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Systematic studies on *Pseudomyrmex* acacia-ants (Hymenoptera: Formicidae: Pseudomyrmecinae)

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Abstract.—The obligate acacia-ants (*Pseudomyrmex ferrugineus* group) are well known as defensive inhabitants of swollen-thorn acacias in the northern Neotropics. A taxonomic revision of these ants leads to the recognition of ten species: *P. ferrugineus* (F. Smith), *P. flavicornis* (F. Smith), *P. janzeni*, sp. nov., *P. mixtecus*, sp. nov., *P. nigrocinctus* (Emery), *P. particeps*, sp. nov., *P. peperi* (Forel), *P. satanicus* (Wheeler), *P. spinicola* (Emery), and *P. veneficus* (Wheeler). The following new synonymy is proposed: *P. nigrocinctus* = *P. alfari* (Forel) = *P. bicinctus* (Santschi) = *P. peltatus* (Menozzi); *P. spinicola* = *P. atrox* (Forel) = *P. gaigei* (Forel) = *P. infernalis* (Wheeler) = *P. scelerosus* (Wheeler). Diagnostic descriptions and taxonomic comments are also provided for ten other unrelated species of *Pseudomyrmex* which have become secondarily associated with swollen-thorn *acacias* either as obligate and, in at least one case, parasitic occupants (*P. nigropilosus* (Emery), *P. simulans* Kempf and *P. subtilissimus* (Emery); *P. reconditus*, sp. nov., may also belong in this category) or as facultative inhabitants (*P. boopis* (Roger), *P. gracilis* (Fabricius), *P. hesperius*, sp. nov., *P. ita* (Forel), stat. nov., *P. kuenckeli* (Emery) and *P. opaciceps*, sp. nov.). A cladistic analysis of the *P. ferrugineus* group yields the following result which appears to be fairly robust insofar as there is congruence among the trees derived from worker-, queen-, and male-based character sets: ((*nigrocinctus* + *particeps*) + (*peperi* + ((*satanicus* + *spinicola*) + *ferrugineus complex*))). The "*ferrugineus complex*" comprises five species whose phylogenetic relationships are not fully clarified. The composite data set (47 characters from all three castes) supports the following partial resolution: (*ferrugineus* + *janzeni* + (*flavicornis* + (*mixtecus* + *veneficus*))). The cladogram of the *P. ferrugineus* group indicates that speciation in the group has occurred primarily as a consequence of geographical isolation, and that the ants and their host acacias have experienced diffuse coevolution rather than strict cospeciation.

INTRODUCTION

Pseudomyrmex ferrugineus (F. Smith) and related species of ants form a well-defined monophyletic group, the members of which nest exclusively in the hollow, swollen thorns of several New World *Acacia* species. Because of their aggressive behavior and predictable occurrence on the acacias, these ants have received considerable attention from tropical biologists (Belt 1874; Safford 1922; Skwarra 1934a, 1934b; Wheeler 1942; Janzen 1966, 1973). The landmark studies of Janzen (1966, 1967b) provided strong experimental evidence of the mutualistic nature of the *Pseudomyrmex/Acacia* association, and the relationship between the two organisms is often cited in discussions of coevolved mutualisms (e.g. Gilbert 1983; Beattie 1985; Futuyma 1986). At the same time, the systematics of the acacia-ants has been neglected, with the result that misidentifications and misstatements have appeared in the ecological literature. In this paper I present a taxonomic revision of the obligate acacia-ants (*Pseudomyrmex ferrugineus* group) and an assessment of their phylogenetic relationships. I also attempt to clarify the identities of other, unrelated species of *Pseudomyrmex* which have become secondarily associated with swollen-thorn acacias.

The earlier taxonomic literature on acacia-ants is scattered in more than a dozen papers containing descriptions of various species, subspecies, and "varieties". Two of the more comprehensive treatments are those of Emery (1890) and Wheeler (1942). In presenting the results of his ecological studies Janzen (1966, 1967b, 1973) summarized his understanding of acacia-ant taxonomy. Ward (1989) provided a brief diagnosis of the *P. ferrugineus* group, together with taxonomic and nomenclatural notes on the commoner species.

MATERIALS AND METHODS

COLLECTIONS

Material for the present study was examined in the following collections:

- AMNH American Museum of Natural History, New York, NY, USA
- ANSP Academy of Natural Sciences, Philadelphia, PA, USA
- BMNH The Natural History Museum, London, U.K.
- CASC California Academy of Sciences, San Francisco, CA, USA
- CHAH C.H.A. Hespenheide Collection, University of California at Los Angeles, CA, USA
- CISC California Insect Survey, University of California at Berkeley, CA, USA
- CUIC Cornell University Insect Collection, Ithaca, NY, USA
- EBCC Estación de Biología Chamela, Jalisco, Mexico
- FFIC Fernando Fernández Collection, Santa Fe de Bogotá, Colombia
- GBFM Graham B. Fairchild Museo de Invertebrados, Universidad de Panamá, Panama
- GCWC G.C. & J. Wheeler Collection, Silver Springs, FL, USA
- INBC Instituto Nacional de Biodiversidad (collections previously held in MNCR: Museo Nacional de Costa Rica), San José, Costa Rica
- INHS Illinois Natural History Survey Insect Collection, Champaign, IL, USA
- JTLC J.T. Longino Collection, Evergreen State College, Olympia, WA, USA
- KSUC Kansas State University Insect Collection, Manhattan, KS, USA
- LACM Natural History Museum of Los Angeles County, Los Angeles, CA, USA
- MCSN Museo Civico di Storia Naturale, Genoa, Italy
- MCZC Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
- MHNG Muséum d'Histoire Naturelle, Geneva, Switzerland
- MNHN Muséum National d'Histoire Naturelle, Paris, France
- MZSP Museo 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, USA
- SEMC Snow Entomological Museum, University of Kansas, Lawrence, KS, USA
- UCDC Bohart Museum of Entomology, University of California at Davis, CA, USA
- UCRC UCR Entomological Collection, University of California at Riverside, CA, USA
- USNM National Museum of Natural History, Washington, DC, USA
- WPMC W.P. MacKay Collection, El Paso, TX, USA
- ZMHB Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
- ZMUC Zoologisk Museum, University of Copenhagen, Denmark
- ZMUH Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Germany
- ZSMC Zoologische Staatssammlung, Munich, Germany

Special mention should be made of the very large and important series of *Pseudomyrmex* collected by D.H. Janzen from 1963 to 1974 and now housed in the Natural History Museum of Los Angeles County (LACM). The Janzen material includes a large number of pinned specimens (usually glued to the side of the pin rather than point-mounted) and an extensive alcohol collection (partly overlapping with the pinned series but including additional accessions). Janzen's field notes pertaining to the collection of these ants have also been deposited in LACM. Obligate acacia-ants (*P. ferrugineus* group) constitute the bulk of the collected material. They occur as long nest series from throughout Central America, with very useful queen-male-worker associations, making this material of inestimable value to the current revision.

When the Janzen collection was received at LACM in 1984 most specimens had only code numbers associated with them—among the pinned specimens a single individual per nest series typically contained a code number, with the remaining specimens being unlabelled—and in some instances difficulties arose in retrieving full data for coded specimens from Janzen's field notes. In other cases the field notes contradicted the apparent identity or composition of a nest series. This latter problem applied mainly to pinned specimens; the alcohol material appeared to be reliably labelled or coded, i.e. the contents of the vials agreed with the field notes. Thanks to the efforts of Roy Snelling and Jack Longino, who incorporated the Janzen collection into the LACM, many of these discrepancies or uncertainties were resolved, but there remains a residue of "problem material" for which collection data are lacking or ambiguous. Among the pinned specimens this comprises twelve drawers in the LACM collection which have been specifically set aside from the main collection. None of this problematical material has been cited in the present study, but I have examined it and determined that no additional species are represented there. Although omission of this material means the potential loss of some locality data, I have examined the entire alcohol collection and point-mounted representative samples so that geographic coverage remains extensive. The main pinned series of LACM acacia-ants, i.e. that for which accurate data labels are available, comprises 30 drawers and approximately 20,000 specimens, the great majority of which were collected by Janzen.

