuenckeli (Emery, 1890) Mexico to Argentina
 = *P. dichrous* (Forel, 1904a) (synonymy by Kempf, 1961)
 = *P. bierigi* (Santschi, 1932) (synonymy by Kempf, 1961)
 = *P. crenulatus* (Enzmann, 1944) (synonymy by Kempf, 1961)
P. malignus (Wheeler, 1921b) Venezuela, Trinidad, Guyana, French Guiana, Brazil
 = *P. cholericus* (Wheeler, 1921b) (synonymy by Ward, 1989)
 = *P. crucians* (Wheeler, 1921b) (synonymy by Ward, 1989)
 = *P. auripes* (Wheeler, 1922) (synonymy by Ward, 1989)
P. mordax (Warming, 1894) **n. comb., stat. rev.** Panama, Colombia, Venezuela
 = *P. symbioticus* (Forel, 1904a) **syn. nov.**

P. penetrator (F. Smith, 1877) **stat. rev.** Venezuela, Guyana, Surinam, Brazil
= *P. nigrescens* (Forel, 1904a) **syn. nov.**
= *P. coronatus* (Wheeler, 1942) **syn. nov.**
= *P. coronatus* (Enzmann, 1944) (synonymy, under *coronatus* (Wheeler), by Brown, 1949)
P. tachigaliae (Forel, 1904c) Peru, western Brazil
= *P. bradleyi* (Wheeler, 1942) (synonymy by Ward, 1989)
= *P. bradleyi* (Enzmann, 1944) (synonymy, under *bradleyi* (Wheeler), by Brown, 1949)
P. triplaridis (Forel, 1904c) Colombia, Venezuela, Guyana, Ecuador, Peru, Brazil
= *P. boxi* (Wheeler, 1942) (synonymy by Ward, 1989)
= *P. boxi* (Enzmann, 1944) (synonymy, under *boxi* (Wheeler), by Brown, 1949)
P. triplarinus (Weddell, 1850) Colombia, Ecuador, Peru, Brazil, Bolivia, ?Argentina
= *P. arborissanctae* (Emery, 1894) (synonymy by Wheeler, 1942)
= *P. cordobensis* (Forel, 1914) **syn. nov.**
= *P. rurrenabaquensis* (Wheeler & Mann, 1942b) **syn. nov.**
= *P. ecuadorianus* (Enzmann, 1944) (synonymy by Brown, 1949)
P. ultrix **sp. nov.** Ecuador
P. viduus (F. Smith, 1858) Mexico (and Cuba?) to Peru, Brazil, Bolivia
= *P. caroli* (Forel, 1899) (synonymy by Ward, 1989
= *P. opacior* (Forel, 1904b) **syn. nov.**
= *P. sapii* (Forel, 1904c) (synonymy by Ward, 1989)
= *P. ulei* (Forel, 1904c) (synonymy by Ward, 1989)
= *P. baileyi* (Wheeler, 1942) (synonymy by Ward, 1989)
= *P. tigrinus* (Wheeler, 1942) (synonymy by Ward, 1989)
= *P. biolleyi* (Enzmann, 1944) (synonymy, under *baileyi*, by Brown, 1949)
= *P. trigonus* (Enzmann, 1944) (synonymy, under *tigrinus*, by Brown, 1949)
P. vitabilis **sp. nov.** Colombia

All castes (workers, queens, males) are known in each species except *P. insuavis* (worker and queen only) and *P. vitabilis* (queen only).

Key to workers and queens (including other Tachigali- *and* Triplaris-*associated* Pseudomyrmex*)*

To improve its utility this key covers all species of *Pseudomyrmex* that have been found inhabiting *Triplaris* or *Tachigali* plants. The *Pseudomyrmex viduus* group is treated in couplets 2–13. The remaining couplets of the key are concerned with other *Triplaris* and *Tachigali* associates, both obligate and facultative. Information on the host plant association(s) of each species is given in parentheses.

1 Eyes relatively short, half the head length (HL) or less (worker REL 0.32–0.48, queen REL 0.33–0.50); frontal carinae usually not closely contiguous and usually separated by an amount greater than basal scape width (worker MFC >0.079 in all species except *P. tachigaliae* and *P. viduus*) 2
1′ Eyes longer than half the head length (worker REL 0.53–0.68, queen REL 0.51–0.63); frontal carinae more closely contiguous (worker MFC <0.080) 14

2 Head notably broader than long (worker CI 1.08–1.16, queen CI 1.06–1.08); compound eye located on the posterior third of head; body pilosity long and

abundant (Fig. 36), worker MSC approximately 95–150, worker HTC 25–50; Mexico to Argentina, Paraguay and Brazil (not a specialized inhabitant of plant domatia) .... *kuenckeli* (Emery)

2′ Head usually longer than broad, less commonly as broad as long (worker CI 0.70–1.04, queen CI 0.56–0.98); compound eye positioned about the middle of the side of the head; body pilosity less abundant (Figs 12–22), worker MSC <90, worker HTC <22 3

3 Head, eyes and propodeum elongate (worker CI <0.80, queen CI 0.56–0.67; worker REL2 >0.49, queen REL2 0.56–0.68; worker DPL/HW >0.96) (Figs 4, 15, 37, 38) 4

3′ Head, eyes and propodeum less elongate (worker CI 0.81–1.04, queen CI 0.72–0.98; worker REL2 0.35–0.48, queen REL2 0.40–0.52; worker DPL/HW 0.76–0.97) (Figs 1–3, 5–14, 16–22) 5

4 Head extremely elongate, queen CI 0.56 (Fig. 38), worker unknown but expected to have CI <0.70; body size smaller, queen HW 0.71, queen LHT 0.76, worker expected to have HW and LHT <0.80; Colombia (known only from holotype queen; biology unknown) .... ***vitabilis*, sp. nov.**

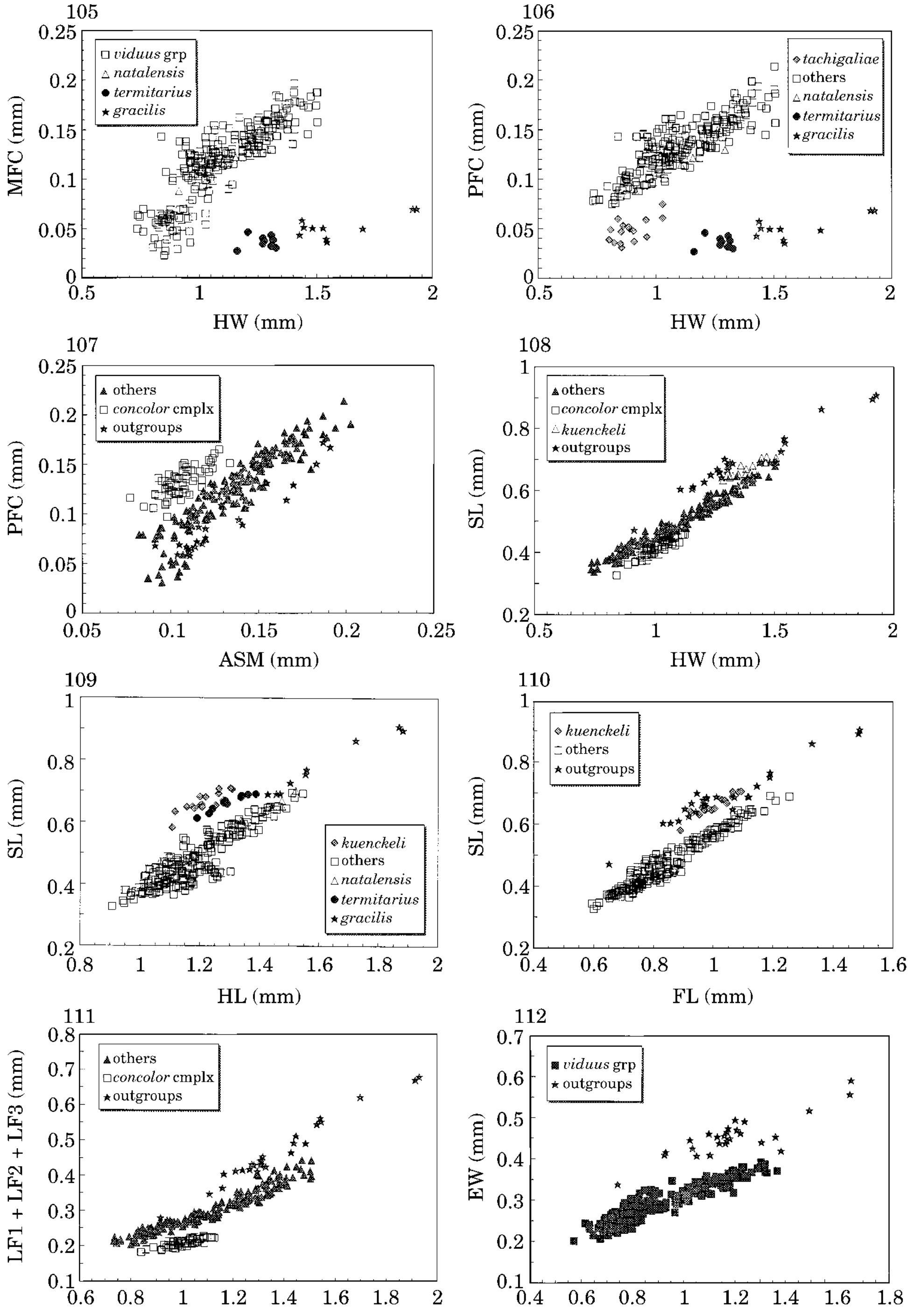
4′ Head less elongate, worker CI 0.70–0.79, queen CI 0.60–0.67 (Fig. 37); larger body size, worker HW 0.74–0.97, queen HW 0.86–0.96, worker LHT 0.63–0.88, queen LHT 0.81–0.94; Mexico to Bolivia, Brazil (recorded from live cavities of various plants including *Cordia, Coussapoa, Macrolobium, Ocotea, Pterocarpus, Pseudobombax, Sapium, Triplaris*) .... *viduus* (F. Smith)

5 Frontal carinae closely contiguous and median lobes of the antennal sclerites correspondingly well exposed (Fig. 7) (worker MFC 0.023–0.065, worker PFC/ASD 0.27–0.48; queen FCI2 0.34–0.51); standing pilosity relatively scarce on mesosoma dorsum (worker MSC 6–26) and absent from external faces of tibiae (worker HTC = 0); median clypeal lobe of worker laterally angulate (Fig. 7), that of queen in the form of a tongue-like anterodorsal protrusion; head subopaque to sublucid, densely punctulate; Peru, western Brazil (*Tachigali* inhabitant) .... *tachigaliae* (Forel)

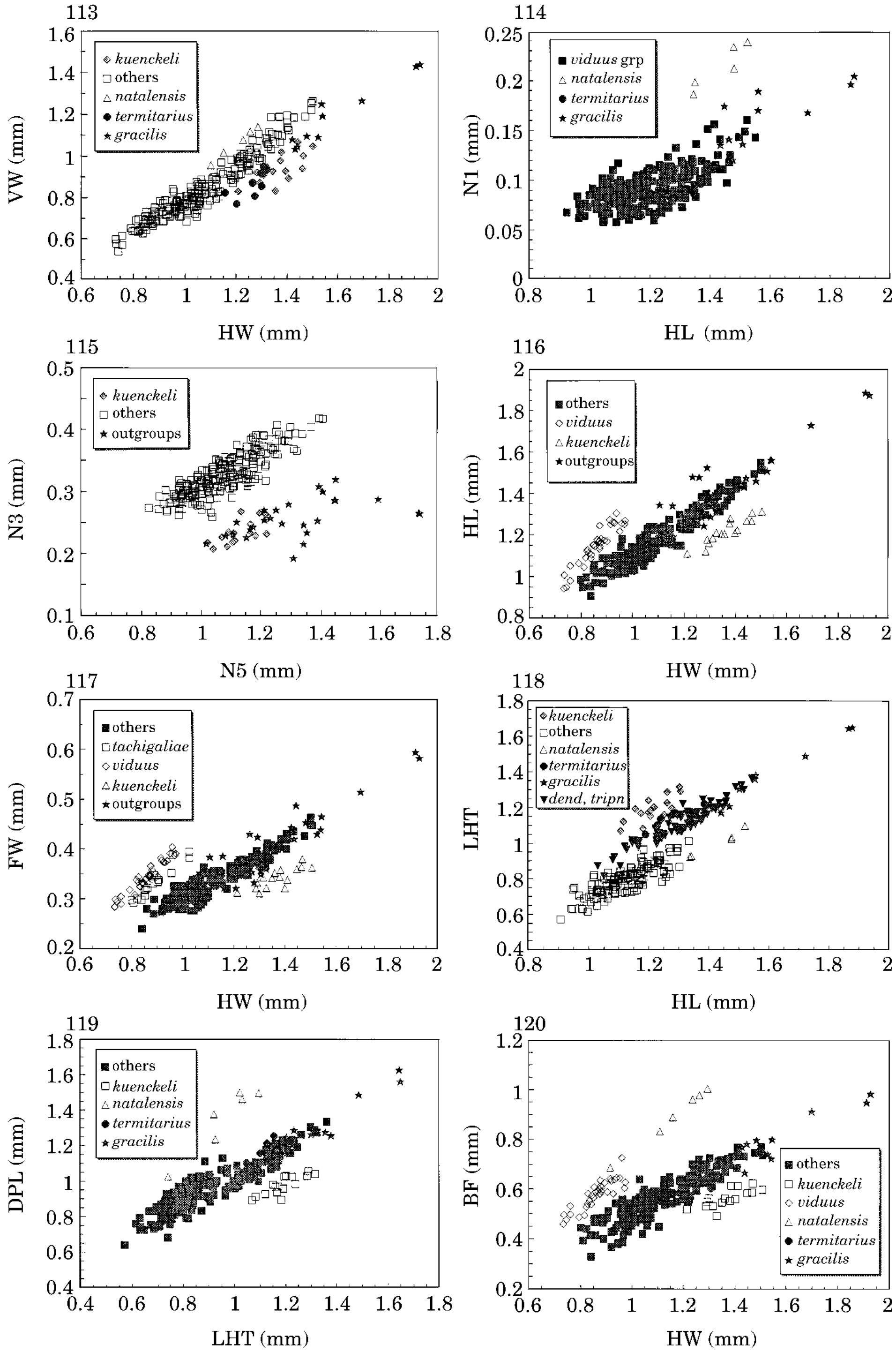
5′ Frontal carinae better separated and median lobes of the antennal sclerites less exposed (Figs 1–3, 5, 6, 8–11) (worker MFC 0.080–0.196, worker PFC/ASD 0.54–0.91, queen FCI2 0.45–0.95); standing pilosity usually more common on mesosoma dorsum (worker MSC 6–84) and present on external faces of tibiae (worker HTC 1–21); median clypeal lobe of both worker and queen usually laterally rounded, but if angulate (*P. malignus*) then upper third of head with sparse punctures and extensive shiny interspaces 6

6 Scape and funicular segments shorter; worker FLI 0.97–1.44, queen FLI 1.11–1.54; see also plot of worker SL on HW (Fig. 108) and (LF1 + LF2 + LF3) on HW (Fig. 111); punctures on upper third of head sparse, of uneven density, mostly small and separated by many diameters, leaving extensive smooth interspaces; palp formula 4,3 (*Tachigali* inhabitants) 7

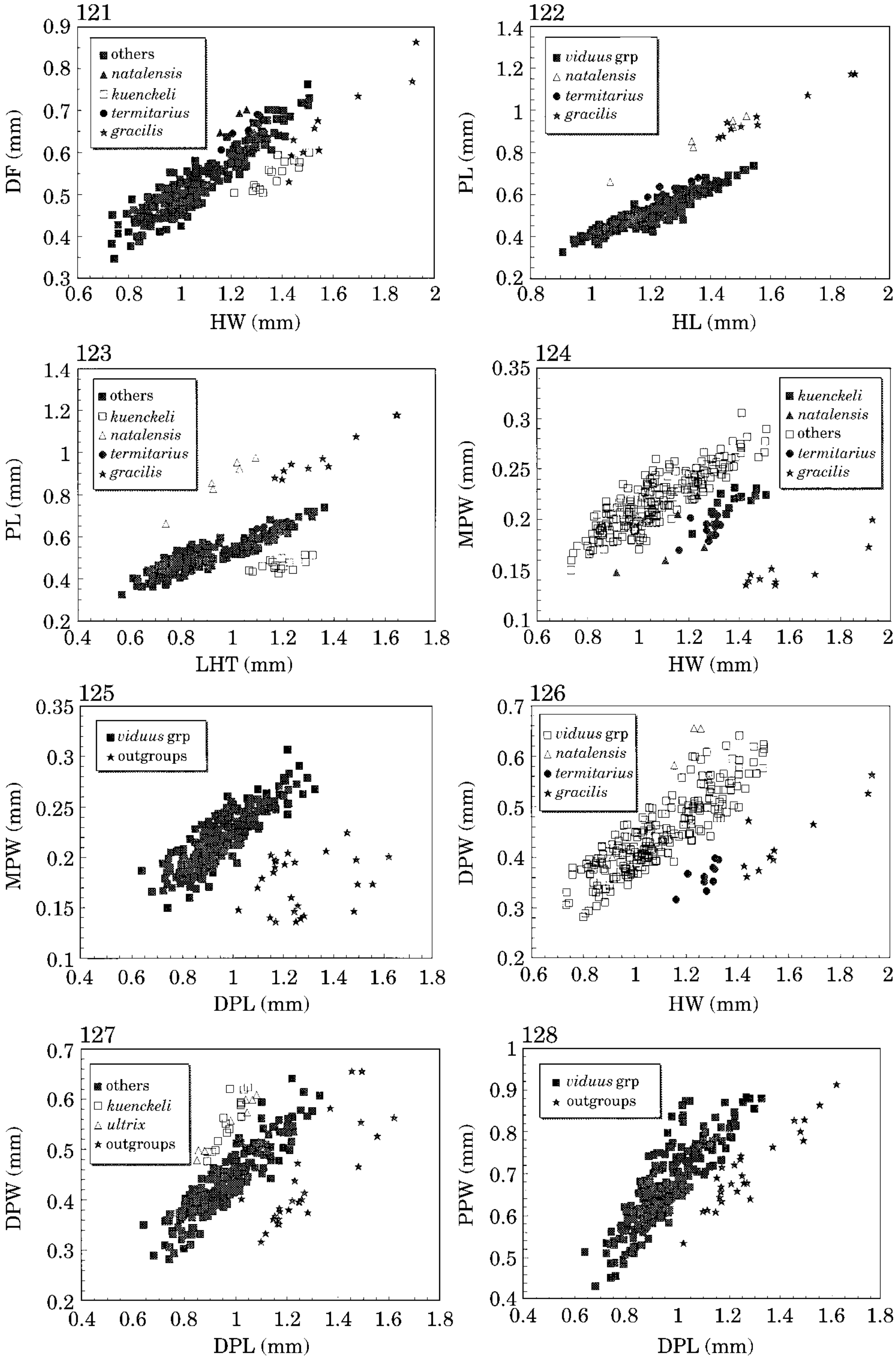
6′ Scape and funicular segments longer; worker FLI 1.36–2.24, queen FLI 1.48–2.22; see also Figs 108, 111; punctures on upper third of head moderately dense, uniformly dispersed, most punctures separated by one to several diameters; palp formula 6,4 or 5,3 (*Triplaris* inhabitants) 10



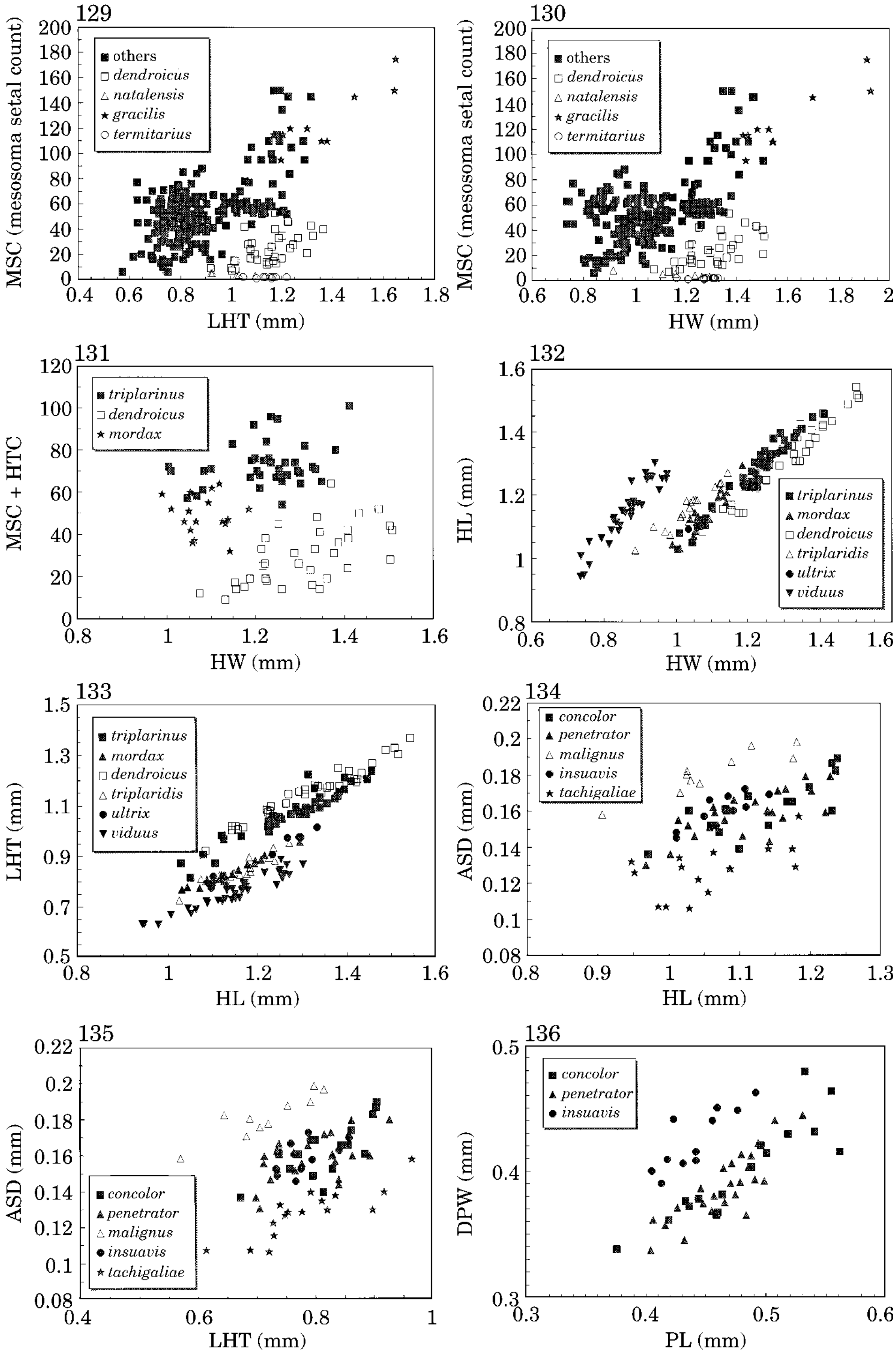
Figures 105–112. *Pseudomyrmex viduus* group plus outgroup taxa, workers. Bivariate plots of various metric measurements. The term 'others' refers to other species in the *P. viduus* group; the '*concolor* cmplx' comprises *P. concolor*, *P. insuavis*, *P. malignus* and *P. penetrator*. The outgroup taxa are *Tetraponera natalensis*, *Pseudomyrmex gracilis* and *P. termitarius* (see text).



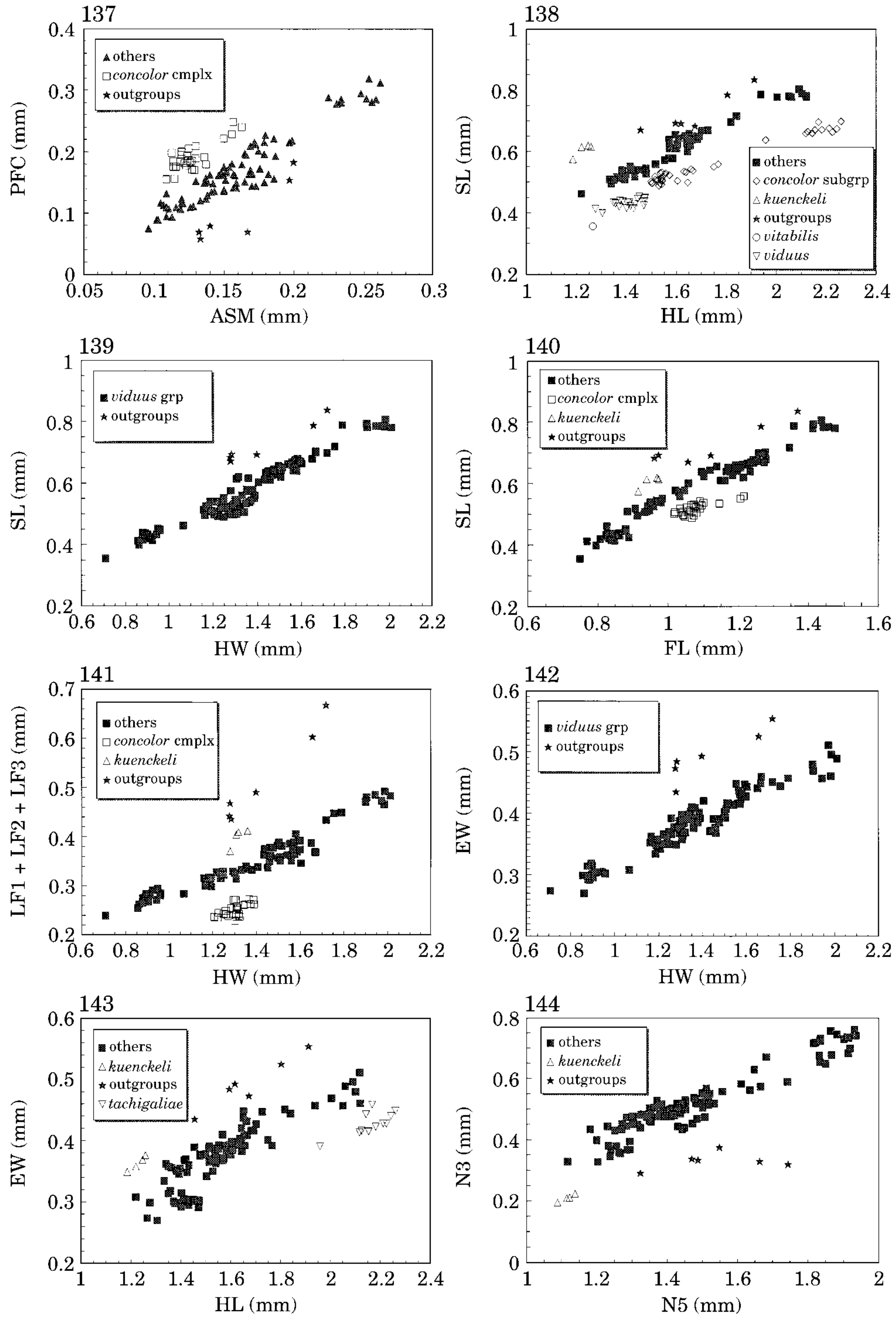
Figures 113–120. *Pseudomyrmex viduus* group plus outgroup taxa, workers. Bivariate plots of various metric measurements; 'dend' and 'tripn' refer to *P. dendroicus* and *P. triplarinus*, respectively.