Metric Measurements and Indices

All measurements were made under a Wild microscope at 50X power, using an orthogonal pair of Nikon micrometers wired to a digital readout. Measurement conventions follow those described in Ward (1985, 1989). Note that a full-face or dorsal view of the head involves positioning the posterior margin and the anterolateral margins (above the mandibular insertions) so that they lie in the same plane of view.

The following measurements and indices are cited in this study (the first six measurements are taken with the head in a full-face, dorsal view):

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 anterior clypeal margin to the midpoint of a line drawn across the "occipital" (i.e. posterior) margin.

EL Eye length: length of compound eye; note that this is measured with the head in full face, dorsal view, unlike EW(below).

OD Ocellar distance: distance from the middle of the median ocellus to the midpoint of a line drawn between the lateral ocelli.

OOD Oculo-ocellar distance: distance from the middle of the median ocellus to the midpoint of a line drawn across the posterior margins of the compound eyes (this distance is negative in value if the posterior margin of the compound eye exceeds the median ocellus).

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.

ASO Antennal sclerite distance, outer margins: maximum distance between the outer, lateral margins of the antennal sclerites.

CLW Width of median clypeal lobe, measured between the anterolateral angles (in *Pseudomyrmex satanicus* and *P. spinicola* only; see Figs. 10, 11).

MD4, MD5, MD8, MD9 A series of mandibular measurements (see Ward 1989, figure 2). 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 usually hidden).

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, figure 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 the "metapleural" lobe to the metanotal groove (see Ward 1985, figure 2).

BF Length of the basal (=dorsal) 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 "metapleural" 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, figure 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, figure 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, figure 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, measure in dorsal view.

LHT Length of metatibia: maximum measurable length of metatibia, excluding the proximal part of the articulation which is received into the distal end of the metafemur (see Ward 1989, figure 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

OOI Oculo-ocellar index: OOD/OD

VI Vertex width index: VW/HW

FCI Frontal carinal index: MFC/HW

FCI2 Frontal carinal index, using ASD: MFC/ASD

ASI Antennal sclerite index: ASD/ASO

SI Scape index: SL/HW

SI2 Scape index, using EL: SL/EL

FLI Funicular length index: (LF2 + LF3)/WF2

FI 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

Other terminology follows the usage in Ward (1989). Note that descriptions of surface sculpture and integument reflectance apply to observations made under soft light, with an opaque (Mylar) filter placed between the specimens and source of illumination. Palp formula refers to the number of maxillary palp segments followed by the number of labial palp segments; 5p4,3 indicates a condition intermediate between 5,3 and 4,3, i.e. partial fusion of the fourth and fifth maxillary palp segments.

Listing of synonymy under each species is restricted to citation of the original descriptions (with full reference given for all previously proposed junior synonyms) and new nomenclatural combinations. For ecologists a more useful summary of name usage is offered in Table 1, which indicates the correspondences between the names appearing in the biological literature on acacia-ants and the currently valid scientific names. The reader will appreciate that there has been considerable misidentification of these ants.

In the lists of material examined of each species, I have cited only locality and collector ("c.u." signifies collector unknown), with the source collections listed together at the beginning. Additional locality information is sometimes provided in square brackets, to facilitate location of the collecting site. Considerable effort was expended to determine the coordinates (latitude and longitude) of each collecting site, and this was then used in conjunction with the public domain software program Versamap (version 1.20) to plot the distributions of each species (Figs. 67-72).

Cladistic Analysis

A set of 47 characters, representing the most discrete or quantifiable differences among species or groups of species in the *P. ferrugineus* group, was used for phylogenetic analysis. Twenty of these characters were worker-based (11 of these manifested the same conditions in queens), 8 were queen-based, and 19 were taken from male morphology, primarily male genitalia. The characters and character states are as follows:

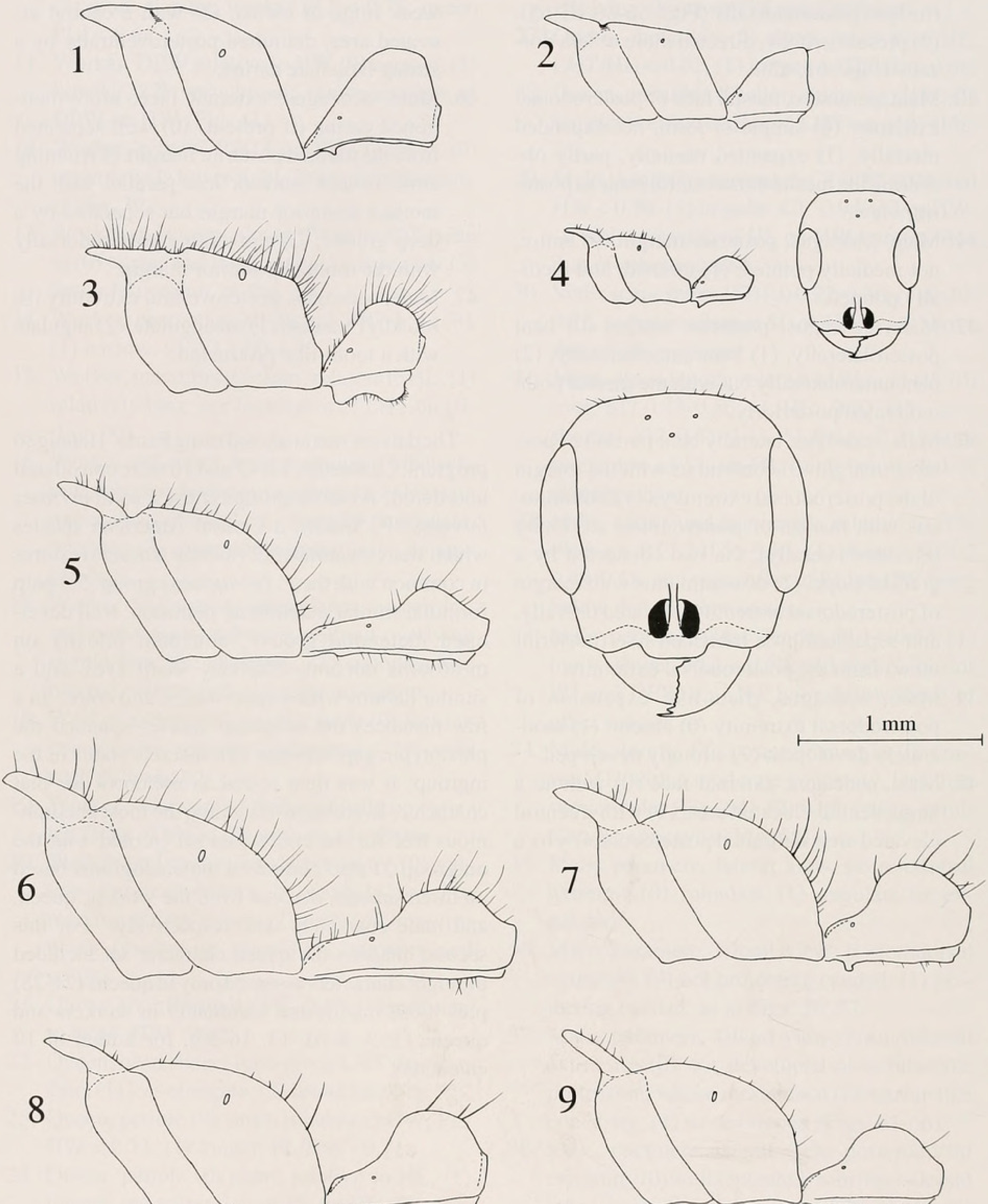
1. Worker, median clypeal lobe (0) laterally rounded or subangulate, (1) laterally with sharp angles or teeth (Figs. 10, 11).
2. Worker and queen, frontal carinae (0) relatively well separated, median lobes of antennal sclerites less exposed (Figs. 12-19, 32), (1) closely adjacent and median lobes of antennal sclerites more exposed (Figs. 10, 11, 32).
3. Worker and queen, palp formula (0) 5,3, (1) 4,3.
4. Worker, head (0) broader, relative to HL, DPL and PL, (1) narrower; see regressions of HL, DPL and PL on HW (Figs. 36-38).
5. Worker, scape (0) short, relative to HL, (1) longer; regression of SL on HL lying above that of other species.
6. Worker, conspicuous pit-like impression on midline of head (0) absent, (1) present.
7. Worker, petiole (0) short relative to postpetiole, PLI2 0.77, (1) longer relative to postpetiole, PLI2 < 0.77.
8. Worker and queen, petiole (0) without a well differentiated anterior peduncle, i.e. weakly constricted in dorsal view and with little or no inflection of the anterior face of the petiole in lateral profile (Figs. 22, 23), (1) with a well differentiated peduncle (Figs. 20, 21, 24-29).
9. Worker and queen, petiole, dorsal view, angulate posterolateral corners (0) absent, (1) moderately developed, preceded by convex or sinuate sides (e.g. Figs, 20, 27), (2) very prominent, preceded by more or less straight sides (Fig. 24).
10. Worker and queen, petiole (0) shorter and higher, worker PLI 0.71, queen PLI 0.64,

(1) more slender, worker PLI < 0.72, queen PLI < 0.64.
11. Worker, DPW relative to HW (0) narrow, (1) broader, (2) very broad; see regression of DPW on HW (Fig. 41).
12. Worker, plot of PWI3 by HW lying in (0) upper left (1) lower right (2) lower left region, of Fig. 39.
13. Worker and queen, plot of PWI4 by HW lying in (0) center and lower right (1) upper left (3) lower left region, of Fig. 40.
14. Worker, postpetiole (0) broad, PPWI > 1.30, (1) narrow, PPWI 1.00-1.30.
15. Worker, metatibia (0) short, relative to HL, (1) relatively long; see regression of LHT on HL (Fig. 30).
16. Worker and queen, head sculpture (0) densely punctulate, subopaque to sublucid, at least on upper third of head, (1) densely punctulate, opaque, (3) punctulate-coriarious, opaque (matte).
17. Worker and queen, propodeum, posterolateral portions (0) sublucid, without overlying rugulo-punctate sculpture, (1) supopaque to opaque, with rugulo-punctate sculpture.
18. Worker and queen, petiolar node (0) lacking conspicuous suberect pubescence, (1) with such pubescence.
19. Worker and queen, standing pilosity on external faces of tibiae (0) present, (1) absent.
20. Worker and queen, head and gaster (0) yellow- to orange-brown, (1) reddish-brown to medium or dark brown, (2) very dark brown to black (excluding mandibles, clypeus and scape).
21. Queen, size (0) small, HW 0.85, (1) medium to large, HW 0.85.
22. Queen, head shape, for a given LHT (0) elongate, (1) less elongate, (2) broad (see Fig. 52).
23. Queen, petiole (0) short, relative to HW, PL/HW < 0.71, (1) longer, PL/HW 0.71.
24. Queen, petiole (0) short, relative to HL, (1) longer: see regression of PL on HL (Fig.46).
25. Queen, regression of PH on HW lying in (0) upper (1) middle (2) lower region, in Fig. 47.
26. Queen, petiole, dorsal view (0) narrow, relative to HL, (2) broader; regression of DPW on HL lying above that of other species.
27. Queen, metatibia (0) short, relative to HL, LHT/HL < 0.62, (1) longer, LHT/HL > 0.66.
28. Queen, metatibia (0) short, relative to HW, (1) longer; see regression of LHT on HW (Fig. 31).
29. Male, head (0) narrower, CI 0.82-0.94 and HW < 0.96, (1) broader, CI 0.94 and/or HW 0.96 (regression of HL on HW lying below that of other species).
30. Male, scape index (SI) (0) 0.22-0.30, (1) 0.29-0.35, and regression of SL on HW lying above that of other species.
31. Male, scape length, relative to EL and HL (0) long, SI2 0.43-0.56, SL/HL 0.22, (1) shorter, SI2 0.33-0.43, SL/HL 0.21 (and regression of SL on HL lying below that of other species).
32. Male, compound eye length, relative to HW (0) long, REL2 0.56-0.63, (1) shorter, REL2 0.49-0.58, and regression of EL on HW lying below that of other species.
33. Male, petiole (0) less slender, PLI > 0.45, (1) more slender, PLI < 0.50, and regressions of PH and DPW on LHT lying below those of other species.
34. Male, sternite IX, posterior margin (0) convex, (1) with a moderate concavity, less than semicircular (Fig. 54), (2) with a deep, semicircular concavity (Fig. 55).
35. Male, paramere, lateral view, posterodorsal extremity(0) rounded, (1) angulate or expanded.
36. Male, paramere, lateral view, posterodorsal extremity (0) not projecting caudad, (1) projecting caudad, as in Figs. 56, 57.
37. Male, paramere, lateral view, posterodorsal extremity (0) not developed as a lobe-like protrusion, whose mesial face is a saucer-like concavity, (1) so developed (Figs. 61-66).
38. Male, paramere, lateral view, posterodorsal extremity (0) well separated from mesiodorsal lobe, (1) close to mesiodorsal lobe, enclosing a narrow space between it and the lobe (Figs. 58, 61-66).
39. Male, paramere, digitiform mesiodorsal lobe (0) absent, (1) present, slender, directed poste-

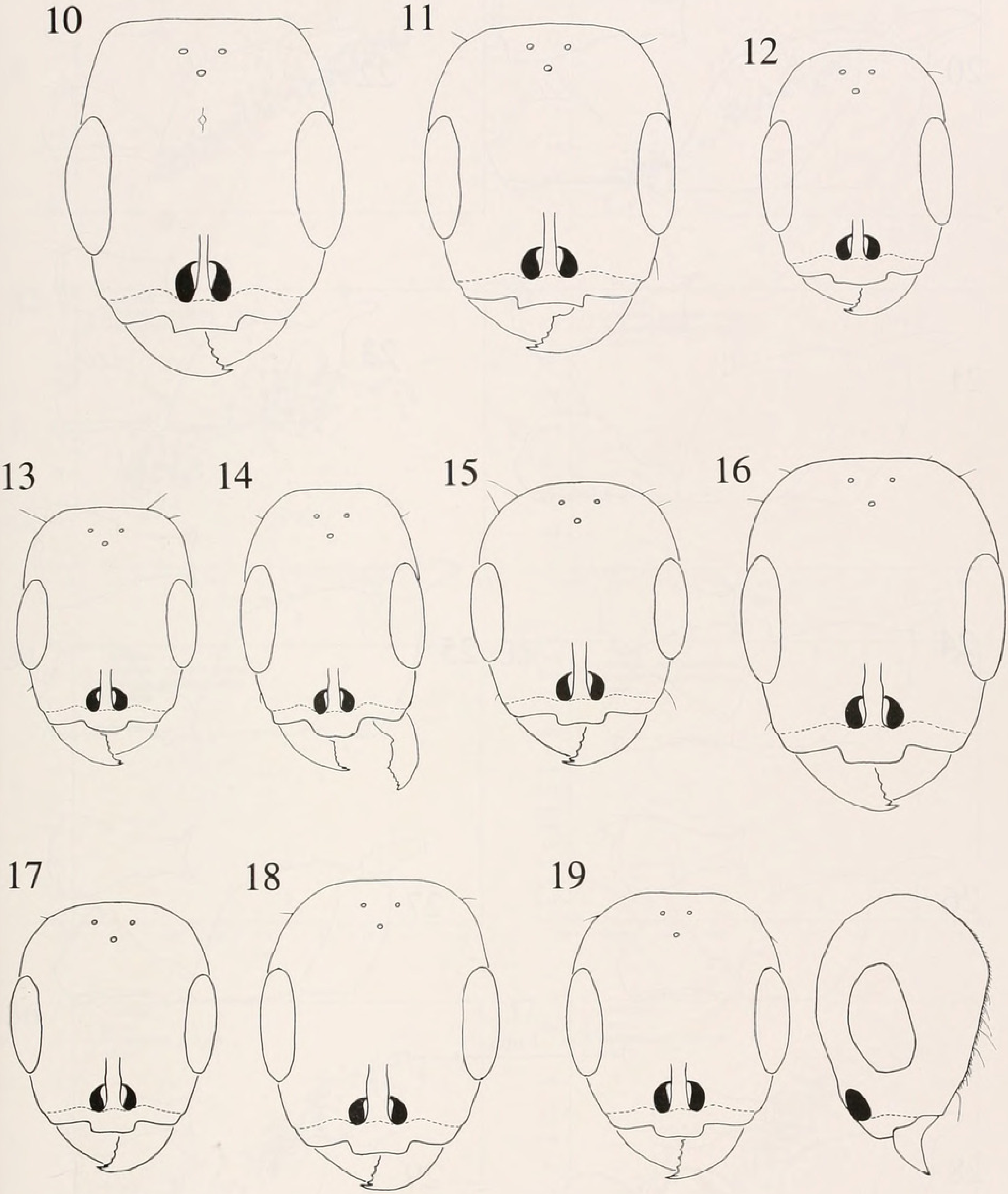
riorly or posterodorsally (Figs. 56-60, 63-65), (2) present, stubby, directed more or less dorsally (Figs. 61, 62).