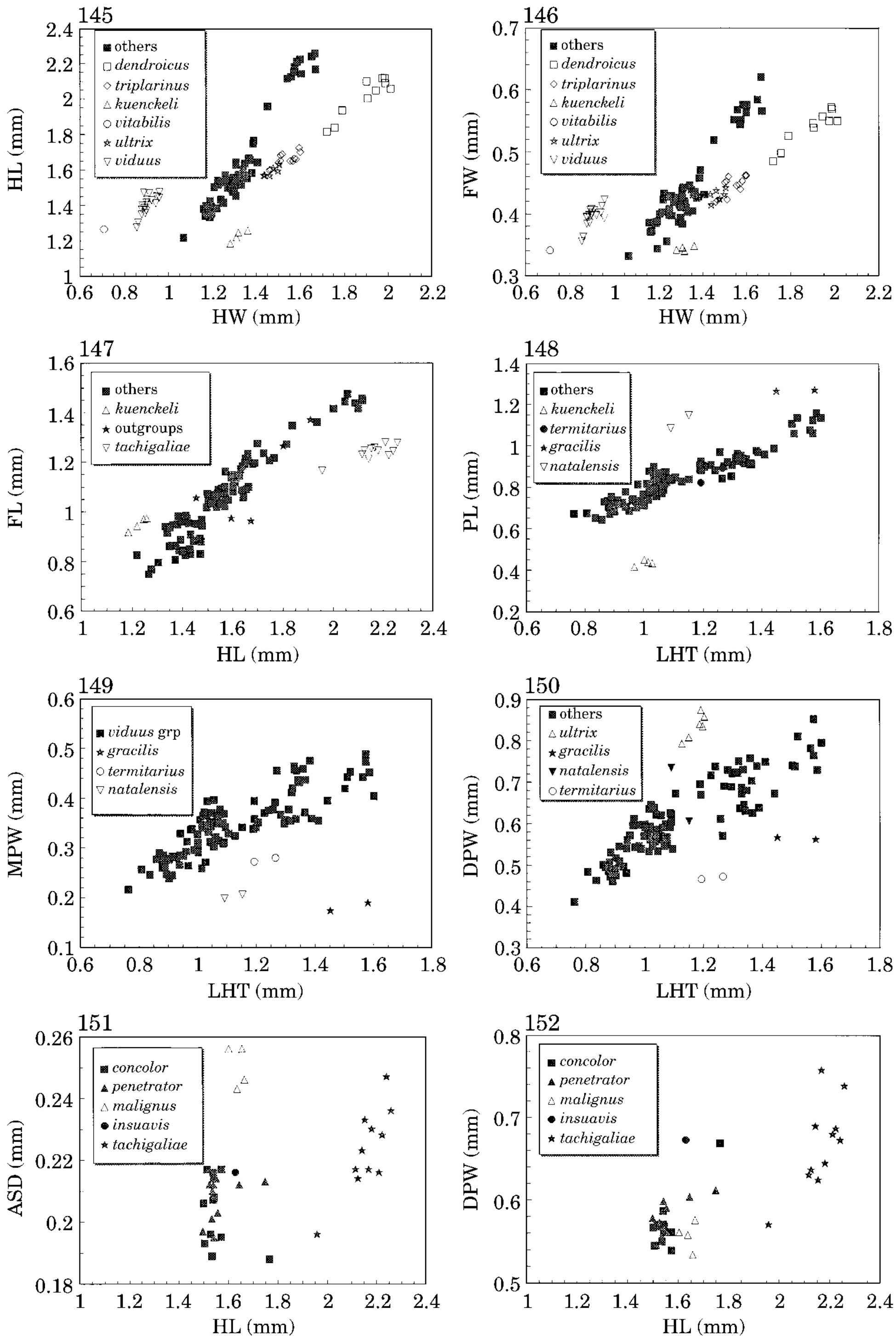
Figures 121–128. *Pseudomyrmex viduus* group plus outgroup taxa, workers. Bivariate plots of various metric measurements.



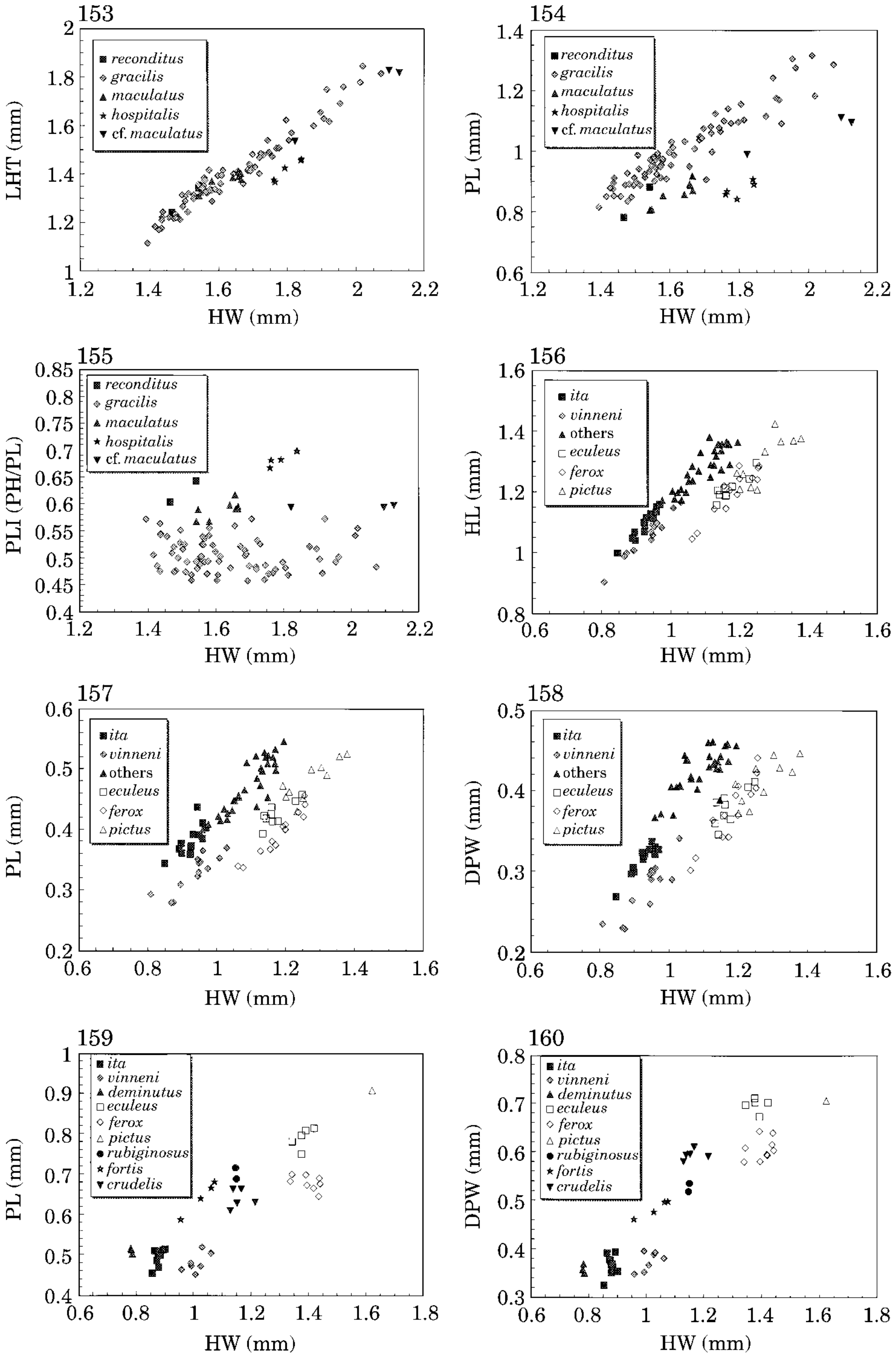
Figures 129–136. *Pseudomyrmex viduus* group plus outgroup taxa, workers. Bivariate plots of various metric measurements. Figs 131–133 and 134–136 are concerned only with the *P. triplarinus* subgroup and the *P. concolor* subgroup, respectively.



Figures 137–144. *Pseudomyrmex viduus* group plus outgroup taxa, queens. Bivariate plots of various metric measurements. The '*concolor* cmplx' comprises *P. concolor*, *P. insuavis*, *P. malignus* and *P. penetrator*; the '*concolor* subgrp' is the same plus *P. tachigaliae*.



Figures 145–152. *Pseudomyrmex viduus* group plus outgroup taxa, queens. Bivariate plots of various metric measurements. Figs 151 and 152 are concerned only with the *P. concolor* subgroup.



Figures 153–160. *Pseudomyrmex* workers (153–158) and queens (159, 160). Bivariate plots of various metric measurements. 153–155: *P. gracilis* group; 156–160: *P. sericeus* group. The term 'others' in Figs 156–158 refers to *P. crudelis*, *P. fortis* and *P. rubiginosus*.

7 Erect pilosity lacking on sides of head above eyes and on posterior margin of head (frontal view), and scarce on the external face of the metatibia (worker HTC 1–6); median clypeal lobe laterally angulate (Fig. 8); queen mandible with a marked basal incision on its outer face; Venezuela, Trinidad, Guianas, Brazil .... *malignus* (Wheeler)

7′ Erect pilosity present (usually common) on the sides and posterior margin of the head, and conspicuous on the external face of the metatibia (worker HTC 6–16); median clypeal lobe laterally rounded (Figs 9–11); queen mandible lacking a basal incision on its outer face 8

8 Petiolar node expanded posterolaterally (Fig. 32), such that worker PWI 0.92–1.04 and queen PWI ≈0.79; pubescence on worker abdominal tergite IV sometimes sparse, the tergite correspondingly lucid; Colombia, Ecuador(?) .... ***insuavis*, sp. nov.**

8′ Petiolar narrower (Figs 31, 33), worker PWI 0.74–0.90, queen PWI 0.63–0.73; pubescence on worker abdominal tergite IV usually rather dense 9

9 Worker and queen concolorous orange-brown; Colombia, Venezuela, Guyana, Brazil .... *concolor* (F. Smith)

9′ Worker and queen with gaster and (usually) most of mesosoma dark brown; remainder of mesosoma and head variable in colour, often a contrasting bright orange-brown; possibly conspecific with *P. concolor*, see discussion in text; Venezuela, Guyana, Surinam, Brazil .... *penetrator* (F. Smith)

10 Petiole very short and broad (Figs 17, 28); worker PLI 0.96–1.05; queen PLI 0.76–0.81; worker PWI 1.04–1.14, queen PWI 0.92–0.99; junction of basal and declivitous faces of worker propodeum marked by slight angular protuberance, laterally on either side (Fig. 17); standing pilosity conspicuous on the posterior margin and upper sides of the head (Fig. 6); uniform dark brown; Ecuador .... ***ultrix*, sp. nov.**

10′ Petiole longer and narrower (Figs 12–14, 16, 23–25, 27); worker PLI 0.70–0.94, queen PLI 0.61–0.74; worker PWI 0.72–0.98, queen PWI 0.63–0.86; junction of basal and declivitous faces of worker propodeum without angular protuberance (Figs 12–14, 16); head pilosity and color variable 11

11 Posterior margin and upper sides of head with conspicuous standing and decumbent pilosity (Fig. 5); dorsum of head with coarse, dense punctures, 0.010–0.020 mm in diameter, subcontiguous on anterior half of head and usually separated by about their diameters on upper half; subpetiolar process with a recurved tooth, directed posteroventrally (Fig. 16); smaller species, with more elongate head (worker HW 0.89–1.14, worker CI 0.85–0.93, queen HW 1.07–1.25, queen CI 0.83–0.89) (Figs 5, 132); palp formula 5,3; Colombia to Peru, Brazil .... *triplaridis* (Forel)

11′ Standing and decumbent pilosity lacking on sides of head and generally sparse or absent on the posterior margin (Figs 1–3); punctures on head usually finer, less dense, separated by one to several diameters on upper half of head; subpetiolar process variable but if furnished with a posteroventral tooth then worker HW >1.06, worker CI >0.93, queen HW >1.70, and queen CI >0.89; palp formula 6,4 12

12 Worker body light- to medium-brown, nearly always with a contrasting dark

brown head; standing pilosity less dense on mesosoma dorsum and tibiae (worker MSC 7–53, worker HTC 1–11), especially in relation to body size (see Fig. 131); subpetiolar process usually conspicuously recurved and directed posteroventrally (Fig. 12); queen large, HW >1.70; Colombia, Venezuela to Bolivia .... *dendroicus* (Forel)

12 Worker body varying in colour (light or dark) but head concolorous with or only slightly darker than mesosoma; standing pilosity denser on mesosoma dorsum and tibiae (worker MSC 25–84, worker HTC 5–21) in relation to body size (Fig. 131); subpetiolar process usually not conspicuously recurved and directed posteroventrally (Figs 13, 14); queen smaller (HW <1.62) 13

13 Legs short in relation to other measures of body size (worker LHT/HL 0.70–0.74, worker EL/LHT 0.57–0.60) (see also Fig. 133); smaller average size, worker HW 0.99–1.19, queen 1.20–1.41; Panama, Colombia, Venezuela .... *mordax* (Warming)

13′ Legs longer (worker LHT/HL 0.78–0.93, EL/LHT 0.48–0.55); larger species, worker HW 1.00–1.41, queen HW 1.46–1.60; Colombia to Peru, Bolivia and Brazil .... *triplarinus* (Weddell)

14 Standing pilosity abundant on body, including outer surfaces of the tibiae (worker MSC >90, worker and queen HTC >8) (Fig. 40); petiole much longer than high (worker PLI 0.46–0.70, queen PLI 0.48–0.71) and with a well differentiated anterior peduncle in lateral view (Figs 40, 41) 15

14′ Standing pilosity less common (worker MSC <40), and absent from the outer surfaces of the tibiae (worker and queen HTC = 0); petiole relatively shorter and higher (worker PLI 0.79–1.26, queen PLI 0.68–1.10) and without a distinctly differentiated anterior peduncle in lateral view (Figs 51–59) 16

15 Petiole relatively short and broad (Fig. 40) (worker PLI 0.67–0.70, queen PLI ≈ 0.70, worker PWI 0.55–0.59, queen PWI ≈ 0.59); standing pilosity on propodeum and petiole consisting of some thick, long, black setae intermingled with finer, pale-silvery hairs; Peru (*Tachigali* inhabitant) ..... ***hospitalis*, sp. nov.**

15′ Petiole more slender (Fig. 41) (worker PLI 0.46–0.57, queen PLI 0.48–0.57, worker PWI 0.38–0.54, queen PWI 0.42–0.56); standing pilosity on propodeum and petiole uniformly fine, pale-silvery; widespread and common throughout the Neotropics (generalist inhabitant of dead twigs and branches, recorded occasionally from *Triplaris*) .... *gracilis* (Fabricius)

16 Very small species, with elongate head (worker HW 0.56–0.68, queen HW 0.56–0.61, worker CI 0.66–0.79, queen CI 0.59–0.66); standing pilosity common on body dorsum (worker MSC >15); found throughout the Neotropics (generalist inhabitant of dead twigs, recorded occasionally from *Triplaris*) .... *elongatus* (Mayr)

16′ Larger species, with broader head (worker HW >0.70, queen HW >0.75, worker CI usually >0.80, queen CI >0.64); standing pilosity relatively uncommon on body dorsum (worker MSC 2–12) (*sericeus* group) 17

17 Worker head broad (CI 0.91–1.03), with strongly convex sides (Figs 42–44, 156); worker petiole short and subtriangular in lateral view (Figs 51–53); worker PL/(HW × LHT) 0.30–0.40; worker legs relatively long (LHT/HL 0.72–0.91); queen very large in size (queen HW 1.34–1.62) (*Tachigali* inhabitants) 18

17′ Worker head more elongate (CI 0.81–0.91), with less strongly convex sides (Figs 45–49, 156); worker petiole typically longer and often subtrapezoidal or subglobose in lateral view (Figs 54–58); worker PL/(HW × LHT) 0.44–0.64; worker legs shorter (LHT/HL 0.62–0.72); queen smaller in size (queen HW 0.78–1.22) 20

18 Legs shorter in relation to head length (worker LHT/HL 0.72–0.77, queen LHT/HL 0.63–0.71); worker profemur broader (worker FI 0.43–0.47); Colombia, Peru, Brazil .... ***ferox*, sp. nov.**

18′ Legs longer (worker LHT/HL 0.82–0.91, queen LHT/HL 0.73–0.76); worker profemur more slender (worker FI 0.36–0.42) 19

19 Body, including appendages, predominantly orange-brown in colour, although parts (especially the mesosoma and petiole) may have darker infuscated patches; dorsal face of worker propodeum convex in profile, with the propodeal spiracle located some distance from it (Fig. 53); larger in size (worker HW 1.19–1.38, queen HW ≈1.62); Colombia, Peru, Brazil, Bolivia .... *pictus* (Stitz)

19′ Body uniformly dark brown to black, with all or parts of the appendages a contrastingly light orange-brown; dorsal face of worker propodeum flattened, submarginate laterally; in profile, propodeal spiracle located just below the level of the dorsal face of propodeum (Fig. 51); smaller in size (worker HW 1.13–1.25, queen HW 1.34–1.42); Ecuador, Peru .... ***eculeus*, sp. nov.**

20 Small (worker HW 0.81–1.03, queen HW 0.78–1.06) with disproportionately short and narrow petiole (worker PL 0.28–0.44, queen PL 0.45–0.52, worker DPW 0.23–0.34, queen DPW 0.32–0.40, worker DPW/HW 0.26–0.35) (see also Figs 66–68, 157–160); worker eye relatively elongate (worker REL 0.63–0.68) 21

20′ Averaging larger in size (worker HW 0.96–1.19, queen HW 0.96–1.22), with longer and broader petiole (worker PL 0.40–0.55, queen PL 0.59–0.72, worker DPW 0.37–0.46, queen DPW 0.46–0.61, worker DPW/HW 0.34–0.42) (Figs 63–65, 157–160); worker eye shorter (worker REL 0.57–0.62) 23

21 Smaller in size, with very elongate head; queen HW ≈0.78, queen CI 0.65–0.66 (Fig. 50); worker unknown but by extrapolation expected to have HW <0.85 and CI <0.80; Brazil (known from only one collection, from *Tachigali*) .... ***deminutus*, sp. nov.**

21′ Larger (worker HW 0.81–1.03, queen HW 0.85–1.06) with broader head (worker CI 0.83–0.91, queen CI 0.73–0.81) 22

22 Head broader (worker CI 0.87–0.91, queen CI 0.77–0.81, queen HW 0.96–1.06); petiole shorter (worker PL/LHT 0.44–0.50), subtriangular or subglobose in lateral view, with a convex anterodorsal face that rounds gently into the posterior face (Fig. 58); Colombia, Venezuela, Peru, Brazil (*Tachigali* inhabitant) .... *vinneni* (Forel)

22′ Head more elongate (worker CI 0.83–0.86, queen CI 0.73–0.77, queen HW 0.85–0.90); petiole longer (worker PL/LHT 0.51–0.61), subtrapezoidal in profile, with differentiated anterior and dorsal faces, the latter meeting the vertical face at a sharply rounded angle (Fig. 57); Mexico to Colombia (generalist inhabitant of dead twigs, occasional in *Triplaris*) .... *ita* (Forel)

23 Worker bicoloured, with head mostly dark grey-brown, gaster medium-brown,

and remainder of body including legs dusky yellow-or orange-brown, with variable amounts of infuscation on the mesosoma dorsum; queen darker overall, but with contrastingly lighter propleuron and protibia; head relatively broad (worker CI 0.84–0.91, queen CI $\approx$0.78); petiole relatively long (worker PLI 0.86–1.02, queen PLI $\approx$0.80); Colombia, Brazil, Peru (recorded as an inhabitant of *Gustavia, Ocotea, Pleurothyrium, Tachigali* and *Triplaris*) .... *rubiginosus* (Stitz)

23′ Most of body, including legs (except sometimes protibia), uniformly dark grey-brown or blackish-brown to black; *either* head tending to be more elongate (worker CI 0.81–0.86, queen CI 0.72–0.73, in *P. fortis*) *or* petiole shorter (worker PLI 1.01–1.13, queen PLI 0.91–1.01, in *P. crudelis*) 24

24 Petiole somewhat angular in lateral profile, with more or less differentiated anterior and dorsal faces (Fig. 54); worker profemur relatively slender (FI 0.43–0.47); queen large (HW 1.13–1.22), with broad petiole (DPW 0.58–0.61, PWI 0.90–0.95) and long eyes (REL 0.60–0.63); Peru (*Tachigali* inhabitant). ... . ***crudelis*, sp. nov.**

24′ Petiole rounded in profile, with a single convex anterodorsal face (Fig. 55); worker profemur broad (FI 0.48–0.50); queen smaller (HW 0.96–1.07), with more slender petiole (DPW 0.46–0.50, PWI 0.73–0.79) and relatively short eyes (REL 0.53–0.56); Mexico to Colombia, Venezuela (recorded from *Triplaris* but not restricted to this plant) .... *fortis* (Forel)

Key to males of the Pseudomyrmex viduus *group*

Males of most species in the *P. viduus* group have diagnostic genitalia. The following key may be used to confirm the identity of nest series from which males have been collected, but it will be necessary to extract and dissect the male terminalia for better viewing of some characters. Limited use is made of metric measurements and indices, and sample sizes ($n = \ldots$) are indicated when they are cited. Males of *P. insuavis* and *P. vitabilis* are unknown but I have indicated where they are likely to key out.

1 Posterior margin of paramere broadly rounded, as seen in lateral view (Fig. 81); aedeagus of distinctive form, with two large teeth on the posterior margin (Fig. 104); petiole short and broad, PLI 0.88–1.04, PWI 0.87–1.10 ($n = 4$) ..... *kuenckeli*

1′ Posterior margin of paramere somewhat truncated, as seen in lateral view (Figs 69–74, 82–84); aedeagus without a pair of large teeth on posterior margin; petiole longer and narrower, PLI 0.51–0.85, PWI 0.45–0.79 ($n = 49$) 2

2 Posterodorsal extremity of paramere, as seen in lateral view, angular (Figs 82–84); posteromesial concavity of paramere directed ventromesially (Figs 86–88); posterior margin of aedeagus with a conspicuous row of teeth (Figs 101–103) 3

2′ Posterodorsal extremity of paramere, as seen in lateral view, rounded (Figs 69–74); posteromesial concavity of paramere directed dorsomesially (Figs 75–80); posterior margin of aedeagus entire or with at most a single posteroventral tooth (Figs 95–100) 5

3 Pygidium with a marked posteromedial spine; posterior margin of hypopygium (sternite IX) with a very shallow concavity (Fig. 92); posterodorsal surface of

paramere simple in form, lacking a prominent, transverse impression (Fig. 82); head slightly longer than broad, CI 0.93–0.98 ($n=6$) .... *tachigaliae*

3′ Pygidium without a posteromedial spine; posterior margin of hypopygium (sternite IX) with a deep semicircular concavity (Figs 93, 94); posterodorsal surface of paramere with a prominent, transverse, cylindrical impression (Fig. 83, 84); head broader than long, CI 1.07–1.13 ($n=12$) 4

4 Paramere as in Figs 83 and 87, its posterodorsal extremity extended mesially; aedeagus as in Fig. 101, the teeth on the posterior margin coarser and fewer in number .... *malignus* (Wheeler)

4′ Paramere as in Figures 84 and 88, its posterodorsal extremity not extended mesially; aedeagus as in Figure 102, the teeth on the posterior margin smaller and more numerous ... *concolor, penetrator* (*insuavis* also expected to key out here)

5 Posteromesial concavity of paramere with an almost continuously lamellate margin (Figs 69–72, 75–78); mesial dorsoventral lobe without a strong, acute, subtriangular mesial protrusion; posteroventral tooth on posterior margin of aedeagus weak or absent (Figs 95–98); eyes smaller, REL2 0.45–0.52, SI2 0.50–0.60 ($n=23$) 6

5′ Posteromesial concavity of paramere carinate, not lamellate; mesial dorsoventral lobe with a strong, acute, subtriangular mesial protrusion (Figs 79, 80); posteroventral tooth on posterior margin of aedeagus well developed (Figs 99, 100); eyes tending to be larger, REL2 0.52–0.61, S12 0.40–0.50 ($n=10$) 9

6 Posteromesial concavity of paramere emarginate dorsally and ventrally (Fig. 71); posterior margin of aedeagus lacking posteroventral tooth (Fig. 97); smaller species, HW 0.98–1.05 ($n=5$) .... *mordax*

6′ Posteromesial concavity of paramere not emarginate dorsally and ventrally (Figs 69, 70, 72); posterior margin of aedeagus with small posteroventral tooth (Figs 95, 96, 98); larger species, HW 1.06–1.33 ($n=16$) 7

7 Posteromesial concavity of paramere subcircular in outline (Fig. 72); pygostyles relatively short and stubby, about 2–2.5 times as long as broad; legs and petiole relatively short, LHT/HW 0.82–0.86, PLI 0.77–0.85 ($n=3$) .... ***ultrix*, sp. nov.**

7′ Posteromesial concavity of paramere elongate in outline (Fig. 69, 70); pygostyles long and slender, about 5 times as long as their maximum width; legs and petiole longer, LHT/HW 0.96–1.15, PLI 0.57–0.74 ($n=13$) 8

8 Standing pilosity more common and consipicuous on body and appendages; petiolar dorsum, viewed in profile, with about 10–22 long, erect hairs; petiole shorter and broader, on average, PLI 0.62–0.74 ($n=8$) .... *triplarinus*

8′ Standing pilosity less abundant; petiolar dorsum with about 5–10 long, erect hairs; petiole longer and narrower, PLI 0.57–0.64 ($n=5$) .... *dendroicus*

9 Summit of mesial dorsoventral lobe, as seen in lateral view, slightly more protruding (Fig. 73); head broader, petiole broader and higher (CI 1.01–1.06, PLI 0.64–0.65, PWI 0.61–0.62; $n=2$) .... *triplaridis*

9′ Summit of mesial dorsoventral lobe, as seen in lateral view, slightly less protruding (Fig. 74); head and petiole more elongate (CI 0.85–0.93, PLI 0.51–0.61, PWI 0.45–0.54; $n=8$) .... *viduus*
(vitabilis also expected to key out here, but with even more elongate head)

Species accounts

Pseudomyrmex concolor (F. Smith)
(*Figs 9, 20, 31, 84, 88, 94, 102*)

Pseudomyrma concolor F. Smith, 1860:70. Holotype (unique syntype) dealate queen, "St. Paul" [São Paulo de Olivença], Amazonas, Brazil (BMNH) [Examined].

Pseudomyrma latinoda Mayr, 1878:877. Holotype worker, "Amaz." [Barreiras de Unahan, Rio Purus; see Benson & Setz, 1985:590], Amazonas, Brazil (Trail) (NHMV) [Examined] [Synonymy by Ward, 1989:435].

Pseudomyrma latinoda var. *endophyta* Forel, 1912:22. Syntype workers, Rio Ariramba, [near] Rio Trombetas (Ducke) (MHNG, NHMB) [Examined]. **Syn. nov**.

Pseudomyrma damnosa Wheeler, 1921b:139. Syntype workers, queens, males, Kartabo, Guyana (W. M. Wheeler) and Penal Settlement, Guyana (W. M. Wheeler) (MCZC, USNM) [Synonymy, under *P. latinodus* (Mayr), by Kempf, 1961:406]. One syntype worker in MCZC from Kartabo here designated *Lectotype*.

Pseudomyrmex concolor (F. Smith); Kempf, 1961:400 [First explicit combination in *Pseudomyrmex*].

Pseudomyrmex latinodus (Mayr); Kempf, 1961:406 [Description of holotype worker of *P. latinodus*].

Pseudomyrmex concolor (F. Smith); Ward, 1989:435 [Brief diagnosis].

Worker measurements. ($n = 16$). HL 0.97–1.24, HW 0.86–1.11, MFC 0.107–0.149, LHT 0.67–0.91, CI 0.86–0.95, REL 0.35–0.39, REL2 0.39–0.45, FCI 0.10–0.14, SI 0.40–0.43, FLI 1.04–1.41, FI 0.38–0.44, PLI 0.80–1.00, PWI 0.74–0.90, PPWI 1.35–1.65.

Worker description. Relatively small species (HW <1.12, LHT <0.92). Basal margin of mandible with small mesial tooth (often worn), closer to the apicobasal tooth than to the proximal tooth (MD4/MD5 approximately 0.65–0.75); masticatory margin of mandible with five teeth, the fourth tooth (counting from the apex) often very weak and abraded. Palp formula 4,3. Median clypeal lobe laterally rounded (not angulate), its anteromedial surface deflected ventrally (Fig. 9). Frontal carinae merging anteriorly with the antennal sclerites, well separated at this point (by more than basal scape width), diverging even further posteriorly so that PFC/ASM >1.10, and sometimes converging slightly again before becoming obsolete (Fig. 9). Median lobe of antennal sclerite not conspicuously exposed, partly due to the aforementioned lateral expansion of the frontal carinae (PFC/ASD 0.73–0.88; FCI2 0.66–0.83). Scape relatively short (SI <0.44), expanded distally to about twice its basal width; funiculus short, also expanded apically, the terminal segment about 1.7–1.9 times the width of the first segment; funicular segments 3–10 conspicuously broader than long (FLI <1.42). Eye small (REL <0.40, REL2 <0.46), only moderately elongate (OI 0.59–0.66). Head a little longer than broad (CI >0.85), the sides weakly convex, rounding relatively abruptly into the posterior margin, which is flat or very slightly concave, in frontal view. Mesosoma dorsum more or less flattened, but with a deeply incised metanotal groove (MP 0.035–0.063, MPI 0.041–0.062). Dorsal face of propodeum flat to somewhat convex; dorsal and declivitous faces of propodeum subequal in length (PDI 0.91–1.07), and meeting at a well rounded angle. Metapleural gland bulla well-developed and conspicuous. Petiole as in Fig. 20, slightly longer than high (PLI ≤ 1.00), without a differentiated anterior peduncle in lateral profile;

flat anterior face of petiole rising to a summit well behind the midpoint of the petiole (NI 0.60–0.69), then rounding into the steep posterior face. Anteroventral petiolar process well developed (Fig. 20), either rounded or with a blunt posteroventral angle. In dorsal view, the minimum (anterior) width of petiole more than half the maximum width (PWI3 0.51–0.59), and the straight sides of the petiole diverging only moderately (Fig. 20). Postpetiole globular, notably broader than long (PPWI >1.34); postpetiolar sternite protruding ventrally; anterior to this a forward-directed anteroventral process is present. Mandible with scattered punctulae on a smooth background, overlain by variable amounts of fine striolation which dulls the reflectance. Dorsum of head mostly smooth and shiny (a weakly coriarious background is developed on the lower half in some workers), with a variable density of punctulae (about 0.010–0.015 mm in diameter); such punctulae usually separated by less than their diameters on lower portion of head between compound eyes and antennal insertions, and by one to several diameters between the compound eyes, except for a median strip in which the punctulae are less dense and are accompanied by a few scattered coarser punctures. Punctulae becoming sparser towards the vertex, especially above the compound eyes where they are largely replaced by a few scattered, larger, piligerous punctures; area immediately above eyes shiny and unsculptured. Mesosoma dorsum with numerous punctulae (separated by one to several diameters) on a smooth, shiny background; side of mesosoma with punctulae less well defined and with a tendency toward the development of weak corarious-imbricate sculpture, with a corresponding dulling of the integument, especially on the propodeum laterally. Dorsum of petiole and postpetiole largely smooth and shining, with scattered fine punctulae. Abdominal tergite IV sublucid, the reflectance subdued by fine punctulae and associated appressed pubescence. Standing pilosity common and conspicuous on most of body (MSC 26–47, HTC 6–12); at least six, and usually many more, erect setae visible in outline on either side of the head in frontal view (Fig. 9). Appressed pubescence also well developed on most of body; appressed hairs short and inconspicuous on the head, longer and denser elsewhere, forming a moderately dense mat (hairs separated by less than their lengths) on mesosoma dorsum and on abdominal tergites IV and V; pubescence less dense on dorsomedial portions of the petiole and postpetiole where the appressed hairs are separated by more than their lengths. Body uniformly light yellow-brown to orange-brown in colour. Ocellar triangle and femora sometimes lightly infuscated.