40. Male, paramere, mesial face of posterodorsal extremity (0) simple in form, not expanded mesially, (1) expanded mesially, partly obscuring the mesial dorsoventral ridge in posterior view.
41. Male, aedeagus, posterior margin (0) entire, not medially pointed, (1) toothed, and medially pointed.
42. Male, aedeagus, posterior margin (0) bent posterolaterally, (1) bent anterolaterally, (2) bent anterolaterally but with the medial point redirected posteriorly.
43. Male, aedeagus, laterally bent portion of posterior margin (0) continuous with the margin of the posterodorsal extremity,(1) discontinuous with margin of posterodorsal extremity (elevated laterally), the two connected by a gradual slope, (2) discontinuous with margin of posterodorsal extremity, elevated laterally, and separated by a trenchant rise (posterior view) from the posterodorsal extremity.
44. Male, aedeagus, plate-like expansion of posterodorsal extremity (0) absent, (1) moderately developed, (2) strongly developed.
45. Male, aedeagus, external face (0) without a large, central elevated area, (1) with a central elevated area, delimited posteroventrally by a weak ridge or carina, (2) with a central elevated area, delimited posteroventrally by a strong lamellate carina.
46. Male, aedeagus, external face, afore-mentioned carina (if present) (0) well separated from the toothed posterior margin, (1) running close to and more or less parallel with the toothed posterior margin but separated by a deep groove, (2) converging posterodorsally with the toothed posterior margin.
47. Male, aedeagus, posteroventral extremity (0) broadly rounded, (1) subangulate, (2) angulate with a tooth-like protrusion.

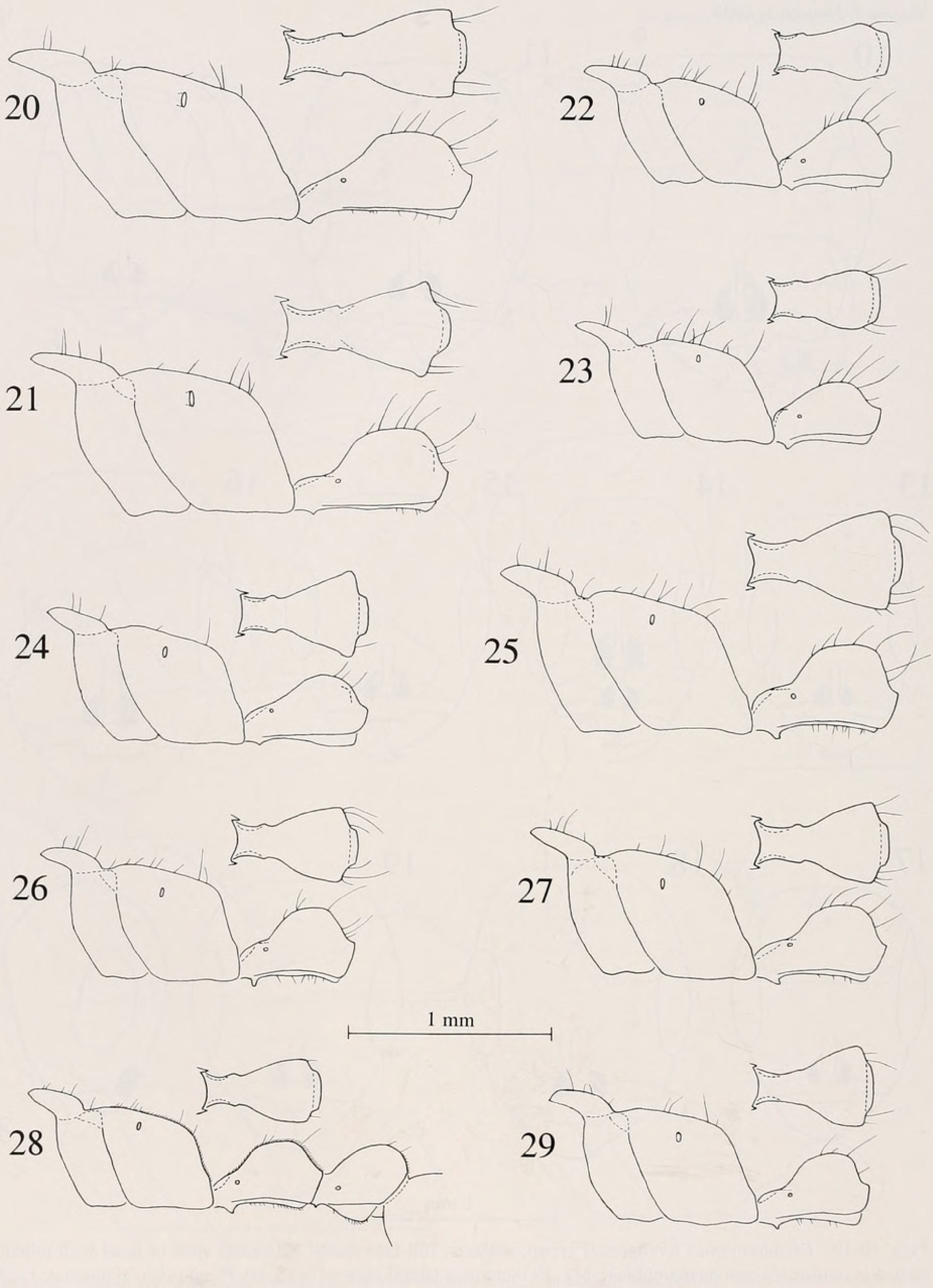
The data set was analyzed using Farris' Hennig86 program. Characters 12, 13 and 16 were considered unordered. As an outgroup I chose *Pseudomyrmex fervidus* (F. Smith), a Central American species which shares a number of (mostly worker) features in common with the *P. ferrugineus* group: 5,3 palp formula, similar mandibular dentition, well developed metanotal groove, abundant pilosity on mesosoma dorsum, relatively small eyes, and a similar habitus with respect to size and color. In a few instances the outgroup species spanned the phenotypic gap between two discrete states in the ingroup; it was then coded as unknown for that character. In addition to seeking the most parsimonious tree for the entire data set (rooted with the outgroup), I also compared the cladograms based on three subsets, derived from the worker, queen, and male characters sets, respectively. For this second analysis the queen character set included the eight characters assessed only in queens (21-28) plus those manifested identically in workers and queens (2, 3, 8-10, 13, 16-20), for a total of 19 characters.