Comments. The worker and queen of this species can be distinguished from all other members of the *P. viduus* group, except *P. insuavis*, *P. malignus* and *P. penetrator*, by the short, broad funicular segments (worker FLI <1.42, queen FLI <1.51, and regression of (LF1 + LF2 + LF3) on HW lying below that of other species: see Figs 111, 141), posterolaterally expanded frontal carinae (see Fig. 9), and palp formula of 4, 3. *P. concolor* differs from *P. malignus* by the presence of several to (usually) many erect hairs on the sides of the head, by the ventrally deflected and laterally rounded median clypeal lobe, by the narrower petiole (worker PW12 0.58–0.66 versus 0.65–0.69 in *P. malignus*), and usually by the occurrence of more conspicuously striolate sculpture on the worker mandible (this last character varies). Workers of *P. concolor* from Amapá, northeastern Brazil tend to have the pilosity on the sides of the head reduced, but the striolate mandibular sculpture is very well developed and in sharp contrast to the smooth mandibles of *P. malignus*. *P. concolor* is very close to *P. insuavis* and *P. penetrator*, differing from the former species by its narrower petiole (worker PWI 0.74–0.90, versus 0.92–1.04 in *P. insuavis*; see also Fig. 136) and from the latter by its lighter orange colour (see discussion under *P. penetrator*).

There is considerable variation in sculpture and pilosity among different populations of *P. concolor*. Workers from northeastern Brazil (Amapá) are perhaps the most distinctly differentiated; they tend to have a shinier integument, reduced head pilosity on the sides of the head, and less dense pubescence on abdominal tergite IV.

Distribution and biology. This species is widely distributed in the central and eastern Amazon basin and adjacent Guianas (Fig. 168), and invariably associated with plants in the genus *Tachigali*. Wheeler (1921a, 1942) discussed the habits of *P. concolor* at Kartabo, Guyana (under the name *Pseudomyrma damnosa*). He described the colonization of *Tachigali paniculata* Aublet saplings by colony-founding queens of *P. concolor*, as well as those of *P. malignus* and *Azteca* species; reported their association with pseudococcids (*Dysmicoccus brevipes* (Cockerell) and *Trionymus petiolicola* (Morrison)); noted the eventual domination of larger trees by single—but polygynous—colonies; and presented a fascinating set of observations on the larger guild of *Tachigali*-associated insects at Kartabo. Studies by Fonseca (1993, 1994; Fonseca & Benson, 1995; Fonseca & Ganade, 1996) near Manaus, Brazil have revealed additional details about the biology of *P. concolor*. In the population near Manaus colonies occupy smaller trees (up to 7 m height) of *Tachigali myrmecophila* (Ducke) Ducke and *T. poeppigiana* Tulasne (cited as *T. polyphylla*), in whose domatia the ants tend pseudococcids of the genus *Cataenococcus*. Although the ants patrol the leaf surfaces of the host plant and aggressively remove herbivores, most of the colony's food appears to be derived from the coccoids. This is consistent with an earlier report from Guyana of coccoid remains in larval food pellets (Bailey, 1923:37). In a sample of 16 colonies Fonseca (1993) found colony sizes ranging from 22 to 1104 workers (1 to 8 dealate queens), and he provided evidence that colony size is strongly constrained by the amount of nesting space available in the host plant. Other host plant records from museum specimens include *Tachigali paniculata* (Rio Yatua, Venezuela) and numerous *Tachigali* unidentified to species.

Material examined. (BMNH, CPDC, INPA, KWJC, MCZC, MHNG, MPEG, MZSP, NHMB, NHMV, PSWC, UCDC, WWBC). BRAZIL AM: AM 010, km. 26 (F. B. Apolinário); Campo Florestal [Faz. Esteio] (W. W. Benson); Campo Florestal, Res.1301 [Faz. Esteio] (W. W. Benson); E.E.S.T., km.44, BR-174, [near] Manaus (W. W. Benson); E.E.S.T., km.45, BR-174, [near] Manaus (W. W. Benson & A. Y. Harada); Faz. Dimona, 80 km N Manaus (D. W. Davidson); Faz. Esteio, 80 km NNE Manaus, 80 m (P. S. Ward); Faz. Esteio, km.24, ZF-3 (A. Y. Harada); Manaus (C. R. Gonçalves); Res. 1301, [near] Manaus [Faz. Esteio] (A. B. Casimiro; A. Batista; H. G. Fowler; K. Carvalho); Res. Campina, km.45, BR-174, [near] Manaus (W. W. Benson); Reserva Ducke (J. A. Rafael); São Paulo de Olivença ["St. Paul"] (Bates); [Barreiras de Unahan, Rio Purus] (Trail); km.24, ZF-3 [Faz. Esteio] (W. W. Benson); km.41 Reserve, north of Manaus (C. R. Fonseca); AP: Curiau (c.u.); Serra Lombard, Limão (J. Bechyne & B. Bechyne); Serra do Navio (K. Lenko; P. Tadeu); PA: Belém, Reserva Guamá ("APEG n. 362"; "APEG n. 814"); ESPAM, Medicilândia (A. J. S. Argolo); Monte Dourado (R. B. Neto); Oriximiná, Rio Trombetas, ALCOA Miner., Mte Branco (A. Y. Harada); Rio Curuá, 60 km E Santarém (R. L. Jeanne); S. Cipó Pitanga, Baixo Rio Xingú (B. Mascarenhas);

Tucuruí (M. Alvarenga); Tucuruí, Ilha Chorona (Nunes de Mello); Tucuruí, Puraquequara (Nunes de Mello); [Rio] Ariramba (at Rio Trombetas) (Ducke). COLOMBIA Amazonas: PNN Amacayu, Rio Cotuhé, Caño Lorena (F. Fernández); Vaupes: Rio Apaporis, Serrania Taraira, ca. Estación Primatológica de Caparú, 150 m (M. Ospina). GUYANA Cuyuni-Mazaruni: Forest Settlement, R. Mazaruni (N. Weber); High Forest (Richards & Smart); Jct. of Mazaruni & Cuyuni Rivers (E. H. Graham); Kartabo (W. M. Wheeler); Penal Settlement (W. M. Wheeler); Upper Demerara-Berbice: Essequibo R., Moraballi Cr. (Oxford Univ. Exped.); Rockstone-Bartica, 0–50 m (J. Longino). VENEZUELA Amazonas: Patanogiteri [= Patanowateri] (H. Herzog); Platanal (H. Herzog); Rio Yatua, 100–140 m (B. Maguire *et al.*).

Pseudomyrmex dendroicus (Forel)
(*Figs 1, 12, 23, 69, 75, 95*)

Pseudomyrma dendroica Forel 1904a:40. Lectotype worker, Rio Purus, Brazil (A. Göldi) (MHNG) [Examined] [Lectotype designation by Ward, 1989:436].
Pseudomyrma dendroica var. *emarginata* Forel, 1904c:684. Syntype workers, queen, Mavany Jurua, Amazonas, Brazil (Ule) (MCSN, MHNG) [Examined] [Synonymy by Ward, 1989:436].
Pseudomyrmex dendroicus (Forel); Kempf, 1961:400 [First explicit combination in *Pseudomyrmex*; treated as junior synonym of *P. triplarinus* (Weddell)].
Pseudomyrmex dendroicus (Forel); Ward, 1989:436 [Removed from synonymy, briefly diagnosed].

Worker measurements (*n* = 34). HL 1.09–1.55, HW 1.07–1.51, MFC 0.126–0.196, LHT 0.92–1.36, CI 0.94–1.04, REL 0.40–0.46, REL2 0.41–0.45, FCI 0.11–0.14, SI 0.42–0.48, FLI 1.74–2.24, FI 0.35–0.40, PLI 0.70–0.85, PWI 0.72–0.86, PPWI 1.29–1.76.

Worker description. Similar to *P. triplarinus* (q.v.) except as follows. Posterior margin of head more markedly concave (frontal view). Frontal carinae better separated, on average. Scape tending to be longer in relation to HL. Petiole less expanded posterolaterally. Subpetiolar process generally subrectangular or fin-shaped, and pointing posteroventrally (Fig. 12). Punctulate sculpture slightly denser on upper third of head, on average. Standing pilosity longer but less common, MSC 7–53, HTC 1–11 (Fig. 131), absent from the posterior margin of the head; erect hairs on the petiole and postpetiole tending to be more notably curved. Head (except for mandibles, scapes and frontoclypeal complex) brown to dark brown and nearly always contrasting with the lighter-coloured mesosoma.

Comments. Workers and queens of *P. dendroicus* and *P. triplarinus* can be separated from all other *Triplaris*-inhabiting *Pseudomyrmex* by the longer legs (Fig. 133) and tendency towards a broader head (Figs 132, 145). *P. dendroicus* can be distinguished from *P. triplarinus* by the worker characters mentioned above and in the key. Queens of the two species are more distinct, those of *P. dendroicus* being absolutely larger (queen HW 1.72–2.01 and queen HL 1.82–2.12 compared with HW 1.46–1.60 and HL 1.60–1.73 in *P. triplarinus*) and having the mandible more modified (with a strong basal incision, and more marked deformation of the upper surface of the mandible).

Distribution and biology. Widely distributed in the western Amazon basin (Fig. 166), *P. dendroicus* is a strict *Triplaris* associate that co-occurs with *P. triplarinus* and *P. triplaridis* at some localities. The workers prune vegetation around the host tree, leaving a cleared area at the base of the tree (Ule, 1906b). Davidson *et al.* (1988) present experimental evidence that this behaviour reduces the invasion success of dominant (and generalist, non-mutualistic) neighbouring ants such as *Crematogaster*. Additional information on the biology of *P. dendroicus* is contained in papers by Ule (1906b, 1907), Wheeler (1942), Schremmer (1984) and Davidson *et al.* (1988, 1989). Schremmer's investigations of *P. "triplarinus"* from Villavicencio, Colombia refer to *P. dendroicus*, while his observations of *P. "triplarinus"* from Sincé, Colombia represent another species, *P. mordax*. Most museum specimens of *P. dendroicus* are labeled as coming from "*Triplaris*" (unidentified to species) but some collections are associated specifically with *Triplaris americana* Linnaeus, including those of Brandbyge, Davidson, Toft, Ule and Ward (part).

Material examined (AMNH, BMNH, CASC, FFIC, IMLA, IZAV, LACM, MCSN, MCZC, MHNG, MNHN, MPEG, MZSP, NHMB, NHMV, PSWC, UASC, UCDC, UNCB, USNM, WPMC, WWBC). BOLIVIA Beni: Est. Biol. Beni, 42 km E San Borja, 210 m (P. S. Ward); Reyes (W. M. Mann); Rio Negro (W. M. Mann); Rurrenabaque (W. M. Mann); Tumichucua (Riberalta) (P. Bettella); La Paz: Blancaflor (W. M. Mann); Santa Cruz: Aserradero Moira, 180 m (P. S. Ward); Guarayos [as "Guaruyos"] (Lizer); Perseverancia (P. Bettella). BRAZIL ac: Cruzeiro do Sul (A. C. Filho & B. C. Lopes; A. S. Filho & B. C. Lopes); Porto Valter (P. L. Herbst); Sena Maduriera, 4 km from rt. marg. Rio Iaco (C. A. Cid & B. W. Nelson); am: Antimary, Rio Acre [= Floriano Peixoto] (A. Göldi); Esperanza [= Esperança] (R. C. Shannon); Marary [as "Mavany"], Jurua (Ule); Rio Purus [prob. Bom Lugar] (A. Göldi); Rio Purus, Bom Lugar (A. Göldi); Seringal Belo Monte [as "Seringal Bela Monte", Acre] (E. L. A. Monteiro); pa: Belém [as "Pará"] (c.u., prob. A. Göldi). COLOMBIA Antioquia: Mpio. Cocorná, La Veta, 980 m (F. Fernández); Boyacá: Pajarito, "Comijaque" (J. Clavijo); San Luis de Gácena, ver. La Unión, 1000 m (R. Ospina); Cundinamarca: Medina, 1500 m (F. Fernández); Medina, 1700–1800 m (F. Fernández); Medina, Meseta del Cura, 1400 m (F. Fernández); Meta: Caño Grande, 450 m (L. Richter); El Buque, nr. Villavicencio (F. Schremmer); Las Salinas, nr. Restrepo (W. W. Lamar); Mpio. Mesetas, Puerto Gabriel (bajo Güejar) (F. Fernández); Mpio. Mesetas, Vereda San Isidro (W. Cubillos); RNN La Macarena, 500–650 m (L. Richter); RNN La Macarena, 500 m (L. Richter); RNN La Macarena, Caño Cristales (C. Kugler); RNN La Macarena, Caño La Cabra (F. Fernández); RNN La Macarena, Vistahermosa, 400 m (F. Fernández); Rio Guayuriba, 500–700 m (L. Richter); S. Villavicencio, Caño El Buque, 480 m (C. Kugler); Villavicencio (F. Schremmer). ECUADOR Morona Santiago: Miazal, 50 km SE Macas, 300 m (M. & J. Wasbauer); Napo: Jatun Sacha, 7 km ESE Pto. Misahuallí, 400 m (P. S. Ward); San Pablo de las Secoyas, 300 m (J. Brandbyge). PERU Cuzco: Callanga (c.u.); Santa Ana (Rio Urubamba), 1100 m (Weyrauch); Santa Ana (Rio Urubamba), 1100 m (Weyrauch); Huánuco: Monson Valley, Tingo Maria (E. I. Schlinger & E. S. Ross); Pachitea (Staudinger); Tingo Maria, 2200 ft. (J. C. Pallister); nr. confl. Rio Pachitea & Rio Llullapichis (N. L. & C. A. Toft); Madre de Dios: 15 km NE Pto. Maldonado (S. P. Cover & J. E. Tobin); 20 km NW Manu, 400 m (P. J. Stern); 30 km SW Pto. Maldonado, 290 m (W. J. Pulawski; D. W. Davidson); Colpa Quebrada, nr. Cocha Cashu (D. W. Davidson); Cuzco Amazonico, 15 km NE Pto.

Maldonado, 200 m (B. L. Fisher); Est. Biol. Cocha Cashu, 400 m (D. W. Davidson; P. Sherman); Machiguenga Colpa Biol. Stn., P.N. Manu (J. Gilardi); Pakitza, Rio Manu, 250 m (Erwin & Farrell); San Martín: La Perla, 21 km NNE Tarapoto, 220 m (P. S. Ward); Rioja (M. Cooper); Ucayali: Middle Rio Ucayali (H. Bassler); Pucallpa (J. M. Schunke; E. I. Schlinger & E. S. Ross). PERU [?] "Tarijacu"[?] (c.u.). VENEZUELA Apure: Bois de Guasdualito (M. Grisol); *Barinas*: 8 km WNW Santa Barbara, 250 m (P. S. Ward); Portuguesa: 3 km NNE Biscucuy, 580 m (P. S. Ward); Qda. La Guata, via Biscucuy Guanare, 600 m (J. E. Lattke); Trujillo: 19 km E Boconó, 600 m (P. S. Ward). VENEZUELA [?] "SE" (Anduze).

Note. The record of this species from Belém ("Pará") appears to represent an introduction which occurred when André Goeldi brought back ant-inhabited *Triplaris* from the Rio Purus and planted them in the botanical garden at Belém (see Forel, 1904a:41). I have seen no recent collections of *P. dendroicus* from anywhere in eastern Amazonia, and consequently this record is excluded from the distribution map (Fig. 166).

***Pseudomyrmex insuavis*, sp. nov**

(*Figs 10, 21, 32, 136, 152*)

Holotype worker. COLOMBIA, Amazonas: Araracuara [0°38′S, 72°15′W] .iv. 1994, G. Gangi#223, ex *Tachigali* cf. *poeppigiana* (UNCB). HW 1.00, HL 1.08, EL 0.39, LHT 0.79, PL 0.46, PH 0.46.

Paratypes. Same locality as holotype, iii–ix. 1994, G. Gangi acc. nos. 11, 20, 177, 185, 223, 224, 269, and 439: Series of workers, 1 queen (to be deposited in BMNH, FFIC, INPA, IZAV, LACM, MCZC, MECN, MPEG, MUSM, MZSP, PSWC, QCAZ, UCDC, UNCB).

Worker measurements ($n = 11$). HL 1.01–1.14, HW 0.94–1.06, MFC 0.101–0.128, LHT 0.73–0.86, CI 0.89–0.94, REL 0.36–0.39, REL2 0.38–0.41, FCI 0.11–0.13, SI 0.41–0.43, FLI 1.04–1.38, FI 0.38–0.41, PLI 0.91–1.00, PWI 0.92–1.04, PPWI 1.53–1.69.

Worker description. Very similar to *P. concolor* (q.v.), except as follows. Petiole shorter, and broader posteriorly (Figs 21, 32); PWI >0.91 (<0.91 in *P. concolor*); PWI3 0.44–0.51 (0.51–0.59 in *P. concolor*); PLI2 0.87–0.99 (0.79–0.93 in *P. concolor*). As in *P. concolor*, standing pilosity is conspicuous on the head, mesosoma, petiole, postpetiole, gaster and legs (MSC 31–66, HTC 8–15). Appressed pubescence on abdominal tergite IV variable, the hairs separated by more than their lengths in some workers, and the area correspondingly more shiny. Body colour much more variable than in *P. concolor*, ranging from concolorous yellow- or orange-brown to dark brown; also intermediate bicoloured conditions with the head and/or (mesosoma + petiole + postpetiole) and/or abdominal segment IV (first gastric segment) lighter in color than the remainder of the body (such variation can be seen within single nest series).

Comments. The posterolaterally expanded petiole (worker PWI >0.91, queen PWI ≈0.79) distinguishes *P. insuavis* from its close relatives *P. concolor* and *P. penetrator* (worker PWI <0.91, queen PWI <0.74) (see also Figs 136, 152). A broad petiole is also seen in some workers of *P. malignus* but *P. insuavis* differs from that species by the conspicuous erect hairs on the sides and posterior margin of the head, by the more abundant pilosity on the mesosoma and legs (compare MSC and HTC values), by the less well separated antennal insertions (see Figs 134, 135, 151), and by the shape of the median clypeal lobe (ventrally deflected and laterally rounded in *P. insuavis*).

Distribution and biology. *P. insuavis* is known only from a few localities in the western Amazon basin (Fig. 168). Greg Gangi's collections came from plants identified as *Tachigali* cf. *formicarum* Harms, *Tachigali hypoleuca* (Bentham) Zarucchi & Herendeen, *Tachigali paniculata* and *Tachigali* cf. *poeppigiana*.

Material examined. Type material listed above plus the following: COLOMBIA AMAZONAS: Corregimiento de Buenos Aires, near Leticia, 16.vii.1987 (L. F. Mendoza) (FFIC, MCZC, PSWC); *Guaviare*: R.N.N. Nukak Maku, 200 m, 31.i.1996 (F. Fernández) (FFIC).

Note. In July 1989, during a brief visit to the Museo Ecuatoriano de Ciencias Naturales (MECN), I noted in that collection three workers of the *P. concolor* complex from Coca, Napo Province, Ecuador (G. Onore leg.), but I did not examine them in sufficient detail to determine their specific identity. A subsequent request to borrow this material could not be met because the specimens have apparently been lost (G. Estévez Jácome, pers. comm.). I would expect the Coca population (indicated by a question mark in Fig. 168) to represent *P. insuavis*, but this will remain uncertain until material is available for examination.

Pseudomyrmex kuenckeli (Emery)
(*Figs 34–36, 81, 85, 89, 104*)

Pseudomyrma kuenckeli Emery 1890:62. Syntype workers, queens, Alajuela, Costa Rica (A. Alfaro) (MCSN) [Examined].

Pseudomyrma kuenckeli var. *dichroa* Forel 1904a:41. Syntype workers, Dibulla, Colombia (A. Forel) (AMNH, BMNH, MCSN, MHNG, NHMB, USNM) [Examined] [Synonymy by Kempf, 1961:402].

Pseudomyrma kuenckeli var. *bierigi* Santschi 1932:412. Holotype worker, Juan Diaz, Panama (A. Bierig) (NHMB) [Examined] [Synonymy by Kempf, 1961:402].

Pseudomyrma crenulata Enzmann, 1944:84. Holotype worker, "Guernavaca", Mexico (not in MCZC) [Not examined] [Synonymy by Kempf, 1961:402].

Pseudomyrmex kuenckeli (Emery); Kusnezov, 1953:214 [First explicit combination in *Pseudomyrmex*].

Pseudomyrmex kuenckeli (Emery); Kempf, 1961:402 [Detailed description].

Pseudomyrmex kuenckeli (Emery); Ward, 1993:158 [Brief diagnosis].

Worker measurements ($n = 16$). HL 1.11–1.31, HW 1.21–1.51, MFC 0.133–0.178, LHT 1.07–1.32, CI 1.08–1.16, REL 0.44–0.48, REL2 0.39–0.42, FCI 0.10–0.13, SI 0.47–0.50, FLI 2.02–2.49, FI 0.31–0.37, PLI 1.01–1.28, PWI 1.08–1.40, PPWI 1.59–1.80.

Worker description. Relatively large species (HW >1.20, LHT >1.05). Masticatory margin of mandible with six or (less commonly) seven teeth. Palp formula 6,4. Median clypeal lobe anterolaterally rounded, its anteromedial surface deflected ventrally (Fig. 35). Frontal carinae widely separated (PFC and MFC >0.12) and subparallel (PFC ≈MFC), the distance between them much greater than basal scape width. Median lobe of antennal sclerite moderately exposed (PFC/ASD 0.63–0.77). Scape long and slender for the species group (SI >0.46, SI2 1.14–1.27). Funiculus only moderately expanded apically, the terminal segment about 1.2–1.5 times the width of the first segment; funicular segment 2 longer than broad; funicular segments 3–10 as long as broad or slightly broader than long. Eye relatively small (see REL and REL2 values), only moderately elongate (OI 0.61–0.66), situated on posterior third of head. Head conspicuously broader than long (CI >1.05), the sides diverging to a maximum width behind the eyes, then rounding gradually into the straight posterior margin (Fig. 35). Mesosoma dorsum more or less flattened, especially the dorsal face of propodeum (Fig. 36); metanotal groove broad but shallow (MP 0.013–0.044, MPI 0.011–0.034). Dorsal face of propodeum laterally submarginate, equal to or longer than the declivitous face (PDI 0.98–1.09), and meeting the latter at a relatively distinct angle of about 120°. Profemur slender. Legs relatively long, LHT/HL 0.92–1.03. Petiole as in Figures 34 and 36, very short and broad, as high as or higher than long (PLI >1.00), with a weakly differentiated anterior peduncle, followed by a straight and steeply ascending anterior face which merges into the convex posterodorsal face; summit of node behind midpoint of petiole length (NI 0.52–0.58). Petiole venter keel-like, with a prominent, blunt anteroventral tooth or lobe and a variably developed (sometimes absent) posteroventral process. In dorsal view, petiolar node broadly transverse and laterally submarginate, tending to be trapezoidal or subrectangular in shape; minimum width of petiole (at the anterior peduncle) notably less than half the maximum petiolar width (PWI3 0.34–0.46), petiolar spiracles usually not prominent in dorsal view. Postpetiole globular, much broader than long (PPWI >1.55); anteroventral process of postpetiole not developed. Mandible usually sublucid, with scattered elongate punctures and variable (sparse to dense) fine striolation overlying the otherwise smooth and shiny integument. Head, mesosoma, petiole, postpetiole and gaster lucid or sublucid, with numerous very fine punctures, mostly less than 0.010 mm in diameter (coarser punctures present anteromesial to the compound eye and on parts of the mesosoma). Standing pilosity abundant, the hairs long and very conspicuous (MSC approximately 95–150, HTC 25–50); standing and decumbent setae present on the posterior margin and sides of head. Appressed pubescence also well developed and conspicuous on most of body, including the head; appressed hairs on abdominal tergite IV separated by much less than their lengths. Body varying in colour from orange-brown to dark-brown; when dark brown then part or all of the head and distal portions of the legs may be a constrastingly lighter orange- or yellow-brown.

Comments. *P. kuenckeli* is a very distinctive species, immediately recognizable by its broad head, widely separated frontal carinae, posteriorly positioned eyes, abundant standing pilosity in the worker, flattened and laterally submarginate dorsal face of worker propodeum, and short broad petiole with keel-like venter. The queen is about the same size as the worker (HW 1.28–1.36, HL 1.18–1.26, LHT 0.97–1.03, in a sample of four queens), a situation not found in most *Pseudomyrmex* species (including other members of the *P. viduus* group).

Distribution and biology. This species is very widely distributed from Mexico to Paraguay and Argentina (Fig. 162), although uncommon or absent from some intervening areas. It tends to be associated with forests in which there is a more or less pronounced dry season. *P. kuenckeli* has large, aggressive, and apparently polygynous colonies, that occupy dead branches of a variety of woody plants. Additional details on behaviour and biology can be found in Forel (1899:89), Wheeler (1901:203–204), and Kempf (1961:405). Although there are old collections from swollen-thorn acacias in Costa Rica (see Ward, 1993:159) it is not clear if these were from living thorns. *P. kuenckeli* has not been found inhabiting any of the ant-plants associated with other members of the *P. viduus* group (*Cordia*, *Tachigali*, *Triplaris*, etc.).

Material examined (AMNH, BMNH, CASC, CKIC, CPDC, EBCC, GCSC, GCWC, IMLA, INBC, IZAV, KWJC, LACM, MCSN, MCZC, MHNG, MNHN, MPEG, MZSP, NHMB, NHMV, PSWC, UASC, UCDC, USNM, WPMC). ARGENTINA Santa Fé: Villa Ana (K. J. Hayward); Santiago del Estero: Icano, bords du Rio Salado (E. R. Wagner). BELIZE Cayo: Las Cuevas, 5 km SE Millionario (J. Beard); Never Delay (N. L. H. Krauss); Orange Walk: 5 mi S Orange Walk at Ferry (D. H. Janzen); Toleda: Punta Gorda (P. Broomfield). BOLIVIA La Paz: Espia ("Espia Rio Bopi") (W. M. Mann); *Santa Cruz*: 10 km NW Terevinto, 380 m (P. S. Ward); Masicuri (P. Bettella); Potrerillo del Guendá, 450 m (P. Bettella). BRAZIL ba: Bela Vista, [near] Belmonte (J. Crispim); CEPEC [near Itabuna] (A. L. B. Souza); Castro Alves (O. Marques); F. Planalto, Barrolândia (J. Crispim); Ilheus (J. Delabie); Pra.do Norte, Ilheus (J. Delabie); es: P.N. Sooretama, Linhares (H. Reichardt); Porto Cachoeira [=Santa Leopoldina] (E. Garbe); go: Campinaçu, Serra da Mesa (Brandão *et al.*); Niquelândia (Silvestre & Dietz; Brandão); Nova Veneza (E. Snethlage); ma: Imperatriz, Ribeirãozinho (F. F. Ramos); Lago Rodrigues (W. França; F. F. Ramos; M. F. Torres); mg: Pedra Azul, 800 m (Seabra & Alvarenga); Pirapora (E. Garbe; c.u.); ms: Faz. Dr José Mendes, Três Lagoas (Exp. Depto. Zool.); Faz. Yamaguti, Cor. da Onça, Mun. Três Lagoas (Exp. Depto. Zool.); mt: Pixaim, 60 km SSW Poconé, 110 m (P. S. Ward); R.S. Base Camp, Serra Roncador (W. D. Hamilton); pa: Conceição do Araguaia (W. França; P. Mauricio; R. B. Neto; W. L. Overal); [Rio] Ariramba (at Rio Trombetas) (Ducke); rj: Guaratiba (A. Silva); Pedra below Rio de Janeiro (W. Schmitt); Porto das Caixas (O. Conde); rr: Ilha de Maracá (F. P. Benton); sp: Agudos (C. Gilbert); Cajuru, Faz. Santa Carlota (R. Silvestre); Faz. Pau d'Alho, Itù (U. Martins); Ituverava (E. Garbe). COLOMBIA cauca: 15 mi S Corinto, 1140 m (E. I. Schlinger & E. S. Ross); Córdoba: Lorica (W. P. & E. MacKay); Huila: 5 km S Villavieja (W. MacKay); La Guajira: Dibulla (A. Forel); Magdalena: Neguange Bay, Parque Tayrona, 0–5 m (C. Kugler); Quebrada Aguja, nr. Cienaga (F. Fernández); Rio Frio to 2000 ft. (Darlington); Valle: Bosque El Vínculo, 980 m (I. Armbrecht); Finca San Luis, nr. Candelaria (c.u.); R.N. Laguna de Sonso, 1000 m (R. C. Aldana). COSTA RICA Alajuela: Alajuela (A. Alfaro); Guanacaste: Lomas Barbudal (G. C. Snelling; S. B. Vinson); Palo Verde, OTS Field Stn. (E. Guerrant & P. Fiedler); Palo Verde, Rio Tempisque (R. C. Kugler); Heredia: Est. Biol. La Selva, 50–150 m (J. T. Longino); Limón: Columbiana Farm, Santa Clara (G. C. Wheeler); Hamburg Farm, Santa Clara (F. Nevermann); Matina (A. Alfaro); Parismina Branch, Santa Clara (F. Nevermann); Santa Clara (A. Alfaro); Puntarenas: Reserva Biol. Carara, 50 m (D. M. Olson); San José: San José (H. Schmidt). EL SALVADOR La Libertad: Quezaltepeque (D. Q. Cavagnaro & M. E. Irwin). GUATEMALA Alta Verapaz: Cacao Trece Aguas (Barber & Schwarz; Schwarz & Barber); Escuintla: Pantaleon, 1700 ft (Champion); Izabal: Lago Izabal, 1.5 km NE El Estor (D. H. Janzen). MEXICO Jal.: Chamela (R. Ayala); Est. Biol.Chamela, 100 m (P. S. Ward); Mor.: Cocoyotla, Mpo. Coatlán del Río (G. Alemán); Cocoyotla, munic. Coatlán del Río, 1120 m (G. Alemán); Cotlán del Río, 1280 m (G. Alemán); Cuernavaca (W. M. Wheeler); N.L.: Los Cavazos, V. de Santiago (J. A. Rodríguez); Montemorelos (W. F. Buren; E. Buren); Q.ROO: 10 km S Boca Paila (J. F. Lynch); VER.: Orizaba (Bilimek); Pueblo Nuevo, nr. Tetzonapa (E. O. Wilson); VER. [?]: Pueblo Viejo (W. M. Mann); *state unknown*: Potrero (Bilimek). PANAMA BOCAS DEL TORO: Changuinola District (G. C. Wheeler); PANAMÁ: Juan Diaz (Bierig). PARAGUAY Colonia Independencia (N. Kusnezov); Colonia Independencia, nr. Villarica (N. Kusnezov). PERU PIURA: Valle Pariños, bei Talara (Weyrauch). TRINIDAD "Trinidad" (Urich).

Pseudomyrmex malignus (Wheeler)
(*Figs 8, 19, 30, 83, 87, 93, 101)*

Pseudomyrma maligna Wheeler, 1921b:143. Syntype workers, males, queens, Kartabo, Guyana (W. M. Wheeler) (MCZC, MZSP) [Examined].

Pseudomyrma maligna var. *cholerica* Wheeler, 1921b:146. Syntype workers, Kartabo, Guyana (W. M. Wheeler) (MCZC) [Examined] [Synonymy by Ward, 1989:440].

Pseudomyrma maligna var. *crucians* Wheeler, 1921b:147. Syntype workers, Kartabo, Guyana (W. M. Wheeler) (MCZC) [Examined] [Synonymy by Ward, 1989:440].

Pseudomyrma auripes Wheeler, 1922:5. Holotype queen, Trinidad (W. M. Wheeler) (MCZC) [Examined] [Synonymy by Ward, 1989:440].

Pseudomyrmex malignus (Wheeler); Kempf, 1961:400. [First explicit combination in *Pseudomyrmex*].

Pseudomyrmex malignus (Wheeler); Ward, 1989:440. [Brief characterization].

Worker measurements ($n = 10$). HL 0.91–1.18, HW 0.84–1.11, MFC 0.117–0.154, LHT 0.57–0.82, CI 0.90–0.96, REL 0.32–0.38, REL2 0.35–0.43, FCI 0.12–0.17, SI 0.39–0.41, FLI 1.14–1.42, FI 0.40–0.44, PLI 0.86–1.05, PWI 0.84–1.08, PPWI 1.48–1.84.

Worker description. Similar to *P. concolor* (q.v.) except as follows. Median clypeal lobe laterally angulate (Fig. 8) and its anteromedial surface not deflected ventrally. Head slightly broader, on average, and the frontal carinae tending to be slightly more separated (compare FCI). Metanotal groove less deeply impressed in some workers. Dorsal face of propodeum shorter than the declivitous face (PDI 0.83–0.99). Petiole generally shorter and broader than that of *P. concolor* but the relevant indices overlap (compare PLI and PWI); least overlap with PWI2 (0.65–0.69, compared to 0.58–0.66 in *P. concolor*). Anteroventral petiolar process well developed and often conspicuously recurved. Mandible smooth and shining, with scattered punctulae, striolae weak and confined to apical portion. Punctulae on upper two thirds of head finer (most with diameter <0.010 mm) and better separated, and the head correspondingly shinier. Mesosomal punctulae also tending to be finer and less dense. Standing pilosity less dense; erect hairs usually absent from the sides of the head (at most one or two may be present below the eyes), and absent from the posterior margin of the head (frontal view); pilosity sparser on the mesosoma dorsum and external faces of tibiae (MSC 6–35, HTC 1–6). Appressed pubescence less well developed, the appressed hairs separated by more than their lengths on abdominal tergite V and parts of abdominal tergite IV. Body colour more variable, ranging from orange-brown to dark brown; head and terminal segments of gaster usually medium to dark-brown, one or more of the remaining parts of body (from the pronotum to the fourth abdominal segment) may be concolorous or a contrastingly lighter orange-brown.

Comments. The workers and queens of this species can be distinguished from all other members of the *P. viduus* group by the combination of well separated frontal carinae (MFC ≫ basal scape width) (see also Figs 134, 135, 151), laterally angulate median clypeal lobe, and the absence of erect hairs from the posterior margin and upper sides of the head (full-face view). The short dorsal face of the propodeum and shiny integument are also characteristic.

Distribution and biology. This is a *Tachigali*-inhabiting species, less frequently encountered than *P. concolor* or *P. penetrator*, but broadly sympatric with them in eastern Hylaea (Fig. 167). Wheeler (1921a, 1942) presented observations on the biology of this species and *P. concolor* in Guyana, where the host tree was *T. paniculata*. The collection from Salto Salas, Venezuela (see below) was made from *Tachigali rusbyi* Harms; for other localities the plant (if mentioned) is identified only as *Tachigali* sp.

Material examined (BMNH, GHPC, INPA, JTLC, LACM, MCZC, MPEG, MZSP, PSWC, UCDC, WWBC). BRAZIL AM: Campo Florestal [Faz. Esteio] (W. W. Benson); Faz. Dimona, 80 km N Manaus, 80 m (P. S. Ward); Municipio Serrinha, Igarapé Serrinha (C. Damião); Res. Campina, [near] Manaus (Rafael & Binda); Reserva Flor. A. Ducke (J. Adis *et al.*); AP: Rio Amaparí, Cachoeira Tatú (J. Lane; Lane & Bicelli); PA: "Alto Parú" [= upper Rio Parú do Oeste] (Sampaio); Cachimbo (H. Sick). FRENCH GUIANA SAINT-LAURENT-DU-MARONI: Saül (G. H. Perrault). GUYANA CUYUNI-MAZARUNI: Camaria (W. M. Wheeler); Forest Settlement (N. Weber); Kartabo (W. M. Wheeler); UPPER DEMERARA-BERBICE: Rockstone-Bartica, 0–50 m (J. Longino). TRINIDAD "Trinidad" (W. M. Wheeler). VENEZUELA AMAZONAS: Haut Orenoque, Mavaca (J. Lizot); Salto Salas (L. Croizat); BOLÍVAR: Río Cuyuni, 66 km SSE El Dorado, 250 m (P. S. Ward)

Pseudomyrmex mordax (Warming) **comb. nov., stat. rev.**
(*Figs 3, 14, 25, 71, 77, 90, 97*)

Pseudomyrma mordax Warming, 1894:173. Syntype workers, queens, Las Trincheras, Venezuela (Meinert) (MHNG) [Examined]. One worker here designated *Lectotype*. [Name previously considered a *nomen nudum* but satisfies the requirements of availability].

Pseudomyrma arboris-sanctae race *symbiotica* Forel, 1904a:38. Syntype workers, males, Dibulla, Colombia (A. Forel) (AMNH, BMNH, MCSN, MCZC, MHNG, MNHN, MZSP, USNM) [Examined]. **Syn. nov.** One syntype worker in MHNG here designated *Lectotype*.

Pseudomyrma arboris-sanctae race *symbiotica* var. *panamensis* Forel, 1912:22. Workers, queens, males, Panama (Christophersen) (MHNG) [Examined]. Unavailable infra-subspecific name; also preoccupied.

Pseudomyrma arboris-sanctae race *symbiotica* var. *loewensohni* Forel, 1918:719. Unavailable infrasubspecific replacement name.

Pseudomyrma mordax; Wheeler, 1942:47 [Considered a *nomen nudum*].

Pseudomyrmex triplarinus; Wheeler & Wheeler (nec Weddell), 1956:386 [Description of larva, misidentified as *P. triplarinus*].

Worker measurements ($n = 18$). HL 1.03–1.30, HW 0.99–1.19, MFC 0.100–0.130, LHT 0.77–0.95, CI 0.92–0.98, REL 0.41–0.44, REL2 0.44–0.47, FCI 0.10–0.12, SI 0.42–0.45, FLI 1.47–1.87, FI 0.37–0.42, PLI 0.77–0.94, PWI 0.82–0.93, PPWI 1.32–1.66.

Worker description. Similar to *P. triplarinus* (q.v.) except as follows. Averaging smaller in size. Profemur tending to be broader (compare FI values). Legs shorter in relation to body size and eye length (LHT/HL 0.70–0.74, EL/LHT 0.57–0.60 compared to 0.78–0.93 and 0.48–0.55, respectively, in *P. triplarinus*) (see also Fig. 133). Anteroventral petiolar process well developed (Fig. 14), subrectangular or bluntly triangular, usually not directed posteroventrally. Punctures on head coarser and denser, especially on upper half of head between compound eye and ocellar triangle, where punctures are mostly 0.010–0.015 mm in diameter and separated by about their diameters. Standing pilosity less dense on average (MSC 25–56, HTC 5–11), absent from the posterior margin of the head (frontal view). Body colour tending to be lighter, but varying from light yellow- or orange-brown to medium brown, the gaster sometimes darker than the rest of the body.

Comments. *P. mordax* can be distinguished from *P. triplarinus* and *P. dendroicus* by the relatively short legs and denser head sculpture. It is also smaller in size than these two species, the difference being absolute in queens (queen HW 1.20–1.41 and queen LHT 0.95–1.09, compared to >1.45 and >1.18, respectively, in the other two species). *P. mordax* differs from *P. triplaridis* by the better separated frontal carinae (worker PFC/ASD 0.64–0.75 and queen PFC/ASD 0.71–0.82, compared with 0.54–0.65 and 0.62–0.71, respectively, in *P. triplaridis*), absence of standing pilosity on the posterior margin of the head (in frontal view), subrectangular or subtriangular anteroventral petiolar process that is not recurved posteroventrally (compare Figs 14 and 16), and lighter color; and from *P. ultrix* by the narrower petiole (compare worker PWI and PLI values; queen PWI 0.72–0.83, compared to 0.93–0.99 in *P. ultrix*), absence of pilosity on posterior margin of head, and lack of an angular protuberance on the worker propodeum.

The name *P. mordax* has languished in the literature since its original appearance (Warming, 1894) but it fulfills the requirements of availability (ICZN, Articles 11, 12), despite the meagerness of the original description. Fortunately, examples of the specimens to which Warming referred (from Las Trincheras, Venezuela) are in the Forel collection in Geneva, and this secures the identity of *P. mordax* and allows designation of a lectotype. Warming (1894) cited Meinert as the author of *Pseudomyrma mordax*, but under Article 50 of the ICZN Warming should be credited with authorship since the description is clearly his.

Distribution and biology. *P. mordax* has a relatively limited distribution in Panama, Colombia and Venezuela (Fig. 165). Among other *Triplaris*-inhabiting ants in the *P viduus* group it overlaps in distribution only with *P. viduus* and, marginally, *P. dendroicus*. Forel (1904a) gives details on the biology of *P. mordax* in the Santa Marta region of Colombia, under the name *Pseudomyrma arboris-sanctae* race *symbiotica*. Based on his observations in the Canal Zone, Panama, Wheeler (1942:58) concluded that *P. mordax* was not very effective at excluding alien (unspecialized) ants from *Triplaris*, and he commented that this species, "though a very vicious and aggressive ant, seems not to sting as severely as the Pseudomyrmas inhabiting *T. surinamensis*, *Tachigali paniculata* and the bull-horn Acacias". Additional information on *P. mordax* is provided by Schremmer (1984), who studied two species of *Triplaris*-associated *Pseudomyrmex* in Colombia but mistook them for a single species (identified as *P. triplarinus*). His observations from Sincé, Departmento Sucré refer to *P. mordax*, while those from Villavicencio refer to *P. dendroicus*. Jaffé *et al.* (1986) investigated worker recruitment, territorial marking, nestmate recognition and alarm behaviour in laboratory colonies of *P. mordax* (identified as *P. triplarinus symbioticus*). *Triplaris cumingiama* Fischer & Meyer ex C. A. Meyer is the host of *P. mordax* in Panama and in at least parts of Colombia. The ant has also been reported from *Triplaris americana* in Venezuela (Jaffé *et al.*, 1986, as *T. felipensis*).

Material examined (AMNH, BMNH, CKIC, CPDC, CUIC, FFIC, GCWC, IZAV, KWJC, LACM, MCSN, MCZC, MHNG, MNHN, MZSP, NHMB, NHMV, PSWC, UCDC, USNM). COLOMBIA Bolívar: Hacienda Monterrey, 10 m (G. Ulloa & F. Fernández); Hacienda Monterrey, 15–75 m (G. Ulloa & F. Fernández); Hacienda Monterrey, 50 m (F. Fernández); Chocó; La Balsa (F. Fernández); La Guajira: Dibulla (A. Forel); Puente Bomba, nr. Dibulla (W. L. Brown & C. Kugler); San Antonio (A. Forel); Magdalena: 5 km SE Rio Frio, 100 m (P. S. Ward); Aracataca (G. Salt); Cañaveral, 50 m (P. S. Ward); Cañaveral, <50 m (J. Longino); Cañaveral-Arrecifes, Parque Tayrona, 0–50 m (C. Kugler); Pueblito, Parque Tayrona (C. Kugler); Rio Frio (G. Salt; Darlington; A. Forel); San Pedro de la Sierra (A. Castillo); San Pedro de la Sierra, 500–1000 m (H.-G. Müller); San Pedro de la Sierra, 700 m (A. Castillo); Sucre: La Guajira, Sincé (F. Schremmer); Sincé (F. Schremmer); Tolima: Armero (Peyton & Suarez); Coyaima, 450 m (R. A. Stirton). PANAMA Colón: France Field (Bierig; G. C. Wheeler; W. M. Wheeler); Frijoles (W. M. Wheeler); Marajal nr. Colón (W. M. Wheeler); Pipeline Road (G. G. Montgomery & Y. Lubin); vic. Pta de los Chivos, 3 km SW Gatun, 100 m (W. L. Brown *et al.*); Darién: Cana, 500 m (D. M. Olson); Cerro Pirre (R. Ruiz); Cruce de Mono (R. Cambra); Panamá: 1.5 km NW Summit Gardens (P. S. Ward); Balboa (W. M. Wheeler); Barro Colorado I. (R. Silberglied & A. Aiello; B. L. Fisher); Cerro Galera (P. S. Ward); Las Cascades (W. M. Wheeler); Maje I., Bayano (E. Mendez); Rio Perequete (D. Quintero); Ruta 1, 14 km W Panama City, 100 m (W. L. Brown *et al.*); Summit (N. L. H. Krauss); Trinidad Rio (A. Busck); *prov.unknown*: "Panama" (Christophersen). VENEZUELA Aragua: 2 km N Ocumare de la Costa (A. S. Menke & D. Vincent); Bahia de Turiamo (H. Romero); Barinas: 17 km SSW Ciudad Bolivia, 240 m (P. S. Ward; J. Longino); Carabobo: Las Trincheras (Meinert); San Esteban (Anduze); Dto. Federal: Caracas (J. E. Lattke); Caracas, Jardín Botánico (J. E. Lattke); El Valle (C. H. Ballow; S. Ballou); Guárico: Paso Real (W. Aragort); Miranda: Campo Centr., Caucagua (K. Jaffé); Caucagua (K. Jaffé; W. Aragort); Cortada de Maturin (E. Yerena); Cúpira, 15 m (W. Goitia); Cúpira, 50 m (P. S. Ward); Panaquire (Machado; W. Aragort); Zulia: Los Angeles del Tucuco (A. S. Menke & L. Hollenberg).

Pseudomyrmex penetrator (F. Smith), **stat. rev.**
(*Figs 11, 22, 33*)

Pseudomyrma penetrator F. Smith, 1877:66. Syntype alate queen, "St. Paul" [São Paulo de Olivença], Amazonas, Brazil (BMNH) [Examined] [Previously synonymized under *P. concolor* by Kempf, 1967:5 and by Ward, 1989:435].

Pseudomyrma latinoda var. *nigrescens* Forel, 1904a:38. Syntype workers, Para, Brazil (Göldi) (MCZC, MHNG) [Examined]. **Syn. nov**.

Pseudomyrma latinoda var. *coronata* Wheeler, 1942:167. Syntype workers, Kamakusa, Guyana (H. O. Lang) (MCZC) [Examined]. **Syn. n** One worker here designated as *Lectotype*.

Pseudomyrma latinoda var. *coronata* Enzmann, 1944:88. Syntype workers, Mouth of Merume, Guyana (H. O. Lang) (MCZC) [Examined]. [Synonymy, under *P. latinodus coronatus* (Wheeler), by Brown, 1949:42] One worker here designated as *Lectotype*.

Pseudomyrmex penetrator (F. Smith); Kempf, 1958:435. [First explicit combination in *Pseudomyrmex*].

Worker measurements ($n = 24$). HL 0.97–1.23, HW 0.89–1.13, MFC 0.093–0.136, LHT 0.70–0.93, CI 0.86–0.97, REL 0.36–0.42, REL2 0.38–0.44, FCI 0.09–0.13, SI 0.39–0.43, FLI 0.97–1.44, FI 0.39–0.46, PLI 0.77–0.92, PWI 0.75–0.89, PPWI 1.48–1.82.

Worker description. Very similar to *P. concolor* (q.v.) in size, shape, sculpture and pilosity (MSC 28–53; HTC 8–16), differing primarily in colour. Gaster, and usually also mesosoma, petiole and postpetiole, dark brown; head concolorous brown or a contrasting orange-brown, with variable amounts of infuscation (especially around the ocellar triangle). Antennae, tarsi and (sometimes) tibiae lighter yellow-brown. Petiole tending to be perhaps lower (compare PLI values), with a smaller subpetiolar process, and postpetiole tending to be broader (compare PPWI values), but these differences, if real, are slight and not diagnostic.

Comments. This is a 'dark form' very closely related to, and possibly conspecific with, *P. concolor*. The circumstances are complicated. In a number of localities the two color forms occur sympatrically and appear to retain their distinctness. Studies in the Manaus region even indicate that the two morphs are ecological differentiated, with *P. penetrator* (= *P. nigrescens*) occupying older *Tachigali* plants than *P. concolor* and achieving larger colony sizes (Fonseca, 1993). Yet elsewhere, the morphological distinctions are blurred, and one collection from 100 km E Humaita in southeastern Amazonas (leg. F. Rickson) contains both dark and light workers within a single nest series. The queen of this nest series is mostly dark brown, but has a contrastingly light head and patches of orange-brown coloration on the pronotum, mesoscutum, and anepisternum. There are also morphologically intermediate individuals in collections made by Benson, Brandão, and others in the Serra do Carajás, Pará. In the Carajás samples some workers and queens appear to be typical dark-bodied *P. penetrator*, but others are more problematic: these have a lighter orange-brown coloration on all or parts of the mesosoma, petiole and postpetiole, and in a few workers the light coloration even extends to the fourth abdominal (first gastric) segment. Finally, the colour differences between the type queens of *P. penetrator* and *P. concolor*, both from São Paulo de Olivença in western Amazonia, are less pronounced than in populations from eastern Amazonia and the Guianas, although this might be due to a loss of colour difference with time.

Similar patterns of colour variation, involving light- and dark-coloured individuals, occur in the related species *P. insuavis* and *P. malignus*, but in those cases the variation is clearly intraspecific. The situation in *P. concolor*/*P. penetrator* is more intriguing, and suggests reproductive isolation between the forms in some regions but not others. Besides the breakdown in colour as a diagnostic character in peripheral (southeastern) populations, another observation indicating gene flow between populations of *P. concolor* and *P. penetrator* is the occurrence of concordant geographical variation in morphology. For example, the type queens of *P. concolor* and *P. penetrator*, from the same locality in western Amazonia, are both exceptionally large (HW 1.39) with elongate heads (CI 0.79). Conversely, queens of *P. concolor* and *P. penetrator* from Guyana and Venezuela tend to have broader (CI 0.84–0.87) and less shiny heads (owing to the greater development of fine striolate-reticulate sculpture on the frons) than their eastern Amazonian counterparts (CI 0.79–0.86). Of course, an alternative explanation for such concordant variation is similar selection pressures on queen morphology in two sibling species. The situation calls for a detailed genetic analysis.

I could find no consistent differences between *P. concolor* and *P. penetrator* in the form of the male genitalia, and this contrasts with the typical situation in the *P. viduus* group in which the male genitalia provide species-diagnostic characters.

Distribution and biology. P. penetrator is associated with *Tachigali* and, like *P. concolor*, is widely distributed in the east/central Amazon basin and adjacent Guianas (Fig. 168). Fonseca (1993) provides information on the biology of this ant (under the name *P. nigrescens*).

Material examined (AMNH, BMNH, CPDC, CUIC, IMLA, INPA, KWJC, LACM, MCSN, MCZC, MHNG, MPEG, MZSP, PSWC, UCDC, USNM, WWBC). BRAZIL AM: 120 km E Humaita, Transamazon Hwy., Rio Carmelos (F. Rickson); Balbina (M. Queiroz); Benjamin Constant (W. L. Brown; K. Lenko); Benjamin Constant & vicinity (W. L. Brown); Campo Florestal [Faz. Esteio] (W. W. Benson); E.E.S.T., km.44, BR-174, [near] Manaus (W. W. Benson); E.E.S.T., km.44.5, BR-174, [near] Manaus (W. W. Benson); Faz. Dimona, 80 km N Manaus (D. W. Davidson); Faz. Esteio, 80 km NNE Manaus, 80 m (P. S. Ward); Santo Antônio do Iça (Ducke); São Paulo de Olivença [as "St.Paul"] (Bates); km.41 Reserve, north of Manaus (C. R. Fonseca); AP: Rio Felicio (J. Lane); PA: BR-010, km 1712 (W. L. Overal); Belém (C. R. Gonçalves); Belém Utinga forest (R. L. Jeanne); Belém [as "Pará"] (G. Arnold; E. Göldi; c.u.); Belém, Reserva Guamá ("APEG"; "APEG n. 297"); Cach. do Breu (Sampaio); Cachimbo (H. Sick); Igarapeaçu (C. R. Gonçalves); Irituia, BR-4 km 98 (S. Vogel); Paragominas, Faz. Cachoeira do Rio Vermelho (B. Mascarenhas); S. J. Pirabas, Boa Esperança (N. Bittencourt); S. Norte, Carajás, Nl Mata plano (C. R. F. Brandão & W. W. Benson; W. W. Benson); S. Norte, Carajás, km 18.5 entre Nl, R. Itacaiúnas (C. R. F. Brandão & W. W. Benson); Serra Norte, Caldeirão (R. B. Neto); Serra Norte, Est. Manganês (N. Degallier; M. F. Torres); Serra Norte, Pedreira (H. Andrade); Serra Norte, Rio Itacaiúnas (W. W. Benson); Serra Norte, Três Alfa (H. Andrade; M. F. Torres); Serra dos Carajas, Vale do Rio Doce (C. R. Fonseca); Tucuruí (W. L. Overal; R. B. Neto; W. L. Overal); RD: Texeirópolis (A. Harada). GUYANA CUYUNI-MAZARUNI: Kamakusa (H. O. Lang); Merumé Mouth (H. O. Lang). SURINAM MAROWIJNE: Janemale, Litani R. (Geijskes). VENEZUELA AMAZONAS: Alto Río Siapa, 530 m (J. E. Lattke); La Culebra (F. Yepez); BOLÍVAR: Río Akanán, 500 m (J. E. Lattke); Río Cuyuni, 66 km SSE El Dorado, 250 m (P. S. Ward).

Pseudomyrmex tachigaliae (Forel)
(*Figs 7, 18, 29, 82, 86, 92, 103*)

Pseudomyrma latinoda race *tachigaliae* Forel, 1904c:686. Syntype workers, queens, Tarapoto, Peru (Ule) (MCSN, MHNG, NHMB) [Examined].

Pseudomyrma latinoda subsp. *bradleyi* Wheeler, 1942:169. Syntype workers, Perene, Peru (Bradley) (MCZC) [Examined] [Synonymy by Ward, 1989:444].

Pseudomyrma bradleyi Enzmann, 1944:82. Syntype workers, Perene, Peru (Bradley) (MCZC) [Examined] [Synonymy, under *P. latinodus bradleyi* (Wheeler), by Brown, 1949:42].

Pseudomyrmex latinodus tachigaliae (Forel); Kempf, 1961:400. [First explicit combination in *Pseudomyrmex*].

Pseudomyrmex tachigaliae (Forel); Ward, 1989:444. [Raised to species. Brief diagnosis].

Worker measurements ($n = 16$). HL 0.95–1.18, HW 0.80–1.03, MFC 0.023–0.065, LHT 0.61–0.96, CI 0.81–0.88, REL 0.37–0.40, REL2 0.42–0.48, FCI 0.03–0.07, SI 0.43–0.49, FLI 1.41–1.80, FI 0.41–0.47, PLI 0.72–0.82, PWI 0.71–0.86, PPWI 1.30–1.63.

Worker description. Relatively small, worker HW <1.04 (but queen large: HW >1.44). Basal margin of mandible with one or two very weak mesial teeth; masticatory margin of mandible with six or seven teeth. Palp formula 5,3. Median clypeal lobe tectiform, with a distinctive, inflected, lamellate anterior margin which appears straight or concave in frontal (dorsal) view, and subangulate laterally (Fig. 7). Below the lamellate margin of the clypeus is a small tongue-like medial protrusion, visible in anterodorsal view. Frontal carinae not well separated (for the *P. viduus* group), converging posteriorly, MFC usually less than basal scape width. Median lobe of antennal sclerite more exposed than in other species in the *P. viduus* group (worker FCI2 0.22–0.45, worker ASI2 0.75–0.87), in particular because of a smaller PFC such that worker PFC/ASD 0.27–0.48 (>0.50 in all other species) and worker PFC/ASM 0.33–0.62 (>0.74 in all other species) and scape tending to be relatively longer (compare SI values). Scape expanded distally to about twice its basal width; funiculus also expanded apically, the terminal segment about 1.8 times the width of the first segment; funicular segments 3–10 conspicuously broader than long. Eye small, only moderately elongate (REL <0.41, REL2 <0.49, OI 0.61–0.66). Head longer than broad (CI >0.80), the sides weakly convex, rounding abruptly into the posterior margin, which is flat or slightly concave, in frontal view (Fig. 7). Mesosoma dorsum more or less flattened, and with a moderately incised metanotal groove (Fig. 18). Dorsal face of propodeum subequal to, or slightly longer than, the declivitous face (PDI 0.95–1.15), the two meeting at a rounded angle. Petiole relatively low, notably longer than high (PLI <0.83), with an evenly convex anterodorsal face in lateral profile, rounding into a steeper posterior face (Fig. 18). Anteroventral petiolar tooth weakly developed or absent. In dorsal view, the minimum (anterior) width of petiole more than half the maximum width (PWI3 0.51–0.62), and the straight sides of the petiole diverging only moderately (Fig. 29). Postpetiole globular, notably broader than long (PPWI >1.29); ventral protrusion of postpetiolar sternite less prominent than in *P. concolor*, and anteroventral process less well developed. Mandible with scattered punctulae and variable amounts of fine striolation which dull the reflectance. Head subopaque to sublucid, densely punctulate, the punctures about 0.012–0.018 mm in diameter and separated by their diameters or less on most of the head, only small marginal areas immediately above and below the eye being shiny and unsculptured. Mesosoma, petiole, postpetiole and gaster mostly subopaque (the episternum sublucid), with fine corarious-imbricate sculpture, punctulae absent or ill-defined, especially posteriorly. Standing pilosity relatively sparse and short on most of body (MSC 6–26; HTC 0); a few (0–6) short, inconspicuous erect setae visible in outline on either side of the head in frontal view. Appressed pubescence very well developed and conspicuous on most of body, especially dense on the petiole, postpetiole, and abdominal tergites. Body uniformly light yellow-brown to (more commonly) dark-brown in colour, the appendages lighter.