Figs. 1-9. *Pseudomyrmex* workers, lateral view of mesonotum, propodeum and petiole, with pilosity shown in outline; Figs. 4 and 5 include a frontal view of worker head. 1, *P. boopis* (Costa Rica); 2, *P. ita* (Costa Rica); 3, *P. kuenckeli* (Costa Rica); 4, *P. hesperius* (Mexico, paratype); 5, *P. opaciceps* (Guatemala, paratype); 6, *P. gracilis* (Mexico); 7, *P. nigropilosus* (Costa Rica); 8, *P. reconditus* (Nicaragua, holotype); 9, *P. simulans* (Panama).



Figs. 10-19. *Pseudomyrmex ferrugineus* group, workers, full-face dorsal (=frontal) view of head with pilosity shown in outline (except on mandibles); Fig. 19 includes a lateral view of head. 10, *P. satanicus* (Panama); 11, *P. spinicola* (Costa Rica); 12, *P. peperi* (Guatemala); 13, *P. nigrocinctus* (Costa Rica); 14, *P. particeps* (Costa Rica, holotype); 15, *P. mixtecus* (Mexico, holotype); 16, *P. flavicornis* (Nicaragua); 17, *P. veneficus* (Mexico); 18, *P. ferrugineus* (Mexico); 19, *P. janzeni* (Mexico, holotype).



Figs. 20-29. *Pseudomyrmex ferrugineus* group, workers, dorsal view of petiole paired with lateral view of mesonotum, propodeum, petiole and, in Fig. 28, postpetiole. Standing pilosity shown in outline. 20, *P. satanicus*; 21, *P. spinicola*; 22, *P. nigrocinctus*; 23, *P. particeps*; 24, *P. peperi*; 25, *P. flavicornis*; 26, *P. mixtecus*; 27, *P. ferrugineus*; 28, *P. veneficus*; 29, *P. janzeni*. These are the same individuals illustrated in Figs. 10-19.

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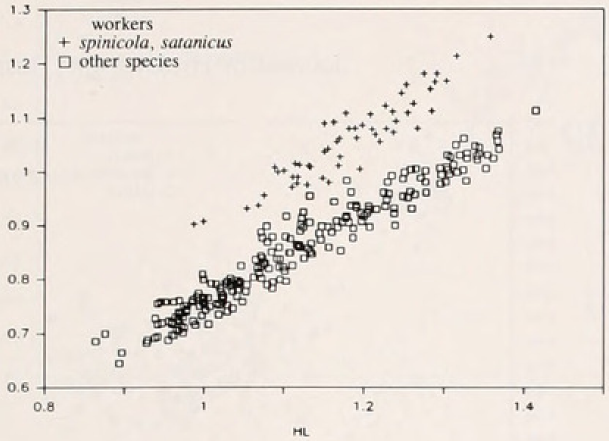

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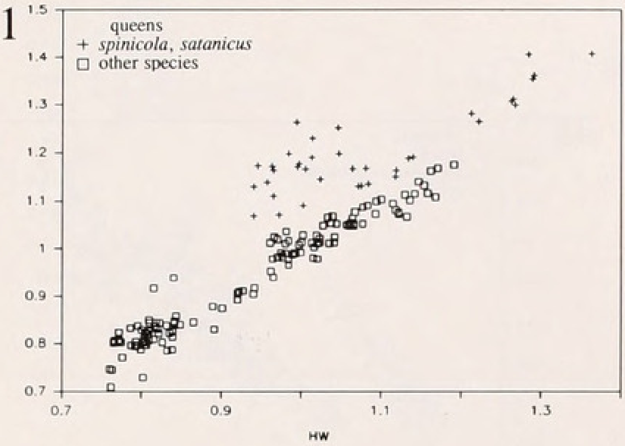

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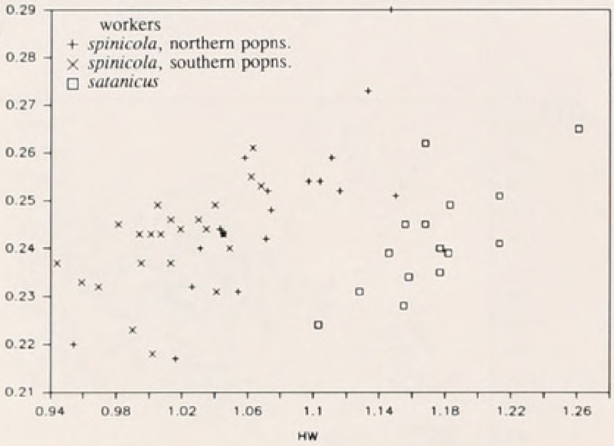