Comments. Queens and workers of *P. tachigaliae* can be recognized by the modified median clypeal lobe. In the worker this is in the form of a tectiform (tent-shaped) lobe with lamellate anterolateral margins that appear subangulate in frontal view. In the queen the clypeal lobe is developed as a striking, tongue-like anterodorsal protrusion. Other characteristic features of the workers and queens of this species are the closely contiguous frontal carinae and correspondingly well-exposed median lobes of the torulus (see worker FCI, FCI2, ASI2 and PFC/ASD values above; queen FCI 0.05–0.08, queen FCI2 0.34–0.51), densely punctulate head sculpture, low petiole (worker PLI <0.83, queen PLI 0.54–0.68) with the dorsal face broadly convex in lateral profile, scarcity of standing pilosity, and conspicuous appressed pubescence.

Distribution and biology. This species is a *Tachigali* associate confined to the western portions of the Amazon basin in Peru and adjacent Brazil (Fig. 167). The workers aggressively defend their host plant, yet Verhaagh (1988) found tenthredinoid sawfly larvae on *Tachigali* foliage that were able to thwart attacks by *P. tachigaliae* workers. Most nest series of *P. tachigaliae* are labelled as coming from unspecified species of *Tachigali*. The type series was collected from *Tachigali formicarum* (Forel, 1904c) and the collection from Cerros Campanquiz, Peru (see below) was taken from *Tachigali tessmannii* Harms.

Material examined (BMNH, LACM, MCSN, MCZC, MHNG, MNHN, MZSP, NHMB, PSWC, UCDC, USNM, WWBC). BRAZIL AC: Serra do Moa (E. L. A. Monteiro); AM: Porto Alegre, Rio Purus (Huber); Porto Alegre, [Rio] Purus (Huber). PERU AMAZONAS: Cerros Campanquiz, nr. Pongo de Manseriche, Río Marañon, 250–350 m (J. J. Wurdack); HUÁNUCO: Panguana, 220 m (M. Verhaagh); nr. confl. Rio Pachitea & Rio Llullapichis (N. L. & C. A. Toft); JUNÍN: El Campamiento, Col.Perene (J. C. Bradley); El Campamiento, Perene (J. C. Bradley); Perene (J. C. Bradley); LORETO: 15 km WSW Yurimaguas, 200 m (P. S. Ward); ACEER, Rio Napo (P. J. Stern); SAN MARTÍN: 17 km NNE Tarapoto, 400 m (P. S. Ward); 24 km NNE Tarapoto, 220 m (P. S. Ward); Convento, 26 km NNE Tarapoto, 220 m (P. S. Ward); Davidcillo, 30 km NNE Tarapoto, 220 m (P. S. Ward); Tarapoto (Ule).

Pseudomyrmex triplaridis (Forel)
(*Figs 5, 16, 27, 73, 79, 91, 99*)

Pseudomyrma triplaridis Forel, 1904c:684. Syntype workers, queens, male, Jurua Miry, Jurua, Amazonas, Brazil (Ule) (AMNH, BMNH, MCSN, MHNG, NHMV) [Examined].

Pseudomyrma triplaridis subsp. *boxi* Wheeler, 1942:184. Lectotype worker, Blairmont, Berbice, Guyana (H. E. Box) (MCZC) [Examined] [Synonymy and lectotype designation by Ward, 1989:444].

Pseudomyrma triplaridis subsp. *boxi* Enzmann, 1944:94. Syntype workers, Blairmont, Berbice, Guyana (H. E. Box) (MCZC) [Examined] [Synonymy, under *P. triplaridis boxi* (Wheeler), by Brown, 1949:43].

Pseudomyrmex triplaridis; Kusnezov (nec Forel), 1953:214. [First explicit combination in *Pseudomyrmex*, but a misidentification of *P. triplarinus* (Weddell).].

Pseudomyrmex triplaridis (Forel); Kempf, 1961:400.

Pseudomyrmex triplaridis (Forel); Ward, 1989:444. [Brief characterization].

Worker measurements ($n = 19$). HL 1.03–1.27, HW 0.89–1.14, MFC 0.080–0.116, LHT 0.72–0.95, CI 0.85–0.93, REL 0.35–0.43, REL2 0.42–0.48, FCI 0.08–0.12, SI 0.43–0.48, FLI 1.36–1.77, FI 0.39–0.43, PLI 0.80–0.92, PWI 0.84–0.97, PPWI 1.38–1.77.

Worker description. Agreeing with the description of *P. triplarinus* except as follows. Averaging smaller in size (compare HW, LHT). Palp formula 5,3. Frontal carinae less well separated, and the median lobe of antennal sclerite correspondingly more exposed (PFC/ASD 0.54–0.65, FCI2 0.45–0.61). Funicular segment 3 broader than long. Head narrower, regression of HL on HW lying above that of *P. triplarinus* (Fig. 132). Metanotal groove tending to be less strongly impressed. Profemur broader (FI >0.38). Legs relatively shorter, LHT/HL 0.70–0.75. Anteroventral petiolar process subtriangular or fin-shaped, recurved posteroventrally (Fig. 16). Postpetiolar sternite with more conspicuous ventral protrusion. Sculpture on dorsum of head coarser, the punctures 0.010–0.020 mm in diameter, subcontiguous on the anterior half of head and separated by about their diameters on upper half of head. Body pilosity common (MSC 43–70, HTC 6–13), somewhat better developed on the head than in *P. triplarinus* so that in frontal view the posterior margin and upper sides of the head always have some erect or subdecumbent hairs visible in outline (absent at least from the sides of the head in *P. triplarinus*). Pubescence on head more conspicuous, the hairs tending to be decumbent or subdecumbent, giving the worker a scruffier appearance. Less variation in body colour: more consistently concolorous medium- to dark-brown, the frontoclypeal complex and appendages typically lighter.

Comments. Workers and queens of *P. triplaridis* can be identified by the combination of relatively short legs (worker LHT/HL <0.77, queen LHT 0.86–1.04, queen LHT/HL 0.70–0.74), moderately elongate head (worker CI 0.85–0.93, queen CI 0.83–0.89) (see also Figs 132, 145), recurved anteroventral petiolar process (Fig. 16), densely punctulate head sculpture (see above), and presence of standing pilosity on the posterior margin and upper sides of the head (in frontal view). The palp formula of 5,3 and the more exposed median lobes of the antennal sclerites (see above; queen PFC/ASD 0.62–0.71, queen FCI2 0.45–0.60) are also characteristic. *P. triplaridis* is intermediate in habitus between *P. viduus* on the one hand and the larger, broad-headed *Triplaris*-inhabiting species on the other hand.

A series of workers from Ilha de Marchantaria, AM, Brazil (leg. J. Adis *et al.*) (INPA) is somewhat atypical (shinier integument, smaller eyes, inflected median clypeal lobe, broader profemur) and may represent a different species.

Distribution and biology. Most records for *P. triplaridis* are from the Amazon basin, but peripheral populations are known from Guyana and southern Brazil (Fig. 164). This species is apparently always associated with *Triplaris*, but little has been published on its biology. Ule (1906b) found that, in contrast to *P. dendroicus*, the workers of *P. triplaridis* did not clear vegetation at the base of their host tree (see also Wheeler, 1942:49). For other information about this species see brief remarks by Forel (1904c:

685, 1906:231) and Wheeler (1942:184), but note that Wheeler's (1942:185–186) comments about "*P. triplaridis baileyi*" and "*P. triplaridis tigrina*" refer to *P. viduus*, not *P. triplaridis*. Collections of *P. triplaridis* have been made from *Triplaris weigeltiana* (Reichenbach) Kuntze (= *T. surinamensis* Chamisso) and *Triplaris dugandii* Brandbyge, in addition to plants identified no farther than genus. See under *P. ultrix* for observations on incipient colonies.

Material examined (BMNH, CASC, CUIC, FFIC, INPA, KWJC, LACM, MCSN, MCZC, MHNG, MNHN, MPEG, MZSP, NHMB, NHMV, PSWC, UCDC, USNM, WWBC). BRAZIL AC: Cruzeiro do Sul (A. C. Filho *et al.*; A. S. Filho *et al.*; W. W. Benson; F. H. Caetano); Jurua Miry, Jurua (Ule); Porto Valter (P. L. Herbst); Rio Moa, nr. airport, Cruzeiro do Sul (W. W. Benson & B. C. Lopes); AM: Ilha de Marchantaria (J. Adis *et al.*); Ilha de Marchantaria, Lago Camaleão (J. Adis *et al.*); Lago Janauaca (W. W. Benson); Lago Mamiraua, Tefé (D. Murawski); Manaus (C. R. Gonçalves); Rio Purus (Förstenberg); Tabatinga (A. Göldi & Huber); Tefé (P. Tastevin); AP: Amicohy, braço sul (Lane & Bicelli); MT: Mato Grosso (Hoehne); PA: Alenquer (W. França); Monte Dourado (R. B. Neto); SP: Castilho, marg. esq. R. Paraná (Exp. Depto. Zool.). COLOMBIA AMAZONAS: Araracuara (G. Gangi); PNN Amacayacu, Caño Lorena (F. Fernández); PNN Amacayacu, Caño Lorena, Río Cotuhe (F. Fernández). ECUADOR NAPO: 13 km NNE Archidona, 960 m (P. S. Ward); Rio Cuyabeno (J. Brandbyge); Río Wai is ayá, 300 m (J. Brandbyge); San Pablo de los Secoyas, 300 m (J. Brandyge); PASTAZA: 25 km NNE Puyo, 800 m (P. S. Ward); SUCUMBIOS: Limon Cocha vic. (H. R. Hermann). GUYANA MAHAICA-BERBICE: Blairmont, Berbice (H. Box; H. E. Box); UP. TAKUTU-UP.ESSEQUIBO: Mataruki R., Upper Essequebo (J. G. Myers); Upper Essequebo (J. G. Myers). PERU LORETO: Pto. America (J. C. Bradley); SAN MARTÍN: "Cumbase" [= San Antonio de Cumbasa] (c.u.); La Perla, 21 km NNE Tarapoto, 220 m (P. S. Ward); Tarapoto, 350 m (P. S. Ward); UCAYALI: Pucallpa (E. I. Schlinger & E. S. Ross; J. Schunke). VENEZUELA AMAZONAS: Alto Río Siapa, 530 m (J. E. Lattke); Patanoviterí [= Patanowa-teri] (H. Herzog).

Pseudomyrmex triplarinus (Weddell)
(*Figs 2, 13, 24, 70, 76, 96*)

Myrmica triplarina Weddell, 1850:263. Syntype workers, Brazil, Bolivia, Peru (not located; see below). **Neotype worker** here designated: Estación Biológica Beni, 42 km E San Borja, Depto. Beni, Bolivia, 210 m, 14°48′S, 66°23′W, P. S. Ward# 9075 (MCZC).

Pseudomyrma arborissanctae Emery, 1894:147. Syntype workers, queens, Bolivia (Balzan) (MCSN, MHNG) [Examined] [Synonymy by Wheeler, 1942:186; here confirmed].

Pseudomyrma arborissanctae var. *cordobensis* Forel, 1914:265. Two syntype workers, "Prov. de Cordoba", Argentina (Bruch) (MHNG) [Examined]. **Syn. nov.**

Pseudomyrma triplarina var. *rurrenabaquensis* Wheeler & Mann, 1942b:188. Syntype workers, Rurrenabaque, Bolivia (W. M. Mann) (AMNH, MCZC) [Examined]. **Syn. nov.**

Pseudomyrma arborissanctae var. *ecuadorianus* Enzmann, 1944:79. Three syntype workers, Ecuador (MCZC) [Examined] [Synonymy by Brown, 1949:44; here confirmed].

Pseudomyrmex triplarinus; Wheeler & Wheeler (nec Weddell), 1956:386 [First explicit combination in *Pseudomyrmex*, but a misidentification of *P. mordax* (Warming)].

Pseudomyrmex triplarinus (Weddell); Kempf, 1961:400.

Worker measurements ($n = 39$). HL 1.03–1.46, HW 1.00–1.41, MFC 0.108–0.158, LHT 0.82–1.23, CI 0.92–1.00, REL 0.40–0.45, REL2 0.42–0.47, FCI 0.10–0.14, SI 0.43–0.48, FLI 1.45–2.09, FI 0.34–0.39, PLI 0.76–0.91, PWI 0.78–0.98, PPWI 1.37–1.76.

Worker description. Relatively large species (HW>1.00, LHT>0.80). Basal margin of mandible with mesial tooth located notably closer to the apicobasal tooth than to the proximal tooth (MD4/MD5 approximately 0.75–0.80); masticatory margin of mandible with six or (less commonly) seven teeth. Palp formula 6,4. Median clypeal lobe anterolaterally rounded or bluntly angled (not sharply angulate), its anteromedial surface deflected ventrally. Frontal carinae well separated (MFC>0.10), subparallel or converging slightly posteriorly (ASM $\approx$ PFC $\geq$ MFC). Median lobes of antennal sclerites not conspicuously exposed (PFC/ASD 0.67–0.83; FCI2 0.57–0.79). Scape of moderate length for the species group, expanded distally to twice its basal width; funiculus short, also expanded apically, the terminal segment about 1.5–1.6 times the width of the first segment; funicular segment 2 about as broad as long, funicular segment 3 as broad as long or slightly broader than long (FLI>1.44); funicular segments 4–10 broader than long. Eye small for the genus, of moderate size for the species group (see REL and REL2 values), only moderately elongate (OI 0.58–0.65). Head rather broad (CI>0.91), the sides convex and either subparallel or diverging slightly posteriorly; side of head rounding relatively abruptly into the posterior margin, which is flat or very slightly concave, in frontal view. Mesosoma dorsum more or less flattened, but mesonotum may be inclined slightly relative to the dorsal face of the propodeum. Metanotal groove deeply incised (MP 0.039–0.093, MPI 0.037–0.075). Dorsal face of propodeum varying from flat to rather convex, subequal to or somewhat longer than the declivitous face (PDI 0.92–1.28), and meeting the latter at a well rounded angle. Metapleural gland bulla well-developed and conspicuous. Legs relatively long, LHT/HL 0.78–0.93 (see also Figs 118, 133). Petiole as in Fig. 13, slightly longer than high (PLI <0.92), with a weakly differentiated anterior peduncle, followed by an increasingly convex anterodorsal face which rounds into the steep posterior face (lateral view). Summit of node behind the midpoint of the petiole (NI 0.52–0.64). Anteroventral petiolar process well developed (Fig. 13), subtriangular in shape and pointing ventrally not posteroventrally. In dorsal view, the minimum (anterior) width of petiole generally less than or equal to half the maximum width (PW13 0.42–0.53), petiolar spiracles forming prominent lateral bulges, and the straight sides of the petiole notably diverging posteriorly (Fig. 24). Postpetiole globular, notably broader than long (PPWI >1.35); ventral protrusion of postpetiolar sternite less prominent than in *P. concolor*; anteroventral process of postpetiole moderately developed. Mandible typically sublucid, with scattered punctulae and fine striolation; the striolae sufficiently dense in some workers to dull the lustre. Head dorsum with numerous fine punctulae (0.005–0.015 mm diameter) on a smooth, shiny background. Punctures more or less evenly spaced and separated by about their diameters or less on anterior portion of head, becoming a little less dense on the upper half of head where they are separated by one to several diameters. Mesosoma dorsum sublucid, with numerous piligerous punctures (separated by one to several diameters), side of mesosoma with punctulae less well defined and with a tendency toward the development of corarious-imbricate and imbricate-costulate sculpture, with a corresponding dulling of the integument, especially on the metapleuron and lateral propodeum. Petiole, postpetiole and gaster sublucid, the reflectance dulled (especially on the gaster) by very fine punctulae and associated appressed pubescence. Standing pilosity common and conspicuous on most of body, including scape, mesosoma dorsum, and external faces of tibiae (MSC 43–84, HTC 9–21); erect setae absent from the side of the head (Fig. 2), present or absent on the posterior margin. Appressed pubescence well developed on most of body; appressed hairs mostly short and inconspicuous on head, longer and moderately dense elsewhere, including the petiole, postpetiole and abdominal tergite IV where hairs are separated by much less than their lengths. Body varying in colour from uniformly light yellow-brown or orange-brown to dark-brown; head concolorous with or only slightly darker than the mesosoma; gaster may be constrastingly darker than rest of body. Scape, appendages, and frontoclypeal complex tending to be lighter in colour than rest of body.

Comments. *P. triplarinus* may be recognized by the following combination of traits: relatively large species (worker HW >0.99, LHT >0.81; queen HW 1.46–1.60, queen LHT 1.19–1.41); head broad (worker CI >0.91, queen CI 0.90–0.95), covered with fine punctures separated by one to several diameters; head not contrastingly darker than the mesosoma; pilosity abundant on mesosoma dorsum and external face of metatibia (worker MSC>40, worker HTC >8) but absent from side of head (frontal view); legs relatively long (worker LHT/HL >0.76) (see also Figs 118, 133); petiole longer than wide, especially in the queen (worker PWI <1.00, queen PWI 0.75–0.84), and with a subtriangular subpetiolar process which is directed ventrally. The relatively slender legs alone separate *P. triplarinus* from all other *Triplaris* inhabitants except *P. dendroicus*, from which it differs by the more abundant pilosity (compare Figs 12 and 13), ventrally directed subpetiolar process, and several other features (see under description of *P. dendroicus*). *P. triplarinus* shows a moderate amount of variation, especially in body colour. Light-and dark-coloured workers may occur in the same population and within single nest series.

Weddell (1850) introduced the name *Myrmica triplarina* in a footnote to a paper containing descriptions of new species of *Triplaris* and other plants. No type material is known to exist for *P. triplarinus* and Weddell's herbarium specimens of *Triplaris* apparently do not contain ants (J. Brandbyge, pers. comm.). Hence I am designating a neotype which agrees with Weddell's original (albeit scanty) description of the ant, and which corresponds to the species which has come to be known in the literature as *P. triplarinus*.

Distribution and biology. This is one of the more widely distributed of the *Triplaris*-inhabiting ants, ranging from southern Colombia through the Amazon basin to Bolivia and the pantanal of southwestern Brazil (Fig. 165). There is also an unconfirmed record from Argentina, marked with a '?' in Fig. 161. Forel (1914) described a new variety, *Pseudomyrma arborissanctae* var. *cordobensis*, from workers collected by Bruch in "Prov. de Cordoba", Argentina (and the types are so labelled), yet *Triplaris* is not known to occur in this region (Brandbyge, 1986). This suggests that an error occurred in labelling or perhaps that Bruch encountered hitchhikers on cargo that had travelled down the Rio Paraná. Consistent with this hypothesis, the *P. cordobensis* types closely match material of *P. triplarinus* from adjacent Bolivia (Santa Cruz) and southern Brazil. Gallardo (1932) repeats Forel's record without shedding further light on the problem.

P. triplarinus has been collected from *Triplaris americana* (= *T. noli-tangere* Weddell), and other *Triplaris* trees not identified to species. The habits of *P. triplarinus* appear to be similar to those of *P. dendroicus*, i.e. workers readily attack and sting intruders and they clear vegetation from the base of the host tree. An ecological study by Oliveira *et al.* (1987) in Brazil demonstrated that *P. triplarinus* workers were more efficient than a co-foraging *Crematogaster* species at finding and capturing termite baits on host foliage.

Material examined (AMNH, BMNH, CBFC, CUIC, FFIC, ICCM, IMLA, INPA, LACM, MCSN, MCZC, MHNG, MUSM, MPEG, MZSP, NHMB, PSWC, UASC, UCDC, USNM, WWBC). ARGENTINA Cordoba: "Prov. de Cordoba" (Bruch) [see discussion above]. BOLIVIA Beni: 47 km SSW San Borja, 420 m (P. S. Ward); Cavinas (W. M. Mann); Espiritu (F. Koya); Est.Biol.Beni, 42 km E San Borja, 210 m (P. S. Ward); Riberalta (W. M. Mann); Rio Mamore at mouth of Rio Ibare (J. K. Bouseman); Rurrenabaque (W. M. Mann); Trinidad (N. Kusnezov; c.u.); Villa Bella (c.u.); Cochabamba: Chapare (Marcus); Cochabamba (Marcus); Valle del Sajta (P. Bettella); La Paz: 20 km E Santa Ana de Alto, 820 m (P. S. Ward); 20 km NNE Coroico, 850 m (P. S. Ward); 40 km N Apolo, 1010 m (G. Pease); 5 km SSW Coroico, 1280 m (P. S. Ward); Chijchijpa, nr. Coroico, 1114 m (M. L. Campbell); Estancia San Pedro, 490 m (F. Koya); Huachi (W. M. Mann); Lower Rio Madidi (W. M. Mann); Puerto Linares, 460 m (F. Koya); Rio Colorado (W. M. Mann); Tumupasa (W. M. Mann); [Puerto] Ixiamas (W. M. Mann); Santa Cruz: 10 km NW Terevinto, 380 m (P. Bettella); 6 km S Santa Cruz (P. Bettella); Buena Vista (Prosen); Buena Vista, 350 m (P. S. Ward); Guarayos ("Guarujo") (Lizer & Delétang); Provincia del Sara [=Gutiérrez] (Steinbach); Provincia del Sara [=Gutiérrez], 450 m (J. Steinbach); Santa Cruz (D. Candia; D. R. Schultz; J. Steinbach); Santa Cruz de la Sierra (Lizer & Delétang); Santa Cruz, 420 m (P. S. Ward); *dpto.unknown*: "Bolivia" (Balzan). BRAZIL ac: Vila Taumaturgo (P. L. Herbst); am: 15 km W Envira (D. Williams); Envira (H. Collins); ms: 24 km ESE Aquidauana, 190 m (P. S. Ward); 24 km SW Miranda, 120 m (P. S. Ward); Passo da Lontra, 80 (M. Orr); mt: Chapada dos Guimarães (C. Aman); Coxipo (Silvestri); Cuiabá-Chapada Hwy, km 25, Rio dos Peixes (J. C. Trager); Cáceres (F. M. Oliveira); Fazenda Ipiranga, 14 km S Poconé, 110 m (P. S. Ward); Fazenda Jofra, Transpantanal Hwy. (K. H. Redford); Ilha de Taiamã, R. Paraguai (C. R. F. Brandão); Limoeiro, 10 km S Ilha de Taiamã (C. R. F. Brandão); Mato Grosso (R. N. Williams); Pantanal, Trans-Pantaneira (W. W. Benson); Piuva, 15 km N Ilha de Taiamã (C. R. F. Brandão); Poconé, IBDF (P. Oliveira); Rondonópolis, Area Indig. Tadarimana (M. T. Tavares); Vila Bela [near Mato Grosso] (R. N. Williams); pa: Monte Alegre (C. R. Gonçalves); Mulata, Monte Alegre (C. R. Gonçalves); Santarém (c.u.); rd: Forte Principe da Beira (c.u.); Rio Madeira, Madeira-Mamore R.R. Co. Camp 43 (Mann & Baker); UHE Samuel, nr. Pôrto Velho (Col. Esquistossomose) (c.u.); sp: Castilho, marg. esq. R. Paraná (Exp. Depto. Zool.); Pto. Cantagalo, Presid. Epitácio (O. P. Forattini). COLOMBIA Amazonas: Araracuara (G. Gangi); PNN Amacayacu, Caño Mata-Mata (F. Fernández; "Martha & Adriana leg."); PNN Amacayacu, Caño Mata-Mata at R. Amazonas (F. Fernández). ECUADOR Morona Santiago: Los Tayos (T. de Vries); Rio Bom Boisa (W. von Hagen). PERU Cuzco: Callanga (Staudinger); Ocobamba (Staudinger); Quincemil (Pena); Santa Ana (Río Urubamba), 1300 m (Weyrauch); Vilcanota (Staudinger); Huánuco: Pachitea (Staudinger); nr. confl. Rio Pachitea & Rio Llullapichis (N. L. & C. A. Toft); Junín: Valle Chanchamayo (c.u.);

Valle Chanchamayo, 800 m (Weyrauch); Loreto: Iquitos (Ducke); Rio Amazonas at Rio Shishito, 100 m (B. L. Fisher); Madre de Dios: Manú (c.u.); Pasco: Puerto Bermudez, Rio Pichis (Cornell Univ. Exped.); Rio Pichis (J. C. Bradley); San Martín: 17 km NNE Tarapoto, 400 m (P. S. Ward); Tarapoto (Ule); Tarapoto, 350 m (P. S. Ward).

***Pseudomyrmex ultrix*, sp. nov.**

(*Figs 6, 17, 28, 72, 78, 98*)

Holotype worker. ECUADOR, Napo: 13 km NNE Archidona, 0°48′S, 77°47′W, 960 m, 7.viii.1991, P. S. Ward# 11393 (MCZC). HW 1.19, HL 1.24, EL 0.50, LHT 0.90, PL 0.52, PH 0.52.

Paratypes. Same locality and date as holotype: series of workers, queens and males (to be deposited in BMNH, IZAV, LACM, MCZC, MECN, MUSM, MZSP, PSWC, QCAZ, UCDC, UNCB).

Worker measurements ($n=8$). HL 1.09–1.34, HW 1.04–1.28, MFC 0.112–0.143, LHT 0.77–1.01, CI 0.95–0.97, REL 0.39–0.41, REL2 0.41–0.43, FCI 0.10–0.13, SI 0.44–0.47, FLI 1.55–2.20, FI 0.36–0.39, PLI 0.96–1.05, PWI 1.04–1.14, PPWI 1.55–1.89.

Worker description. Similar to *P. triplarinus* except as follows. Median lobe of antennal sclerite better exposed, PFC/ASD 0.60–0.70. Legs shorter, LHT/HL 0.70–0.77. Junction of dorsal and declivitous faces of propodeum marked by slight angular protuberance, laterally on either side (Fig. 17). Petiole short and high (PLI ≈ 1.00) with broad posterolateral expansion (PWI >1.00, PWI2 0.73–0.80, PWI3 0.38–0.42). Anteroventral petiolar process reduced in size, in the form of a small spine or tooth, directed ventrally (Fig. 17). Sculpture on dorsum of head coarser, the punctures 0.010–0.020 mm in diameter, and separated by about their diameters or less. Body pilosity common (MSC 47–75, HTC 10–16), with some standing hairs visible in outline on the posterior margin of the head (frontal view) (Fig. 6). Pubescence on head more conspicuous than in *P. triplarinus*, the hairs tending to be decumbent, giving the worker a scruffier appearance. Body dark brown, mandibles and anterior third of head a lighter orange-brown, tarsi yellow-brown.

Comments. This species is easily recognized in the worker and queen castes by the very broad petiole (Fig. 28) such that worker PWI>1.00, worker PWI3 <0.43, queen PWI 0.92–0.99 and queen PWI3 0.40–0.42. The otherwise similar *Triplaris*-inhabiting species, *P. dendroicus*, *P. mordax*, *P. triplaridis* and *P. triplarinus*, have worker PWI <1.00, worker PWI3 0.42–0.59, queen PWI 0.63–0.86 and queen PWI3 0.48–0.62. The angular protuberance on the worker propodeum (at the junction of the dorsal and declivitous faces), the small size of the subpetiolar process, and the densely punctate head sculpture are also distinctive features of *P. ultrix*.

Distribution and biology. P. ultrix is known only from the type locality in eastern Ecuador where both mature and incipient colonies were found, inhabiting *Triplaris dugandii* trees. Observations made at the time of collection provide evidence that *P. ultrix* queens compete with, and act as temporary social parasites of, *P. triplaridis* queens during colony initiation. In a partially-cut *Triplaris* tree I found colony-founding, dealate queens of both species occupying internodes of new shoots, together with eggs and pseudococcids. For eight internodes the contents were individually tallied, with the following results. Four internodes housed single *P. ultrix* queens while the other four internodes contained (i) 7 *P. triplaridis* queens, (ii) 6 *P. triplaridis* queens and 1 *P. ultrix* queen, (iii) 5 *P. triplaridis* queens and 1 *P. ultrix* queen, and (iv) 1 *P. ultrix* queen, 9 *P. ultrix* workers (nanitics) and 1 *P. triplaridis* worker (also nanitic). This last nest also had larvae and worker pupae of unknown specific identity. In no case were multiple queens of *P. ultrix* found within a single internode. The data suggest the hypothesis that *P. ultrix* queens exploit a pleometrotic tendency in *P. triplaridis* by temporarily entering into associations with—and presumably mimicking—*P. triplaridis* queens, while excluding conspecific queens. It is worth noting that *P. ultrix* queens are considerably larger than those of *P. triplaridis*: HW 1.43–1.50 ($n=6$) compared with 1.07–1.25 ($n=11$) in *P. triplaridis*.

Material examined. Type material listed above. No other records are known.

Pseudomyrmex viduus (F. Smith)
(*Figs 4, 15, 26, 37, 74, 80, 100*)

Pseudomyrma vidua F. Smith, 1858:158. Syntype male (unique), Ega, Amazonas, Brazil (BMNH) [Examined].

Pseudomyrma caroli Forel, 1899:89. Syntype workers, queens, Nicoya, Costa Rica (Alfaro) (MCSN, MHNG) [Examined] [Synonymy by Ward, 1989:445].

Pseudomyrma latinoda var. *opacior* Forel, 1904b:170. Holotype worker, Cuba ("coll. Ballion, ex-coll. Puls"), apparently lost, not in ISNB nor LMSG (P. Dessart, pers. comm.). **Syn. nov.** [See discussion below].

Pseudomyrma caroli var. *sapii* Forel, 1904c:688. Syntype workers, queens, Bom Fim, Jurua, Amazonas, Brazil (Ule) (AMNH, MCSN, MHNG) [Examined] [Synonymy by Ward, 1989:445].

Pseudomyrma ulei Forel, 1904c:689. Syntype workers, Jurua Miry, Jurua, Amazonas, Brazil (Ule) (AMNH, MCSN, MHNG, NHMB) [Examined] [Synonymy by Ward, 1989:445].

Pseudomyrma triplaridis subsp. *baileyi* Wheeler, 1942:185. Syntype workers, queens, Camaria, Cuyuni River, Guyana (MCZC, USNM) [Examined] [Synonymy by Ward, 1989:445].

Pseudomyrma triplaridis subsp. *tigrina* Wheeler, 1942:186. Lectotype worker, Blairmont, Berbice, Guyana (MCZC) [Examined] [Synonymy and lectotype designation by Ward, 1989:445].

Pseudomyrma triplaridis subsp. *biolleyi* Enzmann, 1944:93. Syntype workers, queens, Camaria Cuyuni River, Guyana (MCZC) [Examined] [Synonymy, under *P. triplaridis baileyi*, by Brown, 1949:43].

Pseudomyrma triplaridis subsp. *trigona* Enzmann, 1944:94. Syntype workers, males, Blairmont, Berbice, Guyana (MCZC) [Examined] [Synonymy, under *P. triplaridis tigrinus*, by Brown, 1949:43].

Pseudomyrmex caroli (Forel); Wheeler & Wheeler, 1956:382 [Description of larva].

Pseudomyrmex viduus (F. Smith); Kusnezov, 1964:83 [First explicit combination in *Pseudomyrmex*].

Pseudomyrmex viduus (F. Smith); Ward, 1989:445 [Brief characterization].

Worker measurements ($n = 35$). HL 0.94–1.30, HW 0.74–0.97, MFC 0.047–0.079, LHT 0.63–0.88, CI 0.70–0.79, REL 0.39–0.44, REL2 0.50–0.57, FCI 0.05–0.09, SI 0.44–0.50, FLI 1.27–1.67, FI 0.44–0.49, PLI 0.75–0.92, PWI 0.73–0.92, PPWI 1.31–1.70.

Worker description. Relatively small species (HW <1.00). Masticatory margin of mandible with 6 (rarely 5 or 7) teeth. Palp formula 5,3. Median clypeal lobe anterolaterally rounded (not sharply angulate), its anteromedial surface deflected ventrally. Frontal carinae less well separated than in most species of the *P. viduus* group (MFC <0.080, PFC <0.120), tending be parallel or slightly converging along most of their course and then more strongly converging posteriorly (ASM ≥ PFC>MFC). Median lobes of antennal sclerites relatively well exposed (PFC/ASD 0.52–0.64; FCI2 0.31–0.53). Scape expanded distally to twice its basal width; funiculus short, also expanded apically, the terminal segment about 1.4–1.6 times the width of the first segment; funicular segment 2 about as broad as, or broader than, long; funicular segments 3–10 notably broader than long. Head elongate (CI <0.80), the sides relatively straight, usually diverging slightly posteriorly; side of head rounding relatively gradually into the posterior margin, which is concave in frontal view. Mesosoma dorsum more or less flattened, metanotal groove moderately incised (MP 0.034–0.077); dorsal face of propodeum somewhat longer than the declivitous face (PDI 1.01–1.51), and meeting the latter at a well rounded angle. Metapleural gland bulla well-developed and conspicuous. Profemur broad (FI >0.43) and legs relatively short, LHT/HL 0.63–0.71. Petiole as in Fig. 15, slightly longer than high (PLI <0.93), with a weakly differentiated anterior peduncle, followed by an increasingly convex anterodorsal face which rounds into the posterior face; posterior face appearing only slightly steeper than anterior face (lateral view). Summit of node behind the midpoint of the petiole (NI 0.51–0.63). Anteroventral petiolar process usually well developed (Fig. 15), variable in shape, subtriangular, bluntly rounded, or fin-shaped, directed ventrally or posteroventrally. In dorsal view (Fig. 26), the minimum (anterior) width of petiole about half the maximum width (PWI3 0.44–0.56). Postpetiole notably broader than long (PPWI >1.30); ventral protrusion of postpetiolar sternite prominent and anteroventral process of postpetiole moderately well developed. Mandible generally sublucid, with scattered elongate punctures and overlying fine striolation. Sculpture on dorsum of head somewhat variable, punctures on the anterior half to two thirds of head relatively dense, evenly spaced, mostly 0.010–0.020 mm in diameter, and separated by about their diameters or less; punctures on upper third of head less dense and more unevenly spaced, separated by several to many diameters, the interspaces either smooth and shiny or very weakly coriarious. Mesosoma dorsum sublucid, with numerous piligerous punctures (separated by one to several diameters); side of mesosoma with sculpture less uniform, with a tendency towards the development of more extensive smooth shiny or weakly coriarious interspaces on parts of the mesopleuron which contrasts with coarser imbricate-punctulate and imbricate-costulate sculpture adjacent to this on the posterior margin of the mesopleuron, on the metapleuron and on the lateral propodeum. Petiole, postpetiole and gaster sublucid, the reflectance dulled (especially on the gaster) by fine punctulae and associated appressed pubescence. Standing pilosity common (MSC 45–88, HTC 8–18); standing and decumbent hairs conspicuous on the posterior margin of head (frontal view) but absent or sparse along the sides (Fig. 4). Appressed pubescence well developed, most conspicuous on the mesosoma, petiole (sparse medially in some individuals), postpetiole and gaster; postpetiole and abdominal tergite IV with appressed hairs separated by much less than their lengths. Body generally concolorous medium- to dark-brown, although in some populations the gaster is darker than rest of body; antennae, frontoclypeal complex, side of head, and distal portions of legs tending to be lighter yellow- or orange-brown in colour.

Comments. *P. viduus* is readily distinguished from all other species in the *P. viduus* group, except *P. vitabilis*, by the elongate head (worker CI 0.70–0.79, queen CI 0.60–0.67, male CI 0.86–0.94). Other characteristic features are the closely contiguous frontal carinae (worker MFC <0.080, queen MFC 0.054–0.090), long eyes relative to head width (worker REL2 >0.49, queen REL2 0.56–0.61), flattened worker mesosoma, and broad profemur (both worker and queen FI 0.44–0.49). For differences between *P. viduus* and *P. vitabilis* see under the latter species.

P. opacior (Forel, 1904b) was described on the basis of a single worker from Cuba and treated as a variety of *P. latinodus* (= *P. concolor*). The type is apparently lost but the original description, in which *P. opacior* is compared to *P. nigrescens* (= *P. penetrator*), agrees reasonably well with that of *P. viduus*. The following combination of features, in particular, is suggestive of *P. viduus* rather than the *P. concolor* complex: worker size small, less than that of 'var. *nigrescens*'; head slightly broader posteriorly than in front; head densely punctate and subopaque; mesosoma dorsum flattened; and petiole shorter and broader than that of *P. nigrescens*. Moreover, *P. viduus* is known from the adjacent Yucatan Peninsula of Mexico, while members of the *P. concolor* complex are apparently confined to South America. The original description also does not match that of any other *Pseudomyrmex* species known from Cuba. (The other Cuban species are *P. cubaensis*, *P. pallidus*, *P. pazosi*, *P. simplex*, and *P. subater*; see Ward, 1992.) On the other hand, I have seen no specimens of *P. viduus* (or a *P. viduus*-like species) from the island, so the rediscovery of this taxon in Cuba remains a challenge.

Distribution and biology. After *P. kuenckeli*, this is the most widespread species in the *P. viduus* group, ranging from Mexico to Bolivia and Brazil (Fig. 163). It is also the least host-specific of the species inhabiting living plant cavities: colonies have been collected from *Cordia alliodora* (Ruiz & Pavón) Oken (Costa Rica), *Coussapoa* (Brazil), *Ficus* (?) branches (Colombia, Peru), *Macrolobium acaciifolium* (Bentham) Bentham (Ecuador), *Ocotea* (Costa Rica, Peru), *Pseudobombax munguba* (Martius & Zuccarini) Dugand (Brazil, Colombia), *Pseudobombax* cf. *septenatum* (Jacquin) Dugand (Colombia), *Pterocarpus amazonum* (C. Martius ex Bentham) Amshoff (Colombia), *Sapium* (Brazil, Ecuador), *Triplaris melaenodendron* (Bertoloni) Standley & Steyermark (Costa Rica), *Triplaris weigeltiana* (Venezuela, Guyana), unidentified species of *Triplaris* (Colombia, Venezuela), and hollow stems of an unidentified Papilionoideae (Guyana). There is even a record of a colony-founding queen from *Cecropia* (Peru). In his study of ant-plant associations in Costa Rica, Longino (1996) noted that both *Pseudomyrmex viduus* and *Azteca beltii* Emery had exceptionally broad host ranges compared to most other plant-ants.

Earlier literature dealing with *P. viduus* includes Wheeler's (1942) and Bailey's (in Wheeler, 1942:51–52) fascinating observations on this species in Guyana (under the name *P. triplaridis baileyi*). They reported it to be a fierce, aggressive ant, occupying the internodes of *Triplaris weigeltiana* (= *T. surinamensis*) branches and cohabiting with the pseudococcid *Farinococcus multispinosus* Morrison and the coccid *Cryptostigma inquilina* (Newstead) (cited as *Akermes secretus* Morrison), in addition to nematodes and fungi that fed on the ant middens. Bailey's examination of the food pellets of *P. viduus* larvae revealed not only the remains of coccoids but also those of fungal hyphae and nematodes.

In my experience the nests of this species always contain pseudococcids or coccids. In a recent collection of *P. viduus* from live branches of *Sapium utile* (7 km ESE Pto. Misahuallí, Ecuador; P. S. Ward#11320) the coccids were identified as belonging to the genus *Cryptostigma* (plant identification by G. Webster, coccids by P. J. Gullan).

Material examined (AMNH, BMNH, CASC, CELM, CUIC, FFIC, INBC, INPA, IZAV, KSUC, KWJC, LACM, MCSN, MCZC, MHNG, MPEG, MZSP, NHMB, PSWC, UCDC, USNM, WWBC). BELIZE Belize: Belize (c.u.; Baker); Manatee [River] (J. D. Johnson). BOLIVIA Beni: Rurrenabaque (W. M. Mann); La Paz: Asunta [as "Osunto"] (G. MacCreagh); Huachi (W. M. Mann). BRAZIL ac: Jurua Miry (Ule); Jurua Miry, Jurua (Ule); am: "Amazonas" (A. Göldi); Barreirinha (P. Murça Pires); Bom Fim, Jurua (Ule); Ega [= Tefé] (Bates); Furo de Silves ("Exp. Perm. Amaz."); Ilha de Curarí (J. Adis); Ilha de Marchantaria (J. Adis *et al.*); Ilha de Marchantaria, Lago Camaleão (J. Adis *et al.*); Ilha de Marchantaria, Lago Central (J. Adis *et al.*); Itacoatiara (Mann & Baker); Marãa, Rio Japurá, Maguari (J. Dias); Paraná Apara, nr. Lago Mamiraua, Tefé (D. Murawski); Paraná de Tonantins, Tonantins (S. A. More *et al.*); ap: Amicohy, braço sul (Lane & Bicelli); Rio Amapari, Cachoeira Tatú (Lane & Bicelli); Rio Felicio [nr. Serra do Navio] (J. Lane); ap [?]: "Aruagares" [?] [= Rio Araguari?] (c.u.); mt: Sinop (M. Alvarenga pa: Alenquer (W. França); Belém [as "Pará"] (C. R. Gonçalves; c.u.); Cach. Grande (Sampaio); Chaves, Ilha Caviana, Fazenda São Luis (M. Fernandes); Ile Mexiana [Ilha Mexiana] (G. Hagmann); Oriximiná (A. Y. Harada); Rio Cuminá [= lower Rio Parú do Oeste] (Sampaio); Serra Tumuc-Haumac (Sampaio); pa [?]: "Lower Amazon" (J. G. Myers); rd: Abunã, Rio Madeira (Mann & Baker); Porto Velho, Rio Madeira (Mann & Baker). COLOMBIA Amazonas: Araracuara (G. Gangi); Chocó: La Balsa, 50–80 m (L. F. Mendoza); Cundinamarca: Farallones de Medina, 600 m (G. Fagua); Meta: Acacias (I. Zenner); RNN La Macarena, Caño La Curía, 580 m (F. Fernández); RNN La Macarena, Vistahermosa, 400 m (F. Fernández). COSTA RICA Alajuela: 11mi N Florencia (D. H. Janzen); Guanacaste: 6 mi S Cañas (D. H. Janzen); 6mi S, 6mi W Cañas (D. H. Janzen); Est. Biol. Palo Verde, <100 m (J. Longino); Nicoya (A. Alfaro); P.N. Santa Rosa, 300 m (J. Longino); Rio Taboga (C. R. Carroll); Limón: Res. Biol. Hitoy-Cerere, 100 m (J. Longino); Puntarenas: Est. Biol. Carara, 30 m (J. Longino); Guacimal, 300–400 m (J. Longino); Los Loros, near Puntarenas (F. Knab); Pita, 200 m (J. Longino); Reserva Biol. Carara, 40 m (P. S. Ward). ECUADOR Napo: Jatun Sacha, 7 km ESE Pto. Misahuallí, 400 m (P. S. Ward); Reserva Faunistica Cuyabeno (L. J. Vitt). EL SALVADOR La Libertad: Quezaltepeque (D. Q. Cavagnaro & M. E. Irwin). GUATEMALA Alta Verapaz: Cacao Trece Aguas (Barber & Schwarz; Schwarz & Barber); Escuintla: Escuintla (W. M. Wheeler); Finca Caobanal (J. Gilardi); San José (E. S. Ross); Izabal: Izabal (Kellerman); Retalhuleu: 5.3 mi E [NE] Champerico (D. H. Janzen); 5mi W Retalhuleu (D. H. Janzen). GUYANA Cuyuni-Mazaruni: Aurora, Cuyuni R. (L. Gillespie); Camaria (W. M. Wheeler); Cuyuni R. (W. J. Lavarre); Cuyuni R., nr. Camaria (W. M. Wheeler); Kartabo (W. M. Wheeler); Mahaica-Berbice: Blairmont, Berbice (H. Box; H. E. Box). HONDURAS Atlántida: La Ceiba (F. J. Dyer); San Juan Pueblo (W. M. Mann); Comayagua: 15.7 mi N Siguatepeque, 530 m (D. H. Janzen). MEXICO Chis.: 8 km NW Ruinas

Bonampak, 400 m (P. S. Ward); Oax.: 5 mi E Temascal (D. H. Janzen); Tuxtepec (Schneirla); Tab.: Villahermosa (P. J. Spangler); Yuc.: "Yucatan" (G. F. Gaumer). NICARAGUA Chinandega: "Consequina Slope" [Volcán Cosigüina] (M. Willows); León: León (B. Garcete). PANAMA Chiriqui: Caldera (Champion); Colón: vic. Pta de los Chivos, 3 km SW Gatun, 100 m (W. L. Brown *et al.*); Juan Gallegos I. (R. B. Kimsey); Herrera: 5 km NW Chitre, 150 m (E. S. Ross); Panamá: Barro Colorado I. (c.u.; C. W. Rettenmeyer; W. L. Brown & E. S. McCluskey); Summit (N. L. H. Krauss); Trinidad Rio (A. Busck). PERU Huánuco: Panguana, 260 m (M. Verhaagh); Tingo Maria (Rio Huallaga), 700 m (Weyrauch); Madre de Dios: 30 km SW Pto. Maldonado, 290 m (D. W. Davidson); San Martín: 24 km NNE Tarapoto, 220 m (P. S. Ward); La Perla, 21 km NNE Tarapoto, 220 m (P. S. Ward). SURINAM Para: Paramaribo (A. Reyne). TRINIDAD Mayaro: Mayaro Bay (N. Weber); St. George: St. Augustine, upper St. John's Rd. (L. R. Davis, Jr.). VENEZUELA Aragua: Bahia de Turiamo (H. Romero); Maracay, 450 m (P. S. Ward); Barinas: 17 km SSW Cuidad Bolivia, 240 m (P. S. Ward); Bolívar: 111 km S Tumeremo (J. E. Lattke); 12 km ENE Tumeremo, 200 m (P. S. Ward); Campamento Río Grande, 250 m (P. S. Ward); Delta Amacuro: "Orinoco Delta" (N. Weber; N. A. Weber); Dto. Federal: Caracas, Jardín Botánico (J. E. Lattke); Miranda: Caucagua (W. Aragort); Yaguapita (W. Aragort); Monagas: Parque Nacional A. Humboldt, 1150 m (J. E. Lattke); Zulia: El Tucuco, Perija (R. W. Brooks *et al.*).

***P. vitabilis*, sp. nov.**

(*Fig. 38*)

Holotype queen. COLOMBIA, Amazonas: PNN Hamaca-Yacu, Caño Mata-Mata, iii. 1988, Malaise trap, (P. Kelsey) (UNCB). 1 alate queen.

Holotype queen measurements. HL 1.26, HW 0.71, MFC 0.042, LHT 0.76, CI 0.56, REL 0.38, REL2 0.68, FCI 0.06, SI 0.50, FLI 1.64, FI 0.46, PLI 0.61, PWI 0.61, PPWI 1.31.

Queen description. Small species for the *P. viduus* group (see measurements above). Palp formula 5,3. Median clypeal lobe anterolaterally rounded, weakly angulate medially. Frontal carinae separated by more than basal scape width anteriorly (ASM 0.0096, PFC 0.075), strongly converging posteriorly (MFC 0.042). Median lobe of antennal sclerite relatively well exposed (PFC/ASD 0.51, FCI2 0.29). Scape short (SI2 0.73), expanded distally; funiculus short, also expanded apically, the terminal segment about 1.7 times the width of the first segment; funicular segments 2–10 broader than long. Head very elongate (CI 0.56), the sides subparallel, rounding into distinctly concave posterior margin (Fig. 38). Mesosoma dorsum elongate and flattened; dorsal face of propodeum about 1.5 times longer than the declivitous face, and meeting the latter at a well rounded angle. Metapleural gland bulla well-developed and conspicuous. Profemur broad (FI 0.46) and legs relatively short, LHT/HL 0.60. Petiole low and elongate, lacking a clearly differentiated anterior peduncle, gently sloping anterodorsal face rounding gradually into steeper posterior face. Summit of node well behind the midpoint of the petiole (NI 0.63). Anteroventral petiolar process developed as a stout triangular tooth. In dorsal view, the minimum (anterior) width of petiole about half the maximum width (PWI3 0.53). Postpetiole notably broader than long, not strongly protruding ventrally; anteroventral process of postpetiole well developed. Mandible sublucid, with scattered elongate punctures and poorly-defined overlying striolation. Dorsum of head punctate; punctures on the anterior half of head dense, evenly spaced, mostly 0.010–0.015 mm in diameter, and separated by about their diameters or less, except for a median strip where they are less dense and accompanied by larger elongate punctures; punctures on upper half of head becoming much less dense and more unevenly spaced, separated by many diameters, the interspaces smooth and shiny. Venter of head densely punctate throughout. Mesosoma smooth and shining, with numerous punctures (separated by one to several diameters), grading into a coarser imbricate-punctulate sculpture on the lower mesopleuron and parts of the metapleuron. Petiole, postpetiole and gaster sublucid, the reflectance dulled (especially on the gaster) by very fine punctulae and associated appressed pubescence. Standing pilosity common (MSC about 38, HTC 8–9); suberect and subdecumbent hairs conspicuous on the posterior margin of head (frontal view) but essentially absent along the sides (Fig. 38). Appressed pubescence well developed, most conspicuous on the postpetiole and gastric tergites; appressed hairs on abdominal tergite IV separated by much less than their lengths. Light orange-brown to medium-brown in colour, the appendages lighter and the gaster a darker brown.

Comments. Known only from the holotype queen, this curious species has features that suggest an exaggerated version of *P. viduus*. The head is even more elongate (CI 0.56 compared to 0.60–0.67 in *P. viduus* queens; see also Figs 37, 38), with a greater REL2 index (0.68 compared to 0.56–0.61) and smaller size (HW 0.71 and LHT 0.76 compared to HW 0.86–0.96 and LHT 0.81–0.94). The queens of all other species in the *P. viduus* group differ from *P. viduus* in the opposite directions to those listed above. Features in common between *P. vitabilis* and *P. viduus* include the elongate head, closely contiguous frontal carinae, broad profemur and petiole shape.

OTHER *PSEUDOMYRMEX* SPECIES ASSOCIATED WITH *TACHIGALI* AND *TRIPLARIS*

Introduction

The principal ant-plants occupied by members of the *P. viduus* group, *Tachigali* (Fabaceae) and *Triplaris* (Polygonaceae), are also inhabited by other unrelated species of *Pseudomyrmex* in parts of their ranges (Ward, 1991). To assist those interested in studying these ant-plant relationships, I include descriptions of these other taxa (see also couplets 14–24 of the worker/queen key on pages 483–485). All are members of the *P. sericeus* group except *P. elongatus* (*P. oculatus* group), *P. gracilis* (*P. gracilis* group) and *P. hospitalis* (*P. gracilis* group). Diagnoses of these species groups are given in Ward (1989). Nine of the twelve species discussed below appear to be obligate inhabitants of live plant cavities, while the other three (*P. elongatus, P. gracilis, P. ita*) are generalist twig-nesting species which occasionally colonize ant-plants.

The following features are characteristic of all species in the *P. sericeus* group and are not repeated in the descriptions below. Mandibles with 8–10 teeth on the masticatory margin; median clypeal lobe tectiform, with convex anterior margin; distance between frontal carinae slight to moderate (see MFC and FCI values of each species); eyes elongate, eye length more than half head length (see REL values);

standing pilosity sparse, absent from the external faces of tibiae (HTC $=0$); usually fewer than ten standing hairs visible in outline on mesosoma dorsum, typically 1–2 pairs on the pronotum, and 0–1 pair on the propodeum at the juncture of the basal and declivitous faces (worker MSC 2–12); petiole usually with a single pair of stout setae directed posterodorsally; integument densely punctulate and subopaque, and this, in combination with a very dense but exceedingly fine pubescence, imparts a silky lustre to the body.

Synonymic list of species

P. crudelis **sp. nov.** Peru
P. deminutus **sp. nov.** Brazil
P. eculeus **sp. nov.** Ecuador, Peru
P. elongatus (Mayr, 1870) United States (Florida); Mexico to Bolivia and Brazil
For full listing of synonymy see Ward (1989:419).
P. ferox **sp. nov.** Peru, Colombia, Brazil
P. fortis (Forel, 1899) **stat. nov.** Mexico to Colombia, Venezuela
P. gracilis (Fabricius, 1804) United States to Argentina
For full listing of synonymy see Ward (1993:155).
P. hospitalis **sp. nov.** Peru
P. ita (Forel, 1906) Mexico to Colombia
= *P. acaciarum* (Wheeler, 1942) (synonymy by Ward, 1993)
= *P. acaciorum* (Enzmann, 1944) (synonymy, under *acaciarum*, by Brown, 1949)
P. pictus (Stitz, 1913) Colombia, Peru, Bolivia, western Brazil
= *P. heterogyna* (Wheeler & Mann, 1942a) **syn. nov.**
= *P. castus* (Wheeler, 1942) **syn. nov.**
= *P. humboldi* (Enzmann, 1944) **syn. nov.**
P. rubiginosus (Stitz, 1913) **stat. nov.** Colombia, Peru, western Brazil
= *P. huberi* (Santschi, 1922) **syn. nov.**
P. vinneni (Forel, 1906) **stat. nov.** Colombia, Venezuela, Peru, Brazil

Species accounts

***Pseudomyrmex crudelis*, sp. nov.**
(*Figs 45, 54, 63*)

Holotype worker. PERU, San Martín: 24 km NNE Tarapoto, 6°18′S, 76°16′W, 220 m, 23.viii.1986, ex *Tachigali*, P. S. Ward# 8705 (MCZC). HW 1.05, HL 1.24, EL 0.75, LHT 0.88, PL 0.45, PH 0.47.

Paratypes. Same data as holotype: series of workers queens, males (BMNH, LACM, MCZC, MUSM, MZSP, PSWC, UCDC).

Worker measurements ($n=10$) HL 1.20–1.29, HW 1.00–1.13, MFC 0.024–0.053, LHT 0.81–0.93, CI 0.83–0.89, REL 0.59–0.62, REL2 0.68–0.73, FCI 0.02–0.05, FI 0.43–0.47, PLI 1.01–1.13, PWI 0.91–1.03.

Worker description. A member of the *P. sericeus* group. Palp formula 6,4 (rarely 6p5,4). Frontal carinae moderately separated; eyes of short to medium length for the species group (see REL values). Head relatively elongate (CI <0.90), the sides only weakly convex, the posterior margin slightly to moderately concave, in full-face view (Fig. 45). Profemur moderately slender. Dorsal face of propodeum subequal in length to declivitous face, in profile the two faces meeting at a rounded angle. Petiole high and broad (Figs 54, 63), with more or less differentiated anterior and dorsal faces, dorsal face rounding into steep posterior face. Anteroventral petiolar process prominent, with posteriorly-directed tooth (Fig. 54). Standing pilosity sparse, typically one pair of long stout setae on the pronotal humeri, petiole and postpetiole, rarely on the propodeum. Dark brownish-black, the appendages lighter; mandibles, frontoclypeal complex and protibia yellowish-brown.

Comments. Workers and queens of *P. crudelis* are distinguished from other species in the *P. sericeus* group by the combination of medium size (worker HW 1.00–1.13, queen HW 1.13–1.22), relatively narrow worker head, and broad, subtrapezoidal petiole (Fig. 54) (worker DPW/HW 0.39–0.42, queen DPW/HW 0.49–0.52). The mesonotum of the male has an unusual anteromedial protrusion, not seen in any other *Pseudomyrmex* species.

Distribution and biology. This species is known only from *Tachigali* growing in the western foothills of the Amazon basin. Workers keep pseudococcids as well as brood in the *Tachigali* domatia, and they are as aggressive in the defense of their nest sites as species in the *P. viduus* group.

Material examined. Type material listed above plus the following: PERU HUÁNUCO: Panguana, 220–260 m (M. Verhaagh); SAN MARTÍN: Convento, 26 km NNE Tarapoto, 220 m (P. S. Ward); Davidcillo, 30 km NNE Tarapoto, 220 m (P. S. Ward) (BMNH, LACM, MCZC, MUSM, MZSP, PSWC, SMNK, UCDC).

***Pseudomyrmex deminutus*, sp. nov.**

(*Figs 50, 59, 68*)

Holotype alate queen. BRAZIL Amazonas: Rio Juma, near Apui, 400 km E Humaita, Transamazonica Hwy. [7°08′S, 59°57′W], 30.iv.1985, ex *Tachigali*, F. Rickson B-41-85 (MCZC). HW 0.78, HL 1.19, EL 0.70, LHT 0.68, PL 0.52, PH 0.45.

Paratypes. Same data as holotype: two alate queens (MZSP, PSWC).

Queen measurements ($n=3$). HL 1.19–1.21, HW 0.78, MFC 0.015–0.022, LHT 0.67–0.68, CI 0.65–0.66, REL 0.58–0.59, REL2 0.89–0.90, FCI 0.02–0.03, FI 0.52–0.53, PLI 0.87–0.88, PWI 0.69–0.72.

Queen description. A species in the *P. sericeus* group of small stature (HW <0.80, LHT <0.70). Palp formula 5,4. Frontal carinae closely contiguous; head elongate, with straight sides and concave posterior margin, in frontal view; eyes relatively short in relation to head length (REL <0.60); profemur very broad (see FI values). Petiole as in Figs 59 and 68, relatively low, long and narrow, not expanded posterolaterally; petiolar node rounded in lateral view, without differentiated anterior and dorsal faces. Anteroventral petiolar process thin and blunt. Standing pilosity sparse, a pair of long, thin, pale setae on the anterior pronotum, posterior pronotum, mesoscutellum, petiole, and postpetiole. Brownish-black, the antennae, frontoclypeal complex, protibia, and tarsi yellow-brown.

Comments. The worker of *P. deminutus* is unknown, but the queens are so distinct that a description seems warranted. There are no other known species in the *P. sericeus* group in which the queen has such an elongate head (CI $\approx$ 0.66). The small size, relatively short eyes (for the species group), broad profemur and narrow petiole (Fig. 68) are also distinctive. In petiole shape *P. deminutus* is perhaps closest to *P. vinneni* but the queens of that species are larger (HW 0.96–1.06) with broader heads (CI 0.77–0.81) and longer eyes (REL 0.60–0.63).