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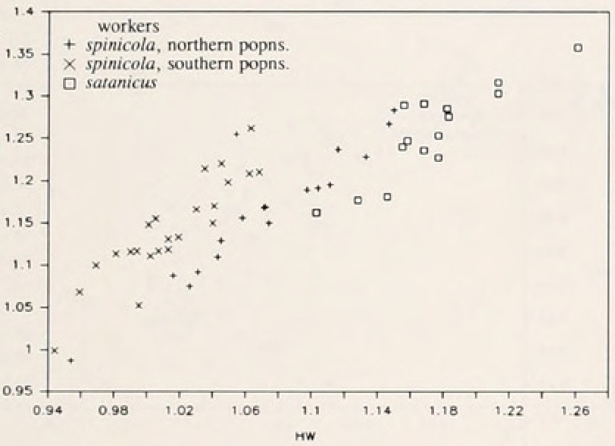
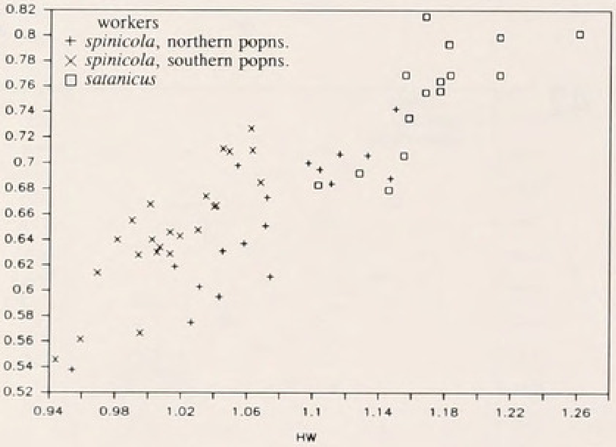
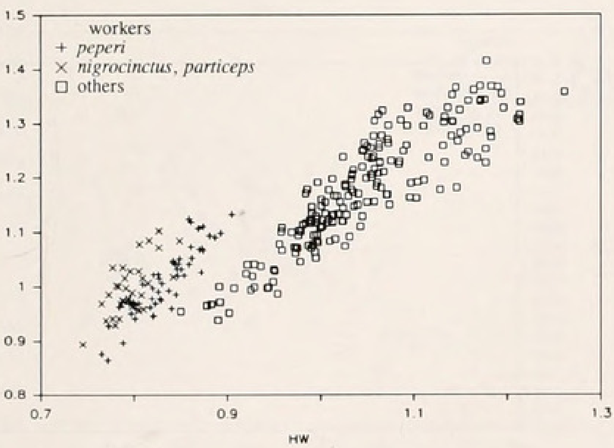
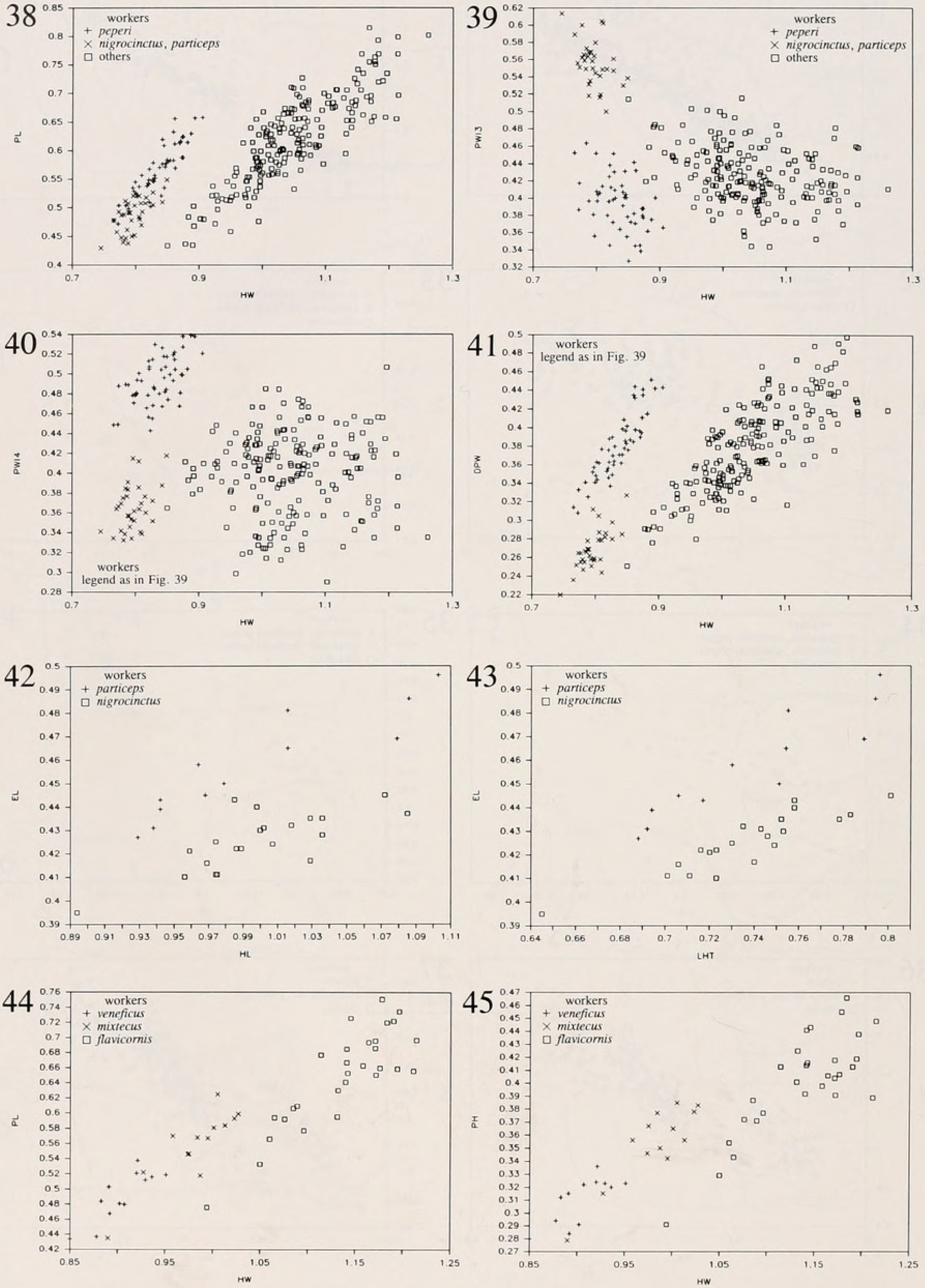


35


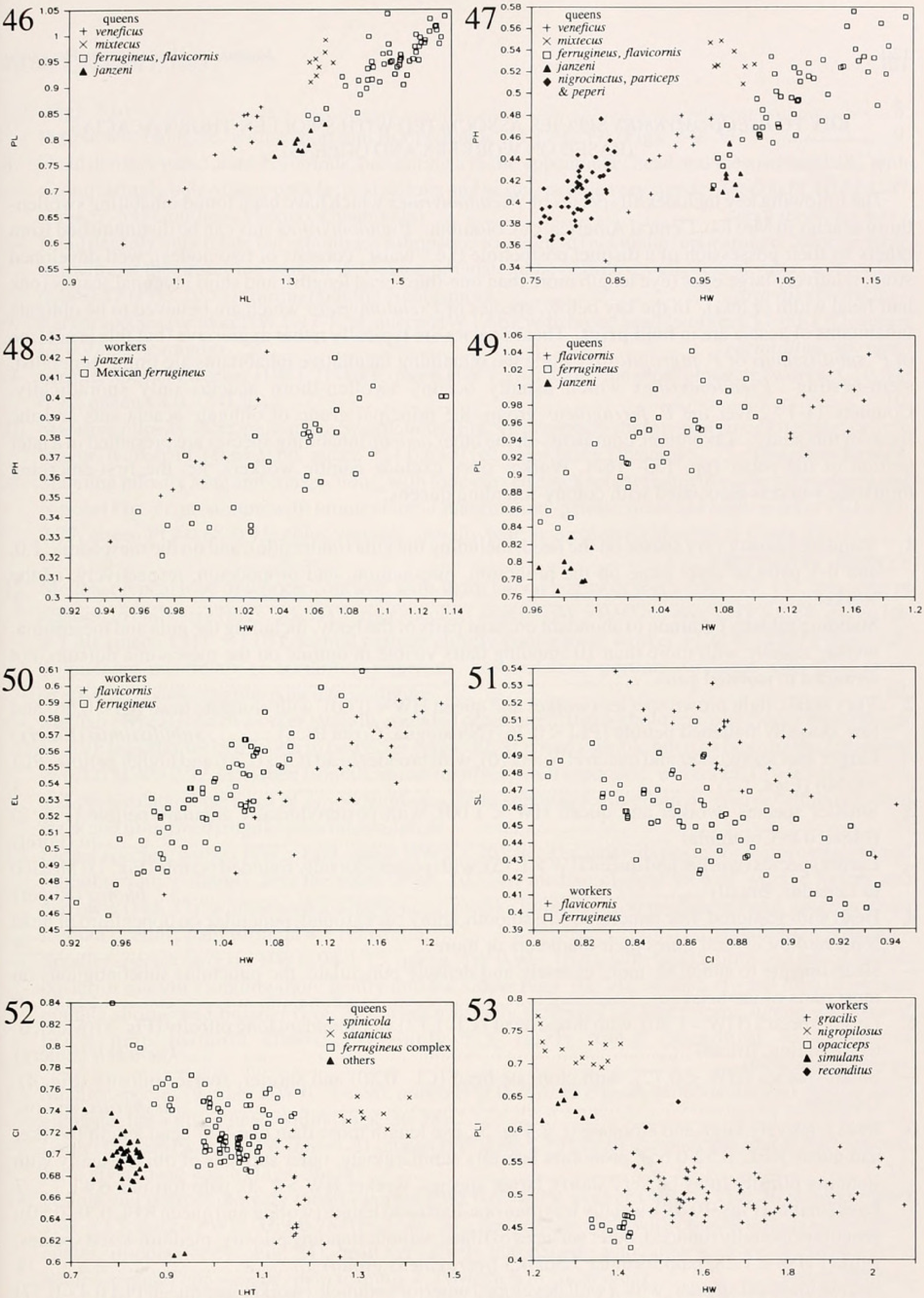
36


37


Figs. 30-37. Scattergram plots of various metric measurements and indices in workers and queens of the *Pseudomyrmex ferrugineus* group. "other species" refers to all others in the *P. ferrugineus* group.



Figs. 38-45. Scattergram plots of various metric measurements and indices in workers of the *Pseudomyrmex ferrugineus* group. "others" refers to all other species in the *P. ferrugineus* group.



Figs. 46-53. Scattergram plots of various metric measurements and indices in *Pseudomyrmex* workers and queens. 46-52, *P. ferrugineus* group; "others" refers to all other species in the *P. ferrugineus* group; "*P. ferrugineus* complex" refers to a complex of five species: *ferrugineus*, *flavicornis*, *janzeni*, *mixtecus* and *veneficus*; 53, *P. gracilis* group.