Distribution and biology. The only known collection is from *Tachigali* in southern Amazonas state, Brazil.

Material examined. Known only from the type material.

***Pseudomyrmex eculeus*, sp. nov.**
(*Figs 42, 51, 60*)

Holotype worker. ECUADOR, Napo: Jatun Sacha, 1°04′S, 77°36′W, 450 m, 13.ix.1992, ex *Tachigali*, B. L. Fisher #458 (MCZC). HW 1.16, HL 1.19, EL 0.76, LHT 1.03, PL 0.43, PH 0.45.

Paratypes. Same data as holotype: series of workers, 1 queen; same locality, ex *Tachigali*, M. Asanza# 86: four workers; same locality, 400 m, ex *Tachigali*, P. S. Ward# 11384: four dealate queens (BMNH, LACM, MCZC, MECN, MUSM, MZSP, PSWC, QCAZ, UCDC).

Worker measurements ($n = 9$). HL 1.16–1.30, HW 1.13–1.25, MFC 0.030–0.054, LHT 0.97–1.11, CI 0.94–0.99, REL 0.61–0.65, REL2 0.63–0.67, FCI 0.03–0.05, FI 0.39–0.42, PLI 1.04–1.14, PWI 0.83–0.93.

Worker description. A member of the *P. sericeus* group. Palp formula: mostly 6,4, but some individuals apparently 5,3. Frontal carinae relatively well separated; head broad, with strongly convex sides; posterior margin of head straight or (less commonly) slightly concave, in frontal view. Profemur very slender (see FI values); legs long (LHT/HL 0.82–0.88). Dorsal face of propodeum flat, submarginate laterally, subequal in length to declivitous face, and rounding into it; propodeal spiracle close to the basal (dorsal) face of propodeum. Petiole short, high, subtriangular in profile, with a single convex anterodorsal face, which rounds gently into the steep posterior face (Fig. 51). Anteroventral process prominent, subrectangular, with a blunt posteroventral angle. Standing pilosity sparse but more common than is usual for the species group. Long, golden, paired (and often curved) setae usually present on pronotum (1–2 pairs), mesonotum (0–1 pairs), on propodeum at the junction of the dorsal and declivitous faces (0–1 pairs), petiole (1–2 pairs) and postpetiole (1–2 pairs); these setae sometimes unpaired, or accompanied by one or two additional shorter setae. Black or very dark blackish-brown, with appendages and frontoclypeal complex contrastingly orange-brown; funiculus and parts of middle and hind legs infuscated.

Comments. This species is related to *P. pictus* and *P. ferox*. All three are characterized by having broad worker heads (CI $\geq$0.91), short petioles with a subtriangular profile, long legs, and large queens (queen HW >1.30). *P. eculeus* can be distinguished from *P. ferox* by its longer legs, more slender worker profemur, and the position of the worker propodeal spiracle close to the flattened dorsal face; and from *P. pictus* by its much darker body color, shape of the propodeum, and smaller size.

Distribution and biology. A *Tachigali* inhabitant with aggressive workers, *P. eculeus* is known only from the type locality and an adjacent region in northern Peru.

Material examined. Type material listed above plus the following: PERU Amazonas: Yamayakat, Rio Alto Marañon, 350 m, ex *Tachigali formicarum* (P. Stern) (MCZC, MUSM, PSWC).

Pseudomyrmex elongatus (Mayr)

Pseudomyrma elongata Mayr, 1870:413. Lectotype worker, S. Fe de Bogota, Colombia (Schaufuss) (NHMV) [Examined] [Lectotype designation by Ward, 1989:419]. For a full listing of synonymy see Ward (1989:419).

Worker measurements (*n* = 55). HL 0.73–0.93, HW 0.56–0.68, MFC 0.011–0.027, CI 0.66–0.79, REL 0.53–0.59, REL2 0.73–0.82, FCI 0.02–0.05, FI 0.43–0.56, PLI 0.79–1.09, PWI 0.62–0.87.

Worker description. With the characteristics of the *P. oculatus* group (i.e. palp formula 6,3; masticatory margin of mandible with 5 teeth; median clypeal lobe protruding, tectiform, in dorsal view its anterior margin convex and laterally rounded; frontal carinae subcontiguous; petiolar node relatively short and high, apedunculate; standing pilosity and appressed pubescence common on most of body, MSC >15) and the following more specific features. Relatively small (HW <0.70), with elongate head and eyes (see CI, REL and REL2 values); petiole short (PLI >0.78), rounded in lateral profile; head densely and finely punctate, predominantly opaque; body medium to dark brown in colour.

Comments. This small species (worker HW <0.70, queen HW 0.56–0.61) with its elongate, densely punctate head is unlikely to be confused with any of the other *Pseudomyrmex* recorded from *Triplaris* or *Tachigali*. For further description see Ward (1989:419).

Distribution and biology. *P. elongatus* is found throughout the Neotropics, from southern United States (Florida) and Mexico to Bolivia and Brazil (Ward 1989). It is a generalist twig-nester which is occasionally found in plant domatia. There is at least one record from *Triplaris cumingiama* (Wheeler, 1942:56, as *Pseudomyrma alliodorae*).

***Pseudomyrmex ferox*, sp. nov.**
(*Figs 43, 52, 61*)

Holotype worker. PERU, San Martín: 8 km ENE Tarapoto, 6°27′S, 76°18′W, 700 m, 19.viii.1986, ex *Tachigali*, P. S. Ward# 8604 (MCZC). HW 1.25, HL 1.24, EL 0.76, PL 0.42, PH 0.46.

Paratypes. Same data as holotype: series of workers, queens, males (BMNH, LACM, MCZC, MUSM, MZSP, PSWC, UCDC).

Worker measurements ($n = 13$). HL 1.05–1.29, HW 1.06–1.26, MFC 0.041–0.064, LHT 0.81–0.96, CI 0.93–1.01, REL 0.60–0.65, REL2 0.61–0.67, FCI 0.04–0.05, FI 0.43–0.47, PLI 1.07–1.26, PWI 0.89–1.00.

Worker description. A member of the *P. sericeus* group. Palp formula: usually 6,4 but 5, 3 in at least one worker. Frontal carinae well separated; head broad, with convex sides; posterior margin of head flat or (more commonly) slightly concave, in frontal view. Profemur moderately slender (see FI values); legs moderately long (LHT/HL 0.72–0.77). Dorsal face of propodeum somewhat convex in profile, subequal in length to declivitous face, and rounding gradually into it; propodeal spiracle distant from basal (dorsal) face of propodeum. Petiole short, high, subtriangular in profile, with a single convex anterodorsal face, which rounds gently into the steep posterior face (Fig. 52). Anteroventral process moderately well developed, usually subtriangular, with a blunt, posteroventrally-directed tooth or angle. Standing pilosity sparse but more common than is usual for the species group. Long, golden, paired (and often curved) setae present on pronotum (2–5 pairs), petiole (1–2 pairs) and postpetiole (1–2 pairs), less commonly on mesonotum or propodeum; these setae sometimes unpaired, or accompanied by one or two additional shorter setae. Dark brown to brownish black, with appendages and frontoclypeal complex orange-brown; antennae and parts of middle and hind legs infuscated.

Comments. P. ferox can be identified by the broad worker head, subtriangular petiolar profile, and intermediate leg length (longer than most species but shorter than *P. eculeus* and *P. pictus*; see key). The well-separated frontal carinae, moderately broad profemur, and convex dorsal face of the propodeum are also characteristic.

Distribution and biology. This is another obligate inhabitant of *Tachigali*, with aggressive stinging workers. It is known from several scattered locations in northern Peru, Colombia and Brazil. Greg Gangi's Colombian collections were made from plants identified as *Tachigali* sp. and *Tachigali ptychophysca* Spruce ex Bentham.

Material examined. Type material listed above plus the following: BRAZIL MT: Aripuaná (M. Gomes & C. Damião); COLOMBIA AMAZONAS: Araracuara (G. Gangi); PERU SAN MARTÍN: Convento, 26 km NNE Tarapoto, 220 m (P. S. Ward); LORETO: 15 km WSW Yurimaguas, 200 m (P. S. Ward) (BMNH, FFIC, LACM, MCZC, MUSM, MZSP, PSWC, UCDC).

Pseudomyrmex fortis (Forel), **stat. nov.**
(*Figs 46, 55, 64*)

Pseudomyrma sericea var. *fortis* Forel, 1899:89. Syntype worker, Atoyac, Veracruz, Mexico (H. H. Smith) (BMNH) [Examined].

Pseudomyrmex sericeus var. *fortis* Forel; Kempf, 1972:223. [First explicit combination in *Pseudomyrmex*].

Worker measurements ($n = 10$). HL 1.14–1.38, HW 0.96–1.15, MFC 0.038–0.068, LHT 0.72–0.93, CI 0.81–0.86, REL 0.57–0.59, REL2 0.67–0.71, FCI 0.04–0.06, FI 0.48–0.50, PLI 0.90–1.10, PWI 0.81–0.92.

Worker description. A member of the *P. sericeus* group. Palp formula: variable (6,4 or 5,4). Frontal carinae well separated; head somewhat elongate, sides weakly convex; posterior margin of head concave, in frontal view. Profemur broad; legs relatively short (LHT/HL 0.62–0.70). Dorsal face of propodeum subequal in length to declivitous face, and rounding gradually into it; propodeal spiracle distant from basal (dorsal) face of propodeum. Petiole subglobose, rounded in profile, with a single convex anterodorsal face, which rounds gently into the steep posterior face (Fig. 55). Anteroventral process well developed, a triangular or subrectangular lobe, usually with a blunt posteroventral tooth or angle. Standing pilosity sparse; stout, paired setae usually present on pronotum (1–2 pairs), propodeum at junction of basal and declivitous faces (0–1 pair), petiole (1 pair) and postpetiole (1–2 pairs), occasionally additional short hairs present on mesosoma. Dark brown to brownish black; mandibles and frontoclypeal complex a lighter castaneous brown; scape, protibia and protarsus may also be a lighter brown.

Comments. Key distinguishing features of *P. fortis* are the relatively large size yet elongate head (worker CI 0.81–0.86, queen CI 0.72–0.73), relatively short eyes in relation to head length (worker REL 0.57–0.59, queen REL 0.53–0.56), broad and subglobose petiole, with prominent anteroventral process (Fig. 55), and unicoloured body. The worker has well separated frontal carinae and a broad profemur (FI>0.47). *P. fortis* bears little close resemblance to *P. sericeus* which is smaller (worker HW <0.95), with closely contiguous frontal carinae, elongate eyes (worker REL $\approx$0.65), a short high propodeum whose basal and declivitous faces meet at an angle, and a petiole which is subtriangular in lateral profile.

Distribution and biology. There are scattered records of this species from Mexico, Guatemala, Costa Rica, Colombia and Venezuela. Little is known about its biology, but Wheeler (1913, 1942) reported the species inhabiting *Triplaris melaenodendron* (as *T. "auriculata"*) at Patulul and Escuintla, Guatemala, and he indicated that the workers sting readily (ant specimens examined in the MCZC and their identity confirmed). Wheeler & Bailey (1920:264) examined larval food pellets of these *P. fortis* and found remains of insects, fungi, and bits of "medullary tissue evidently gnawed from the walls of the myrmecodomatia by the workers". A population of *P. fortis* in northern Colombia—with somewhat divergent morphology, the workers being small with short petioles—also has aggressive workers, which inhabit live *Avicennia* branches and tend coccids of the genus *Cryptostigma* (Ward, 1991). I suspect that *P. fortis* will prove to be a "generalist" plant-ant species, i.e. one which, like *P. viduus*, *P. rubiginousus*, and some *Azteca* species (Longino, 1996), occupies a variety of live plant cavities.

Pseudomyrmex gracilis (Fabricius)
(*Fig. 41*)

Formica gracilis Fabricius 1804:405. Lectotype worker, Essequibo, Guyana (ZMUC) [Examined] [Lectotype designation by Ward, 1989:439].
For a complete listing of synonymy see Ward (1993:155).

Worker measurements ($n = 74$). HL 1.38–1.99, HW 1.39–2.07, MFC 0.033–0.079, LHT 1.10–1.84, CI 0.95–1.08, REL 0.54–0.65, REL2 0.54–0.65, FCI 0.02–0.04, FI 0.36–0.44, PLI 0.46–0.57, PWI 0.38–0.54.

Worker description. With the traits of the *P. gracilis* group (i.e. palp formula 6,4; masticatory margin of mandible with 7–10 teeth; median clypeal lobe laterally rounded; eyes large and elongate; standing pilosity common on mesosoma dorsum and on external faces of tibiae; pronotum dorsolaterally submarginate) and the following more specific features. Head broad, about as wide as long (CI 0.95–1.08); anterior margin of median clypeal lobe straight to broadly convex; in lateral view mesonotum more steeply inclined than dorsal face of propodeum; petiole long and slender (PLI 0.46–0.57) with a well developed anterior peduncle (Fig. 41); head and mesosoma densely and finely punctulate-coriarious to coriarious-imbricate, subopaque to sublucid (not matte) in appearance; standing pilosity abundant, fine, predominantly pale silvery-white (not black). Size and colour extremely variable (HW 1.39–2.07), varying from unicolorous black (appendages lighter) to unicolorous orange-brown, with many intermediate and bicoloured combinations.

Comments. Differences between *P. gracilis* and *P. hospitalis* are discussed under the latter species. See Ward (1993:155) for additional details on the taxonomy of *P. gracilis*.

Distribution and biology. *P. gracilis* is a widespread eurytopic species, found from southern United States to Argentina. The species typically nests in dead twigs or branches of various unspecialized plants, but it is also an occasional occupant of myrmecophytes, including *Triplaris* (Wheeler, 1942:56).

***Pseudomyrmex hospitalis*, sp. nov.**

(*Figs 39, 40*)

Holotype worker. PERU, San Martín: 8 km ENE Tarapoto, 6°27′S, 76°18′W, 700 m, 19.viii.1986, ex *Tachigali*, P. S. Ward# 8612 (MCZC). HW 1.84, HL 1.79, EL 1.10, LHT 1.46, PL 0.91, PH 0.63.

Paratypes. Same data as holotype: series of nine workers (BMNH, LACM, MCZC, MUSM, MZSP, PSWC).

Worker measurements ($n=5$). HL 1.70–1.81, HW 1.76–1.84, MFC 0.060–0.076, LHT 1.37–1.46, CI 1.02–1.04, REL 0.61, REL2 0.58–0.60, FCI 0.03–0.04, FI 0.42–0.43, PLI 0.67–0.70, PWI 0.55–0.59.

Worker description. With the traits of the *P. gracilis* group (i.e. palp formula 6,4; masticatory margin of mandible with 7–10 teeth; median clypeal lobe laterally rounded; eyes large and elongate; standing pilosity common on mesosoma dorsum and on external faces of tibiae; pronotum dorsolaterally submarginate) and the following more specific features. Relatively large species (see worker HW and LHT values); head broad, as wide or wider than long; anterior margin of median clypeal lobe straight to slightly convex; frontal carinae separated by less than basal scape width; in lateral view mesonotum more steeply inclined than dorsal face of propodeum; dorsal face of propodeum longer than declivitous face, and rounding insensibly into it; legs relatively short, LHT/HW 0.78–0.79; petiole relatively high and broad (see PLI and PWI values) with short anterior peduncle (Fig. 40). Mandible subopaque, with scattered coarse punctures and fine striolate sculpture; head and mesosoma densely but finely punctulate-corarious to corarious-imbricate, subopaque to sublucid. Standing pilosity abundant, a mixture of fine pale silvery-white hairs and thicker, longer black setae; latter visible in profile on the head, mesosoma, petiole, and postpetiole. Dense covering of fine, appressed, silvery pubescence on most of body. Colour black; mandibles and frontoclypeal complex yellow-brown, antennae and legs dark brown, becoming lighter at their termini.

Comments. *P. hospitalis* can be distinguished from *P. gracilis* by the shorter, broader petiole (compare Figs 40 and 41) (see also PLI and PWI indices), shorter legs (Fig. 153), and by the presence of thick black setae intermingled with finer, pale silvery pilosity on the head, mesosoma and petiole. In *P. gracilis* such black setae are absent from the propodeum and petiole, and less conspicuous on the head and pronotum. Other species, not associated with *Tachigali* or *Triplaris*, with which *P. hospitalis* might be confused are *P. maculatus* (F. Smith), which is widespread in South America (Kempf, 1958), and *P. reconditus* Ward, known only from Nicaragua (Ward, 1993). Both of these have conspicuous black setae on the mesosoma and petiole, but the petiole and legs are longer (PLI 0.57–0.64, PL/HW 0.52–0.57, LHT/HW 0.83–0.87, compared to 0.67–0.70, 0.47–0.49 and 0.78–0.79, respectively, in *P. hospitalis*) and the overall body size is smaller (HW 1.47–1.67, compared to 1.76–1.84 in *P. hospitalis*). In addition *P. maculatus* is a bicoloured orange-and-black species, with a thinner petiole (PWI 0.43–0.51). These differences must be considered tentative since so few specimens are known of *P. hospitalis* and *P. reconditus*. Finally, there are two problematic collections of large (HW 1.82–2.12), black, *hospitalis*-like workers (1 worker from Jatun Sacha, Ecuador and 3 workers from P. N. Manu, Peru) which have black setae on the mesosoma and petiole, but have the petiole shape and leg length of *P. maculatus* (PLI 0.59–0.60, PL/HW 0.52–0.54, LHT/HW 0.84–0.87). These are labelled "cf. *maculatus*" in Figures 153–155, which summarize the morphometric differences among the taxa discussed here.

Distribution and biology. *P. hospitalis* is known only from two collections from *Tachigali*, in northern Peru. The type series was collected in two different petiole domatia on a single branch of a *Tachigali* tree which was also inhabited by *Camponotus rectangularis* but not by *Pseudomyrmex ferox* or an aggressive *Azteca* sp. (these last two occurred in other *Tachigali* trees at the site). The workers of *P. hospitalis* were not particularly aggressive. It is possible that this species bears the same relationship to *Tachigali* as *Pseudomyrmex nigropilosus* (Emery) does to swollen-thorn acacias in Central America (Janzen, 1975), i.e., it may be a timid and unprotective species which opportunistically colonizes trees that are not inhabited by their usual aggressive occupants. *P. hospitalis* is the species previously referred to as *Pseudomyrmex* sp. PSW-35 in Ward (1991:340) and Ward (1993:161).

Material examined. Type material listed above plus the following: PERU Loreto: 15 km WSW Yurimaguas, 200 m (P. S. Ward) (PSWC).

Pseudomyrmex ita (Forel 1906)
(*Figs 48, 57, 66*)

Pseudomyrma sericea var. *ita* Forel 1906:230. Syntype workers, San Mateo, Costa Rica (P. Biolley) (MHNG) [Examined].

Pseudomyrma sericea var. *acaciarum* Wheeler 1942:176. Syntype workers, Tumba Muerta

Road, Panama (W. M. Wheeler) (LACM, MCZC) [Examined] [Synonymy by Ward, 1993:158].

Pseudomyrma sericea var. *acaciorum* Enzmann 1945:90. Syntype workers, Tumba Muerta Road, Panama (W. M. Wheeler) (MCZC) [Examined] [Objective synonym of *Pseudomyrma sericea* var. *acaciarum* Wheeler; Brown 1949:43].

Pseudomyrmex sericeus ita (Forel); Kempf 1972:223.

Pseudomyrmex ita (Forel); Ward, 1993:158 [Raised to species].

Worker measurements ($n=13$). HL 1.00–1.16, HW 0.85–0.97, MFC 0.015–0.029, LHT 0.64–0.74, CI 0.83–0.86, REL 0.63–0.67, REL2 0.75–0.78, FCI 0.02–0.03, FI 0.49–0.52, PLI 0.99–1.16, PWI 0.75–0.90.

Worker description. Relatively small member of the *P. sericeus* group (compared to other species considered here). Palp formula 6,4; frontal carinae closely contiguous (see MFC and FCI values); eyes and head elongate; posterior margin of head concave; dorsal face of propodeum subequal to, or shorter than, declivitous face and meeting the latter at an obtuse angle; profemur broad (FI ≈ 0.50); legs short (LHT/HL 0.62–0.68). Petiole relatively short, narrow and high (see PLI and PWI values), with sharp dorsolateral margins; petiole subtrapezoidal in profile, with anterior and dorsal faces more or less differentiated (weakly so in populations from northern Central America); dorsal face of petiole rounding sharply into the vertical posterior face (Fig. 57). Standing pilosity very sparse; a pair of stout setae present on the pronotal humeri, petiole, and postpetiole, lacking on the mesonotum and propodeum. Dark brown-black, with lighter brown maculation variably present on the pronotum, petiole, postpetiole, fronto-clypeal complex, and appendages.

Comments. The most important distinguishing feature of *P. ita* is the dorsolaterally marginate petiole with its characteristic angular profile in lateral view and straight diverging sides in dorsal view (Figs 57, 66). The small size (worker HW <1.00, queen HW 0.85–0.90), closely contiguous frontal carinae, elongate eyes (worker REL >0.62, queen REL 0.61–0.64) and relatively narrow petiole (worker DPW 0.32–0.39) are also useful traits for identification.

Distribution and biology. P. ita is found from Mexico to Colombia. Like *P. gracilis*, it is a generalist twig-nesting species which is occasionally found in ant-plants (Ward, 1993). Wheeler (1942) reported it from hollow twigs of *Triplaris melaenodendron* (as *T. "auriculata"*) at Patulul and Escuintla, Guatemala (ant specimens examined in the MCZC and their identity confirmed) and from twigs of *Triplaris cumingiama* (as *T. "americana"*) at Balboa, Panama (ant specimens not seen). It is unclear from Wheeler's (1942) account whether the ants occupied live stems or dead twigs only.

Pseudomyrmex pictus (Stitz)
(*Figs 44, 53, 62*)

Pseudomyrma picta Stitz, 1913:209. Syntype workers, Alto Acre, Brazil (Ule) (ZMHB) [Examined].

Pseudomyrma picta var. *heterogyna* Wheeler & Mann, 1942a:172. Syntype workers, one dealate queen, Cavinas, Bolivia (W. M. Mann) (MCZC) [Examined]. **Syn. nov.**

Pseudomyrma picta subsp. *casta* Wheeler, 1942:173. Syntype workers, La Sombre, Putumayo, Peru (J. C. Bradley) (MCZC) [Examined]. **Syn. nov.**

Pseudomyrma picta var. *humboldi* Enzmann, 1944:75. Syntype workers, one dealate queen, Cavinas, Bolivia (W. M. Mann) (MCZC) [Examined]. **Syn. nov.** (Objective synonym of *heterogyna*).

Pseudomyrmex pictus var. *heterogyna* (Wheeler & Mann); Kusnezov, 1953:214. [First explicit combination in *Pseudomyrmex*]

Worker measurements ($n = 10$). HL 1.21–1.43, HW 1.19–1.38, MFC 0.038–0.059, LHT 1.02–1.26, CI 0.91–1.03, REL 0.60–0.64, REL2 0.61–0.67, FCI 0.03–0.05, FI 0.36–0.41, PLI 1.00–1.10, PWI 0.80–0.94.

Worker description. A member of the *P. sericeus* group. Palp formula variable: 6,4 or 5, 4. Frontal carinae relatively well separated; head broad, with strongly convex sides; posterior margin of head straight or slightly concave, in frontal view. Profemur very slender (see FI values); legs long (LHT/HL 0.82–0.91). Dorsal face of propodeum somewhat convex and rounding gradually into the declivitous face; length of dorsal face subequal to or slightly shorter than that of the declivitous face; propodeal spiracle distant from the basal (dorsal) face of propodeum. Petiole as high as long to slightly higher than long, subtriangular in profile, with a single convex anterodorsal face, which rounds gently into the steep posterior face (Fig. 53). Anteroventral process small, subrectangular or subtriangular, usually with a blunt posteroventral angle or tooth. Standing pilosity variable, more common than is usual for the species group. Long, golden, paired (and often curved) setae present on pronotum (1–6 pairs), mesonotum (0–1 pairs), on propodeum at the junction of the basal and declivitous faces (0–1 pairs), petiole (1–3 pairs) and postpetiole (2–3 pairs); these setae sometimes unpaired, or accompanied by one or two additional shorter setae. Body, including appendages, predominantly orange-brown in colour; legs, mesosoma (especially dorsal face of propodeum), petiole, and gaster with variable amounts of darker maculation.

Comments. *P. pictus* is most easily recognized by its predominantly light (orange-brown) coloration, broad head (worker CI >0.90, queen CI $\approx$0.86), slender worker profemur (FI 0.36–0.41), and long legs (worker LHT/HL 0.82–0.91, queen LHT/HL $\approx$0.75). The superficially similar *P. rubiginosus*, which is also light in colour, has a darker and more elongate head, broader worker profemur, shorter legs, and a more blocky petiole. *P. pictus* appears to be most closely related to *P. eculeus*. For differences between these two see the key (couplet 19) and discussion under *P. eculeus*.

Distribution and biology. Known from Colombia, Peru, western Brazil and Bolivia, *P. pictus* is typically associated with *Tachigali*, but the types of *heterogyna* were reportedly collected from the 'hairy cauline swelling' of a *Platymiscium* species (Wheeler & Mann, 1942a: 173).

Pseudomyrmex rubiginosus (Stitz), **stat. nov.**
(*Figs 47, 56, 65*)

Pseudomyrma sericea var. *rubiginosa* Stitz, 1913:211. Syntype workers, "Brasilien" [Alto Acre, Brazil] (Ule) (NHMV) [Examined].

Pseudomyrma sericea var. *huberi* Santschi, 1922:346. Syntype workers, Rio Puru[s], Amazonas, Brazil (Huber) (NHMB) [Examined]. **Syn. nov.**

Pseudomyrmex sericeus var. *rubiginosus* (Stitz); Kempf, 1972:223. [First explicit combination in *Pseudomyrmex*]

Worker measurements ($n=10$). HL 1.18–1.37, HW 1.01–1.19, MFC 0.035–0.046, LHT 0.77–0.95, CI 0.84–0.91, REL 0.56–0.61, REL2 0.65–0.69, FCI 0.03–0.04, FI 0.44–0.49, PLI 0.86–1.02, PWI 0.81–0.95.

Worker description. A member of the *P. sericeus* group. Palp formula: variable (6,4 or 5,3). Frontal carinae relatively well separated; head only moderately elongate, sides weakly convex; posterior margin of head concave, in frontal view. Profemur moderately broad; legs relatively short (LHT/HL 0.65–0.71). Dorsal face of propodeum subequal in length to declivitous face, and usually rounding rather suddenly into it; propodeal spiracle distant from basal (dorsal) face of propodeum. Petiole relatively long and broad, subtrapezoidal in profile, with weakly differentiated anterior and dorsal faces, and dorsal face rounding relatively suddenly into vertical posterior face (Fig. 56). Anteroventral process moderately well developed, a triangular or rounded lobe, typically without a well-marked posteroventral tooth or angle (but exceptions occur). Standing pilosity sparse; a single pair of stout, paired golden setae rather consistently present on the propodeum at the junction of the basal and declivitous faces, on the petiole, and on the postpetiole; pilosity more variable on the pronotum (1–2 pairs) and mesonotum (0–1 pair); occasionally additional short hairs present on these surfaces. Bicoloured, with head mostly dark grey-brown, gaster medium-brown, and remainder of body, including mandibles, antennae, frontoclypeal complex and legs, dusky yellow- or orange-brown; variable amounts of infuscation on the mesosoma (especially posteriorly), petiole, postpetiole and legs.

Comments. P. rubiginosus can be recognized by the bicoloured body and by the somewhat angular profile to the worker propodeum and petiole (Fig. 56), although there is some variation in the shape of both these structures. Nevertheless, differentiated anterior and dorsal faces of the petiole can be discerned in lateral view, and the dorsal face rounds suddenly into the steep posterior face. Other useful identifying characteristics are the head shape (worker CI 0.84–0.91, queen CI ≈ 0.78), patterns of standing pilosity in the worker (see above), and relatively long petiole (worker PL/LHT 0.52–0.58, queen PL/LHT ≈ 0.70).

Distribution and biology. This species is known from Colombia, Peru and western Brazil. The type specimens were collected from *Triplaris*, and there are additional records of colonies inhabiting *Triplaris, Pleurothyrium poeppigii* Nees, *Gustavia, Ocotea*, and *Tachigali* cf. *formicarum*. It is the only *Pseudomyrmex* plant-ant that has been found inhabiting both *Triplaris* and *Tachigali*.

Pseudomyrmex vinneni (Forel), **stat. nov.**
(*Figs 49, 58, 67*)

Pseudomyrma sericea var. *vinneni* Forel, 1906:230. Syntype workers, [Barcelos], Rio Negro, Amazonas, Brazil (Ducke) (AMNH, MCSN, MHNG) [Examined].

Pseudomyrmex sericeus var. *vinneni* (Forel); Kempf, 1972:223 [First combination in *Pseudomyrmex*].

Worker measurements ($n = 13$). HL 0.90–1.17, HW 0.81–1.03, MFC 0.024–0.039, LHT 0.59–0.77, CI 0.87–0.91, REL 0.63–0.68, REL2 0.71–0.75, FCI 0.03–0.04, FI 0.46–0.51, PLI 1.02–1.17, PWI 0.80–0.92.