KEY TO *PSEUDOMYRMEX* SPECIES ASSOCIATED WITH SWOLLEN-THORN ACACIAS (BASED ON WORKERS AND QUEENS)

The following key includes all species of *Pseudomyrmex* which have been found inhabiting swollen-thorn acacias in Mexico, Central America, or Colombia. *Pseudomyrmex* ants can be distinguished from others by their possession of a distinct postpetiole (i.e. "waist" consists of two nodes), well developed sting, relatively large eyes (eye length more than one-third head length), and short antennal scapes (one half head width or less). In the key below, species of *Pseudomyrmex* which are believed to be obligate inhabitants of acacia are in **bold print.** These species are typically rather aggressive (but this is not true of *P. subtilissimus* or *P. nigropilosus*),while the remaining facultative inhabitants are timid, generalist, stem-nesting *Pseudomyrmex* which usually occupy swollen-thorn acacias only sporadically. Couplets 11-19 cover the *P. ferrugineus* group, the principal group of obligate acacia-ants and the focus of this study. Taxonomic comments on the other *acacia*-inhabiting species are presented in a later section of the paper (pp. 153- 162). Worker sizes exclude nanitic workers, i.e. the first-emerging miniature workers associated with colony-founding queens.

1. Standing pilosity very sparse on the head, including the gula (underside), and on the mesosoma; 1,0, and 0-1 pairs of erect setae on the pronotum, mesonotum, and propodeum, respectively, of the worker 2
— Standing pilosity common to abundant on most parts of the body, including the gula and mesosoma; worker usually with more than 10 standing hairs visible in outline on the mesosoma dorsum, not arranged in isolated pairs 4
2. Very small, light brown species (worker and queen HW < 0.60), with elongate head (CI < 0.66) and low, dorsally flattened petiole (PLI < 0.76) (Nicaragua, Costa Rica) .... ***subtilissimus* (Emery)**
— Larger species (worker and queen HW > 0.70), with broader head (CI > 0.70) and higher petiole (PLI > 0.80) (Figs. 1,2) 3
3. Smaller species (worker and queen HW < 1.00), with posterodorsally angulate petiole (Fig. 2) (Mexico to Colombia) .... *ita* (Forel)
— Larger species (worker and queen HW > 1.15), with posterodorsally rounded petiole (Fig. 1) (Mexico to Ecuador, Brazil) .... *boopis* (Roger)
4. Head with scattered, fine punctulae on a smooth, shiny background; punctulae on upper third of head separated by several times their diameters or more 5
— Head opaque to sublucid, more coarsely and densely punctulate, the punctulae subcontiguous on most parts of the head 6
5. Larger species (HW > 1.20), with broad head (CI 1.12) and abundant long pilosity (Fig. 3) (Mexico to Argentina, Brazil) .... *kuenckeli* (Emery)
— Small species (HW < 0.72), with elongate head (CI 0.80) and shorter, sparser pilosity (Fig. 4) (Mexico) .... *hesperius*, sp.nov.
6. Eyes relatively large and elongate (e.g. Fig. 5), eye length more than one-half head length (worker and queen REL 0.52-0.65); pronotum laterally submarginate; outer surfaces of tibiae usually with standing pilosity (may be very short); larger species, worker HW > 1.20; palp formula 6,4 7
— Eyes smaller (Figs. 10-19), usually less than one-half head length (worker and queen REL 0.38-0.50); pronotum laterally rounded; outer surfaces of tibiae without standing pilosity; medium-sized species, worker HW < 1.28; palp formula 5,3or 4,3 (*ferrugineus* group) 11
7. Petiole long and slender, with a well developed anterior peduncle (worker and queen PLI 0.42-0.57)

(Figs. 5,6) 8
— Petiole less elongate, with a short anterior peduncle (PLI > 0.59) (Figs. 7-9, 53) 9
8. Head densely punctulate-coriarious, presenting a matte appearance; head and mesosoma black, with a contrastingly pale orange petiole, postpetiole, and gaster; petiole very slender, worker PLI 0.42-0.47 (Figs. 5, 53) (southern Mexico, Guatemala) .... *opaciceps*, sp. nov.
— Head densely punctulate but retaining a subopaque to sublucid (not matte) appearance; color variable but without the preceding pattern in Mexico or Guatemala; petiole usually less slender, worker PLI 0.46-0.57 (Figs. 6, 53) (throughout the Neotropics) .... *gracilis* (Fabricius)
9. Larger species (worker HW 1.47-1.54, queen HW 1.66), with broad head (worker CI 1.00-1.02, queen CI 0.92) (Nicaragua) .... ***reconditus*, sp. nov.**
— Smaller species (worker HW 1.21-1.41, queen HW 1.15-1.36); head more elongate (worker CI 0.84-0.90, queen CI 0.77-0.80) 10
10. Standing pilosity short, pale and inconspicuous (Fig. 9); pronotum sharply margined laterally; petiole longer, worker PLI 0.61-0.66, queen PLI 0.63-0.68; color black (Panama) .... ***simulans* Kempf**
— Standing pilosity long and conspicuous, with long curved black setae arising from the propodeum and petiole (Fig. 7); pronotum with blunter lateral margination; petiole short and high, worker PLI 0.69-0.77, queen PLI 0.68-0.75; color variable, usually pale or bicolored (Mexico to Costa Rica) .... ***nigropilosus* (Emery)**
11. Median clypeal lobe of worker concave, with sharp lateral angles or teeth (Figs. 10, 11); legs long in relation to body size (Figs. 30, 31); larger species (worker HW > 0.92, worker LHT > 0.88, queen HL > 1.40, queen LHT > 1.05); frontal carinae closely contiguous, worker FCI2 0.24-0.42 (Fig. 32); propodeum punctulate to coriarious-imbricate, posterolateral portions sublucid with little or no overlying, coarse, rugulo-punctate sculpture 12
— Median clypeal lobe of worker laterally rounded or subangulate (without sharp angles or teeth) (Figs. 12-19); legs shorter in relation to body size (Figs. 30, 31); size variable but if as large as the preceding (worker HW > 0.92, etc.) then frontal carinae relatively well separated, worker FCI2 > 0.43 (Fig. 32), and posterolateral portions of propodeum opaque to subopaque, overlain by coarse (although often weak and ill-defined) rugulo-punctate sculpture 13
12. Larger species (worker HW > 1.09, queen HW > 1.20); head broader, its posterior margin straight and rounding rather sharply into the sides (Figs. 10, 34); median clypeal lobe of worker longer and narrower (Fig. 33); worker with a conspicuous, pit-like impression on midline of head, anterior to the median ocellus; palp formula 4,3 (Panama) .... ***satanicus* (Wheeler)**
— Smaller species (worker HW 0.94-1.15, queen HW 0.94 - 1.14), with head a little less broad and its posterior margin rounding more gently into the sides (Figs. 10, 34); median clypeal lobe of worker notably shorter and broader (Fig. 33); worker usually lacking a pit-like impression on mid-line of head; palp formula almost invariably 5,3, rarely 5p4,3 (Honduras to Colombia .... ***spinicola* (Emery)**
13. Smaller species (worker HW 0.74-0.90, queen HW 0.76-0.85); head, propodeum, and petiole more elongate, for a given head width (Figs. 36-38) 14
— Larger species (worker HW 0.85-1.21, queen HW 0.84-1.19); head, propodeum, and petiole shorter, for a given head width (Figs. 36-38) 16
14. Petiole and postpetiole very broad (worker PWI 0.63-0.75, worker PWI3 0.33-0.46, worker PPWI 1.41-1.83; queen PWI2 0.69-0.78) (Figs. 40, 41), the petiolar node with conspicuous posterolateral angles, in dorsal view (Fig. 24); head very finely and densely punctulate-coriarious, presenting a matte (opaque) appearance; palp formula 4,3 (Mexico to Nicaragua) .... ***peperi* (Forel)**
— Petiole and postpetiole relatively narrow (worker PWI 0.49-0.61, worker PWI3 0.50-0.61, worker PPWI 1.03-1.30; queen PWI2 0.57-0.63), the petiolar node without conspicuous posterolateral angles