Worker description. A member of the *P. sericeus* group. Palp formula: 6,4. Frontal carinae moderately well separated; head longer than broad but not strongly so (see CI values), somewhat quadrate, with almost straight sides, and flat to slightly concave posterior margin; eyes elongate. Profemur broad; legs relatively short (LHT/HL 0.63–0.67). Dorsal face of propodeum subequal in length to declivitous face, and rounding gradually into it. Petiole short, high, subtriangular or subglobose in profile, with a single convex anterodorsal face, which rounds gently into the steep posterior face (Fig. 58). Anteroventral process varying from slightly to moderately well developed, usually lobe-like and without a posteroventral tooth or angle. Standing pilosity sparse; stout, paired setae on pronotum (1 pair), petiole (1 pair) and postpetiole (1 pair), absent from mesonotum and propodeum, and sometimes small and inconspicuous on the petiole and postpetiole. Dark brown to brownish black, with appendages, frontoclypeal complex and (in some workers) promesonotum a lighter medium-brown to orange-brown.

Comments. P. vinneni can be recognized by its small size (worker HW 0.81–1.03, queen HW 0.96–1.06), elongate eyes (worker REL 0.63–0.68, queen REL 0.60–0.63), and rounded (subtriangular to subglobose) petiolar profile (Fig. 58). In addition, in the worker caste, the quadrate head, broad profemur, rounded juncture of the basal and declivitous faces of the propodeum (in lateral view), and scarcity of standing pilosity are characteristic. *P. sericeus* itself has more closely contiguous frontal carinae, a propodeum whose short dorsal face meets the longer declivitous face at an obtuse angle, and a petiole which is subtriangular in lateral profile.

Distribution and biology. This species is widely distributed but infrequently collected. It is known from Colombia, Venezuela, Peru and Brazil. Most of the individuals I have examined were extracted from herbarium specimens of *Tachigali* by Woody Benson. Specific plant records include *Tachigali cavipes* (Spruce ex Bentham) Macbride, *T. paniculata, T. myrmecophila, T. physophora* (Huber) Zarucchi & Herendeen, *T. schultesiana* Dwyer, *T. venusta* Dwyer and *T. odoratissima* (Spruce ex Bentham) Zarucchi & Herendeen.

PHYLOGENY AND BIOGEOGRAPHY OF THE *PSEUDOMYRMEX VIDUUS* GROUP

For the purposes of investigating the relationships among species in the *Pseudomyrmex viduus* group, *P. penetrator* was combined with *P. concolor* into a single composite taxon, *P. concolor* (*sensu lato*). This was done because there is evidence of gene flow between these two entities (see above, under *P. penetrator*). Moreover, with respect to the set of characters developed for phylogenetic analysis, including male genitalia, these two taxa are virtually identical. They differ primarily in body colour, and this was not used as a cladistic character because it shows considerable intraspecific variation in other members of the *P. viduus* group and even breaks down as a diagnostic character for *P. concolor* and *P. penetrator* in some regions.

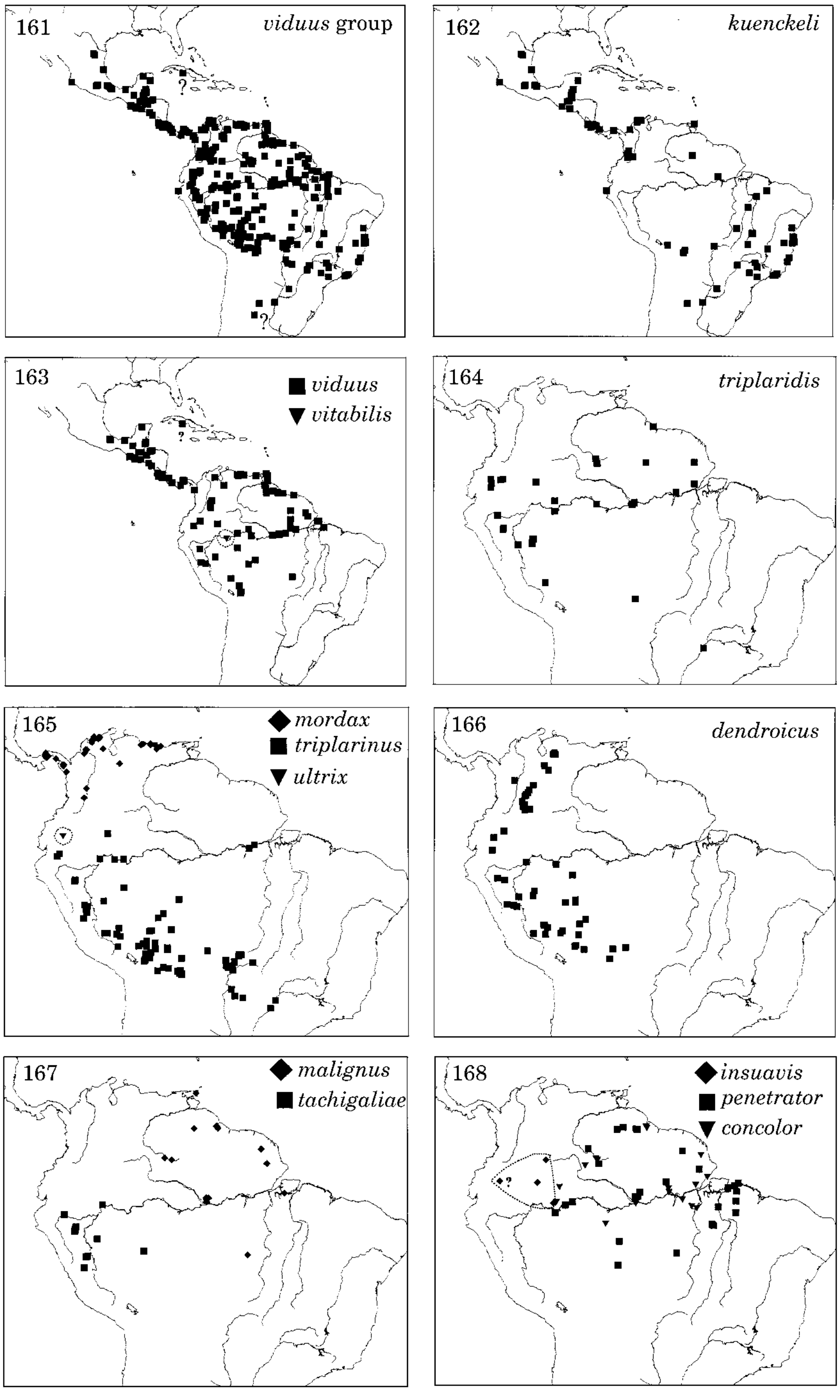
The coded character state matrix for the morphological data is given in Table 1. Cladistic analysis, using the implicit enumeration ('ie') option of Hennig86, yielded two most parsimonious trees (length 143, consistency index 0.74, retention index 0.81), of which one is shown in Fig 169. These two trees differ only in the placement of *P. mordax* and *P. ultrix*, which vie as alternate candidates for the sister taxon of the pair of {*P. triplarinus* + *P. dendroicus*}. Successive approximation weighting produced a single tree in which *P. mordax* is the sister species of {*P. triplarinus* + *P. dendroicus*}, and this is considered the preferred tree for purposes of discussion here. None of the conclusions is substantially altered by consideration of the alternate tree.

There is strong support (bootstrap values of 95% and 99%) for the monophyly of both the *Triplaris*-inhabiting and *Tachigali*-inhabiting species, hereafter referred to as the *P. triplarinus* subgroup and the *P. concolor* subgroup, respectively. Moreover, these two subgroups together form a well-supported monophyletic group (bootstrap value of 99%) whose sister group is *P. kuenckeli*. The *P. triplarinus* subgroup consists of two rather well defined clades, the trio of {*P. triplaridis* + {*P. viduus* + *P. vitabilis*}} and the set of four other species (Fig. 169). All of these species are essentially confined to South America—*P. mordax* just enters Panama—except *P. viduus*, which has both an expanded geographical range (Fig. 163) and an enlarged repertoire of host plant associations (discussed below). The members of the *P. concolor* subgroup form a sequential series consisting of *P. tachigaliae*, *P. malignus*, *P. concolor* (s.1.) and *P. insuavis* (Fig. 169), although a sister group relationship between the last two is only weakly supported. This could be tested by the examination of *P. insuavis* males (currently unknown).

Species richness of the *Pseudomyrmex viduus* group reaches a maximum in the Amazon basin, but the ranges of most species are rather extensive (Figs 162–168) and do not show obvious correspondence with the centres of endemism recognized for some plant and animal taxa (e.g., Brown, 1987a; Haffer, 1969, 1987; Prance, 1987), and interpreted as Pleistocene forest refugia (Haffer, 1969; Simpson & Haffer, 1978; cf. Colinvaux, 1993). Five species in the *P. viduus* group have somewhat restricted distributions (see Figs 163, 165, 167, 168) that arguably fall within the Napo (*P. insuavis, P. ultrix, P. vitabilis*), east Peru-Acre (*P. tachigaliae*), and Río Magdalena (*P. mordax*) centres, although the ranges of *P. insuavis* and *P. mordax* also extend considerably beyond these regions as they are usually delimited (e.g., Brown, 1987b: 182; Lynch, 1988:313).

As has been postulated for other Amazonian taxa (Bush, 1994; Cracraft & Prum, 1988; Lynch, 1988; Patton *et al.*, 1997), it seems likely that much of the diversification of the *Pseudomyrmex viduus* group occurred before the Pleistocene. The well resolved phylogeny of the *P. viduus* group (Fig. 169) implies a series of speciation events at differing times in the past. Many of the species in the group have broadly overlapping ranges. *P. kuenckeli*, the sister taxon of the remaining species (and a generalist in nesting habits, hence unconstrained by host plant distribution), is found throughout the Neotropics, encompassing almost the entire range of the rest of the clade (Fig. 162). Within the *P. triplarinus* subgroup, sister taxa such as *P. dendroicus* and *P. triplarinus*, and the trio of *P. triplaridis*, *P. viduus* and *P. vitabilis*, show extensive sympatry (Figs 163–166). All of this argues against recent speciation in the Pleistocene.

In the *P. concolor* subgroup there is a stronger pattern of vicariance, given the sister group relationship between *P. tachigaliae* (southwestern Amazonia) and the remaining species (northwestern, central and eastern Hylaea) and, within the latter group, between *P. insuavis* (northwestern Amazonia) and *P. concolor* (s.l.) (central and eastern



Figures 161–168. Distribution of species in the *Pseudomyrmex viduus* group. 161, entire species group; 162, *P. kuenckeli*; 163, *P. viduus* and *P. vitabilis*; 164, *P. triplaridis*; 165, *P. mordax*, *P. triplarinus* and *P. ultrix*; 166, *P. dendroicus*; 167, *P. malignus* and *P. tachigaliae*; 168, *P. insuavis*, *P. penetrator* and *P. concolor*.

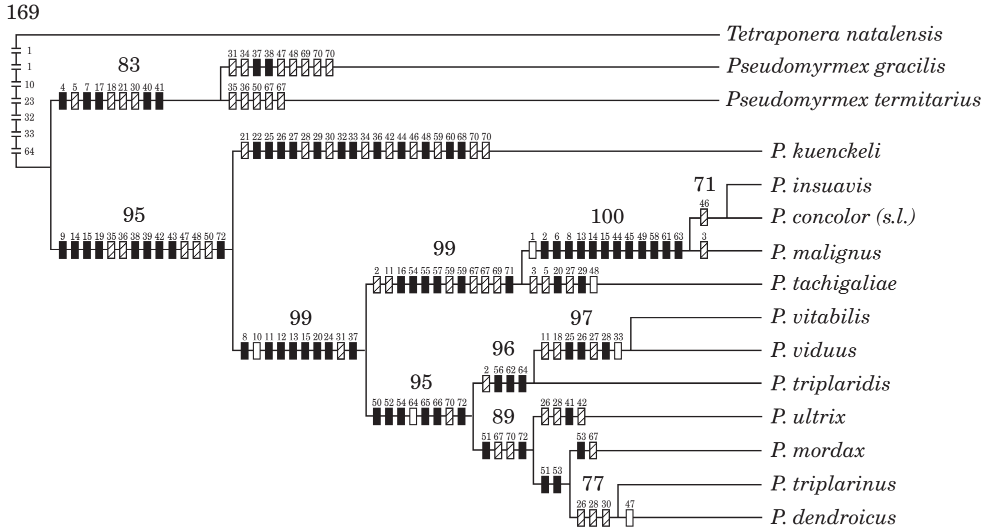


Figure 169. Phylogeny of the *Pseudomyrmex viduus* group. This is one of two most parsimonious trees (length 143, consistency index 0.74) obtained with the 72-character dataset (Table 1). The alternate tree differs only in the positions of *P. mordax* and *P. ultrix*, which are switched. (▮) unique character state changes; (▨) homoplasious changes, due to convergence; (▯) reversals. The smaller numbers refer to the characters, the larger numbers are bootstrap support values (maximum 100). There are other, equally parsimonious, reconstructions of character state change for characters 2, 3, 8, 21, 25, 26, 27, 28, 30, 33, 35, 36, 47, 48, 50, 59 and 70. The reconstruction shown here delays transformation in these characters.

Hylaea) (Fig. 170). If the sister taxa *P. malignus* and {*P. concolor* (s.l.) + *P. insuavis*} are considered to have secondarily overlapped in distribution following divergence in eastern and central/western Hylaea, respectively (see Figs 167–168), then the *P. concolor* subgroup points to the following area relationships for Hylaea: {southwestern Amazonia {eastern Hylaea {central Amazonia + northwestern Amazonia}}}. This is not in accord with the Amazonian area relationships deduced by Cracraft & Prum (1988) on the basis of bird phylogenies. Cracraft & Prum (1988) found the Guiana region to be a sister group to all other areas within the Amazon basin, whereas the phylogeny of the *P. concolor* subgroup indicates a basal divergence between southwestern Amazonia (east Peru-Acre) and the rest of Hylaea. This deepest split within the *P. concolor* subgroup is well supported by character evidence (Fig. 169), and almost certainly dates to the Tertiary. Indeed, the proposed Miocene Amazon seaway (Räsänen *et al.*, 1995) is a potential candidate for the barrier that caused this divergence.

Why is a history of vicariance more evident in the *P. concolor* subgroup than its sister group, the *P. triplarinus* subgroup? The former are restricted to *Tachigali* plants, which typically grow in rainforest or small rainforest clearings, whereas *Triplaris*, the host plant of the *P. triplarinus* subgroup, frequently colonizes waterways and this has perhaps favored greater dispersal capacities in its associated ants. In addition, *Triplaris* arguably provides more abundant and more continuously available (i.e. less fragmented) habitat for its ant hosts. The species of *Triplaris*-ants certainly tend to have larger geographic ranges than those species resident in *Tachigali* (compare Figs 163–166 with Figs 167–168).

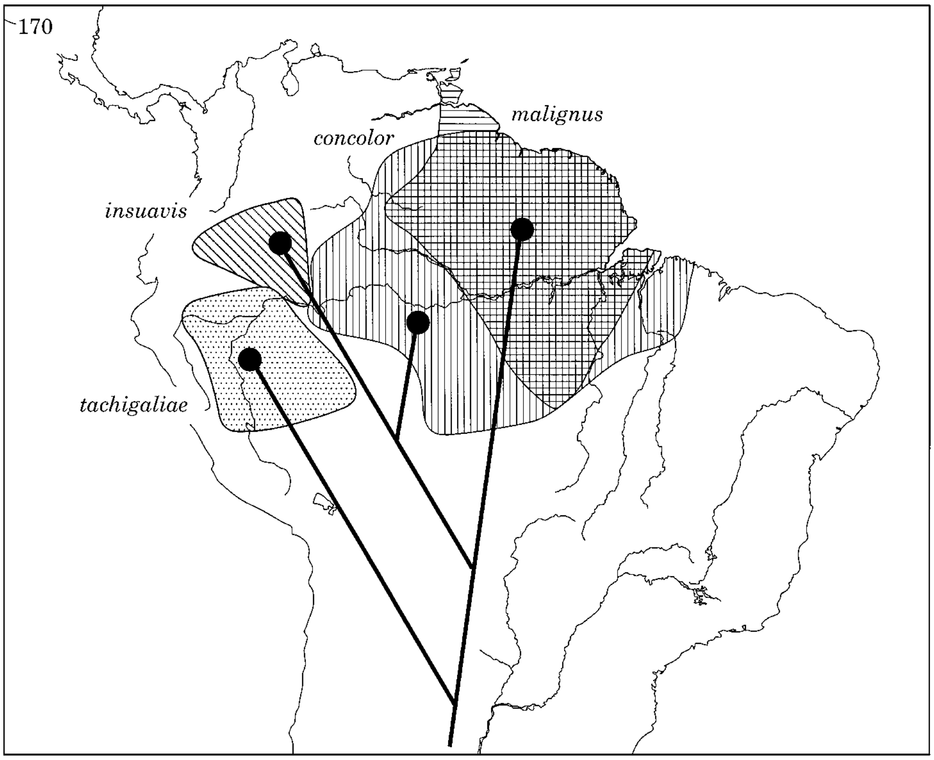


Figure 170. Phylogeny and distribution of the *Tachigali*-ants, *Pseudomyrmex concolor* subgroup. As used here, '*concolor*' includes the two forms, *P. concolor* and *P. penetrator* (see text).

PATTERNS OF HOST PLANT ASSOCIATION

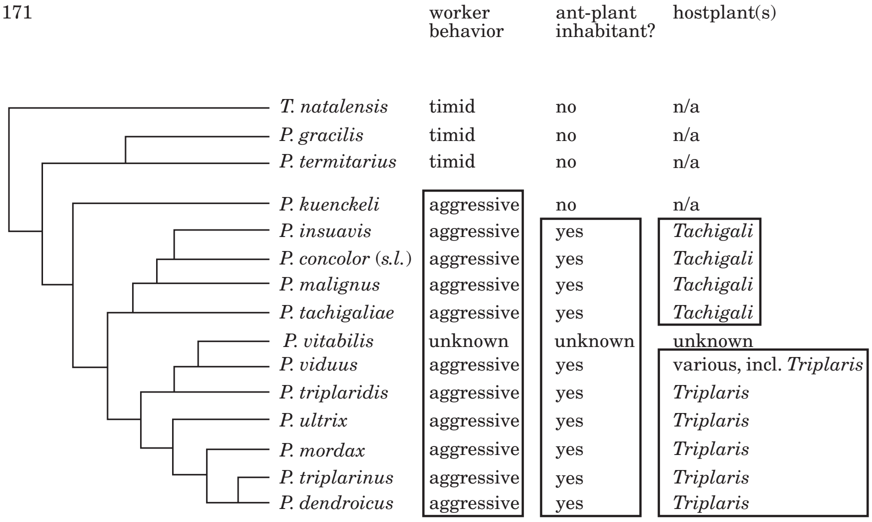
Mapping the available information about worker behaviour (aggressive as opposed to timid demeanour) and host plant associations on the phylogeny of the *P. viduus* group (Fig. 171) reveals several interesting points. First, it is possible to reject the hypothesis put forward tentatively in Ward (1991), based on analysis of a more limited set of taxa and characters, that *P. kuenckeli* is closely related to *P. triplarinus* and represents an unusual case of reversion to generalist nesting habits, with retention of the aggressive behaviour associated with domatia-inhabiting species. Rather, since *P. kuenckeli* is the sister group of all other members of the *P. viduus* group, the aggressive patrolling and stinging behaviour of its workers—behaviour which is rare in most of the 150-odd species of generalist twig-nesting *Pseudomyrmex*—appears to represent the groundplan condition for the species group. By this new interpretation, aggressive behaviour appeared *before* the evolution of mutualistic relationships with ant-plants and may have been an important preadaptation for the evolution of such relationships.

It would be useful to have more information on the life history and habits of *P. kuenckeli*. Ward (1991) presented a model for the evolution of ant-plant mutualisms (involving primary domatia) in which a precursor is the tending of scale insects (Coccoidea) in beetle- and lepidopteran-bored cavities in unspecialized plants.

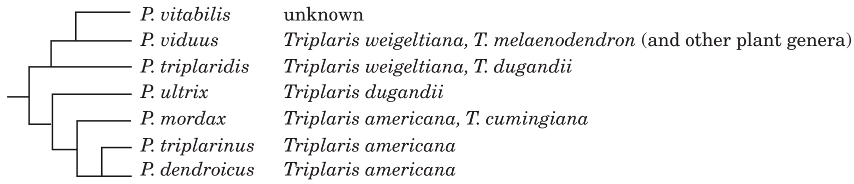
TABLE 1. *Pseudomyrmex viduus* group: dataset for cladistic analysis. The first three taxa are outgroups. '?' signifies unknown, polymorphic or inapplicable

	10	20	30	40	50	60	70	
T. natalensis	0001100001	0000001100	0000111111	0000001101	1000000000	00????0000	0001000002	00
P. gracilis	2000001000	0000000000	10101?1110	1111000000	00000?1100	00????0000	0000000010	00
P. termitarius	2000001000	0000000000	1010111110	0110111100	0000000001	0001000000	0000002002	00
P. concolor	1201110211	2122311111	0011111111	1110112211	1111111111	0000101120	1010002012	11
P. dendroicus	2001100111	1111201111	0011121210	1110112211	1110000?02	2112000000	0001111000	03
P. insuavis	1201110211	2122311111	0011111111	1110112211	11111111??	??????????	??????????	??
P. kuenckeli	2001100?10	0001101110	1110232200	0221121211	1212011201	0001000011	0000000100	01
P. malignus	1211110211	2122311111	0011111111	1110112211	1111101?11	0000101120	1010002012	11
P. mordax	2001100111	1111201111	0011111111	1110112211	1110001102	2122000000	0001112000	03
P. tachigaliae	2111000111	2111211112	0011110121	1110112211	1110001001	0000101020	0000002012	11
P. triplaridis	2101100111	1111201111	0011111111	1110112211	1110001102	0102010000	0102110001	02
P. triplarinus	2001100111	1111201111	0011121210	1110112211	1110001102	2112000000	0001111000	03
P. ultrix	2001100111	1111201111	0011121211	1110112211	2210001102	1102000000	0001111000	03
P. viduus	2101100111	2111201011	0011000011	1100112211	111?001102	0102010000	0102110001	02
P. vitabilis	?1??100?1?	2?1?2?1011	?011?0?01?	????1122??	1??00??1??	??????????	??????????	??

171



172



Figures 171, 172. Fig. 171. Distribution of worker behaviour (timid/aggressive) and ant-plant associations in the *Pseudomyrmex viduus* group. The first three taxa are outgroups. Fig. 172. The species of *Triplaris* recorded serving as host plants in the *Pseudomyrmex triplarinus* subgroup, mapped on the phylogeny of the ants.

Although *P. kuenckeli* appears to nest primarily in dead branches, these can be large in size and have substantial contact with live plant tissue (Ward, pers. obs.), suggesting the possibility that the nest cavities extend into live branches, where scale insects are tended. Davidson (1997) argues that the carbohydrate-rich diet of homopteran-tending ants facilitates their adoption of 'high tempo' foraging activity and aggressive behaviour. In this way, the common ancestor of *P. kuenckeli* and the other *P. viduus* group species could have been primed for a plant-protective role.

The ancestral host plant for the ant-plant mutualists of the *P. viduus* group (i.e. for the *P. triplarinus* subgroup plus *P. concolor* subgroup) cannot be inferred with certainty, since each subgroup is more or less restricted to its own host plant (Fig. 171). Of the two clades, however, the *P. concolor* subgroup appears to have more apomorphic workers and queens, at least with respect to morphology (Fig. 169), suggesting that association with *Tachigali* may be a derived condition relative to association with *Triplaris*.

How species-specific are the associations between the ants and their host plants? The data are insufficient to provide a detailed answer, since many of the plant records are at the level of genus only. The best information comes from the *Pseudomyrmex triplarinus* subgroup, and here there is an indication of some degree of specificity (Fig. 172), especially in view of the partial sympatry of the taxa involved. Thus, in at least some locations, *P. dendroicus* co-occurs with *P. triplaridis*, with the former inhabiting *Triplaris americana* while *P. triplaridis* occupies *T. weigeltiana*. There is also a tendency for related species of *Pseudomyrmex* to use the same species of *Triplaris* (Fig. 172). It must be emphasized, however, that for most collections of these ants the host plant is simply given as "*Triplaris*", so additional field data are needed to confirm this pattern. There is a recent taxonomic revision of *Triplaris* (Brandbyge, 1986) but no phylogenetic analysis, so the question of cospeciation between the ants and the plants must remain open. Given the association of some *Pseudomyrmex* species with more than one species of *Triplaris*, and vice-versa, it seems unlikely that strict parallel cladogenesis is the prevailing mode. A similarly diffuse pattern of coevolution was inferred for the acacia-ants of the *P. ferrugineus* group (Janzen, 1966; Ward, 1993).

Ruprechtia, a close relative of *Triplaris*, is reported to have several species with hollow stems, at least one of which houses ants (Brandbyge, 1989; Brandbyge & Øllgard, 1984), but I have not had the opportunity to examine any ant specimens associated with this genus.

The 'generalist' plant-ant, *Pseudomyrmex viduus*, merits additional study given its association with a variety of domatia-bearing plants besides *Triplaris*. Some populations continue to utilize *Triplaris*, presumably the ancestral host plant for the species, but others have been found inhabiting live stems or cavities of *Cordia*, *Coussapoa*, *Ocotea*, *Pseudobombax*, and *Sapium*, among others. This species deserves increased scrutiny to determine the amount of within- and between-population variation in host plant choice. It suggests that host plant shifts in ant-plant-inhabiting *Pseudomyrmex* may involve an intermediate condition of expanded host plant use. It is tempting to predict that *P. vitabilis*, a close relative of *P. viduus* with a seemingly restricted geographical distribution (and whose biology is unknown), will prove to be a specialist on a plant other than *Triplaris*.

As documented above (under the section 'Other *Pseudomyrmex* species associated with *Tachigali* and *Triplaris*') both *Triplaris* and *Tachigali* are inhabited by other aggressive species of *Pseudomyrmex* besides those of the *P. viduus* group. An earlier cladistic analysis (Ward, 1991) indicated that these associations evolved independently from those of the *P. viduus* group. The *P. sericeus* group is the major contender, and it is interesting to note that most plant-ant species from this group are associated with *Tachigali* rather than *Triplaris*, and they occur primarily in regions of western Amazonia where there is only one representative of the *P. viduus* group living in *Tachigali*. This suggests that there is greater ecological opportunity for secondary colonization here. The ant genus *Azteca* (Formicidae: Dolichoderinae) also has species that are specialized inhabitants of *Triplaris* and *Tachigali* (Wheeler, 1942), and occur sympatrically with *Pseudomyrmex* in some localities. The nature of competitive interactions among these species, and the possible mediating roles of scale insects (Coccidae and Pseudococcidae) and the particular species of plant, are fascinating but largely unexplored areas.

CONCLUSIONS

The *Pseudomyrmex viduus* group comprises about 13 species of ants whose collective distribution covers much of the New World tropics. Most species are confined to the South American mainland, however, and species richness is highest in the western Amazon basin. Twelve of the 13 species are specialized inhabitants of live plant cavities (myrmecodomatia), in which they keep brood and scale insects (Coccidae and Pseudococcidae) and which they defend with alacrity. In spite of the evident deterrent effect of these stinging ants on browsers, botanists, and other curious humans, there has been no experimental verification of a mutually beneficial relationship between the ants and the plant. Any such studies need to include the effects of the homopterans on the interaction, making the experimental analysis of this system more complex than that of swollen-thorn acacias and *Pseudomyrmex* ants, in which coccoids play no role.

On the whole, the ants of the *P. viduus* group show considerable conservatism of host plant use. Thus, there are two well-defined clades within the group, showing high fidelity to *Tachigali* (Fabaceae: Caesalpinoideae) and *Triplaris* (Polygonaceae), respectively. There has not been rampant host switching between plant genera. Yet, in an exception to this pattern, one species, *P. viduus*, is remarkably general in its use of live plant cavities, having been recorded from ten plant genera belonging to eight different families. *P. viduus* is a member of the clade of *Triplaris* associates (Fig. 171) and some populations of *P. viduus* still use this, the presumptive ancestral host plant. This suggests that host plant switching in these ants involves an intermediate period of expanded host plant use. This is supported by the observation of a few other 'generalist' plant-ants in *Pseudomyrmex* (e.g., *P. rubiginosus*, in the *P. sericeus* group). Longino (1996) has documented a similar phenomenon in Costa Rican ants of the genus *Azteca*, i.e., specificity of host plant usage in most live-stem inhabiting species, but promiscuous associations by some.

Patterns of *intraspecific* morphological variation that are observed in widespread taxa such as *P. concolor* (*s.l.*), *P. triplarinus* and *P. viduus* may be partly attributable to a greater degree of isolation of some populations in arid and/or cool periods of the Pleistocene, but a consideration of the *Pseudomyrmex viduus* group as a whole—the phylogenetic relationships and geographic ranges of the species, and the sympatry of sister taxa—indicates that the group is an old one, with most speciation events preceding the Quaternary. Given the observed conservatism of host plant use, this implies that associations with the myrmecophytes *Tachigali* and *Triplaris* are at least several million years old and perhaps much older.

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