(Figs. 22,23); head densely punctulate, sublucid to subopaque, but without a matte appearance; palp formula 5,3 15

15. Workers and queens light orange-brown, with a fuscous patch on anterior third of abdominal tergite IV (first gastric tergite); eyes relatively short (worker EL/LHT 0.56-0.61, queen REL2 0.58-0.66) (Figs. 13, 42, 43); queen head less elongate (queen CI 0.67-0.72) (Guatemala to Costa Rica) .... ***nigrocinctus* (Emery)**

— Workers and queens entirely dark brown; eyes longer (worker EL/LHT 0.59-0.64, queen REL2 0.69-0.70) (Figs. 14, 42, 43); queen head more elongate (CI 0.61, in the two known specimens) (Costa Rica) .... ***particeps*, sp. nov.**

16. Small species (worker HW 0.85-0.95, queen HW 0.84-0.96) with head, gaster, and at least part of mesosoma very dark brown to black; body pubescence dense, decumbent to suberect, and conspicuous, especially on the petiolar node (Fig. 28); standing pilosity often (not always) sparse; head weakly shining (western Mexico) .... ***veneficus* (Wheeler)**

— Body pubescence dense but predominantly appressed, petiolar node without conspicuous suberect pubescence; usually larger (worker HW 0.89-1.21, queen HW 0.96-1.19) with more conspicuous standing pilosity; color and head sculpture variable 17

17. Head and gaster (typically also mesosoma) very dark brown to black; head densely punctulate and opaque 18

— Body lighter in color: light orange-brown to medium brown, rarely dark brown; head at least weakly sublucid between ocelli and upper margin of the compound eye 19

18. Smaller species, worker HW 0.89-1.03, queen HW 0.96-1.01; petiole relatively longer and higher (Figs. 44-47) (southern Mexico) .... ***mixtecus*, sp. nov.**

— Larger species, worker HW 0.99-1.21, queen HW > 1.10; petiole relatively shorter and lower (Figs. 44-47) (Guatemala to Costa Rica) .... ***flavicornis* (F. Smith)**

19. Head and mesosoma light orange-brown, the gaster similar or slightly darker; underside of head (gula) with conspicuous suberect pubescence (Fig. 19); profile of worker mesosoma as in Fig. 29; smaller species (worker HW 0.93-1.03, queen HW 0.96-1.00) with shorter, higher petiole (Figs. 46-49) (western Mexico) .... ***janzeni*, sp. nov.**

— Gaster (and usually head) medium to dark brown, mesosoma variable; gular pubescence usually more appressed and inconspicuous; in profile worker mesosoma usually with basal face rounding more gradually into declivitous face (Fig. 27); size variable but larger on average (worker HW 0.92-1.15,queen HW 0.92-1.12), with longer and lower petiole (Figs. 46-49) (eastern and southern Mexico to Honduras) .... ***ferrugineus* (F. Smith)**

KEY TO MALES OF THE OBLIGATE ACACIA-ANTS, *PSEUDOMYRMEX FERRUGINEUS* GROUP

Although isolated acacia-ant males are unlikely to be encountered, the following key is offered as a supplement for determination of species in the *P. ferrugineus* group. It can be used to confirm worker- or queen-based identifications, but some couplets require examination of the male genitalia.

1. Posterior margin of subgenital plate (sternite IX) with a shallow (less than semicircular) concavity (Fig. 54); scape short, SI2 0.33-0.43, SL/HL 0.21 2

— Posterior margin of subgenital plate (sternite IX) with a deep, semicircular concavity (Fig. 55); scape longer, SI2 0.43-0.56, SL/HL 0.22 3

2. Paramere, in lateral view, with a slender finger-like mediodorsal lobe and angulate posteroventral corner (Fig. 57) .... *particeps*

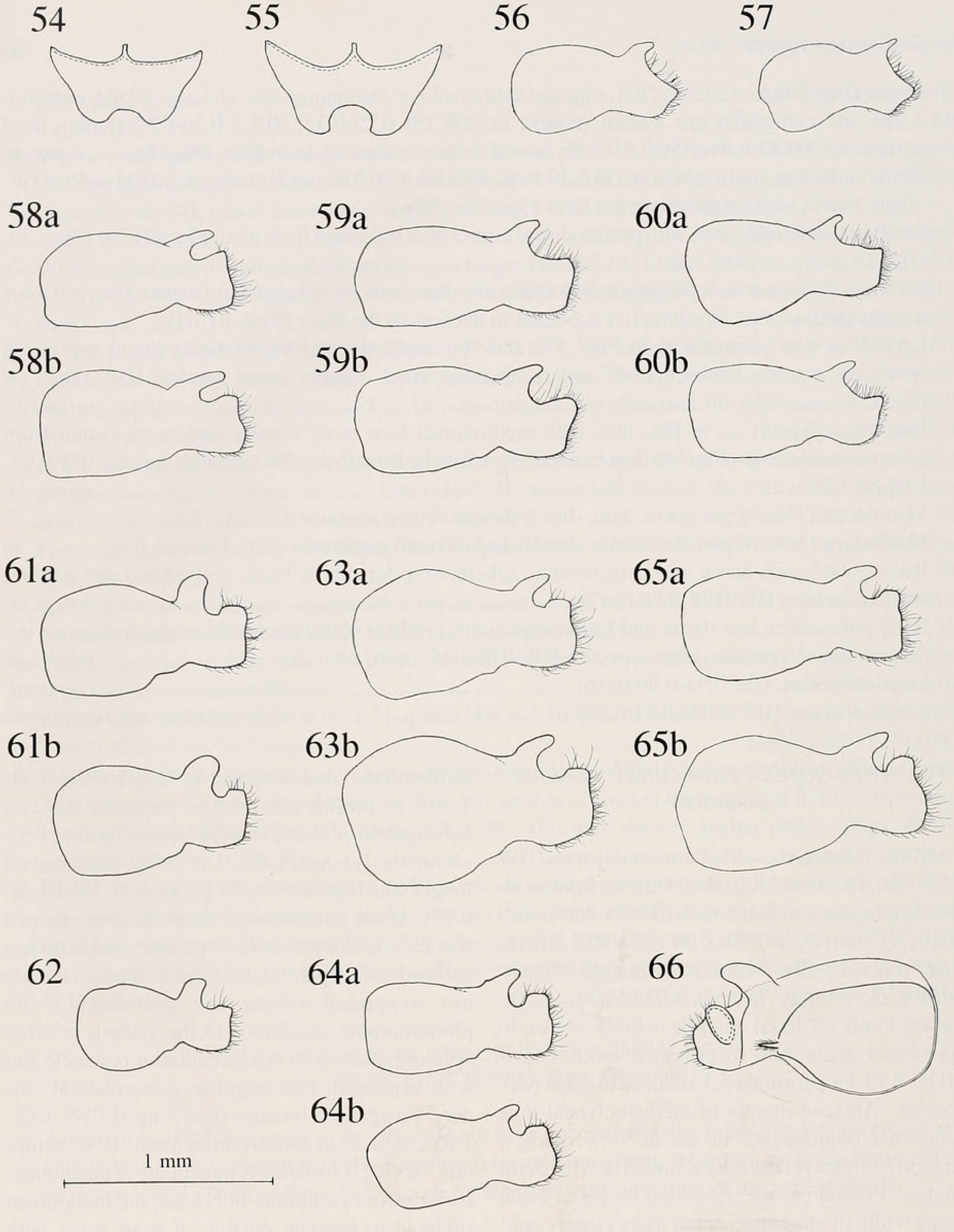
— Paramere, in lateral view, with a stubbier mediodorsal lobe and more gently rounded posteroventral corner (Fig. 56) .... *nigrocinctus*

3. Scape and compound eye longer, relative to HW (SI 0.29-0.35; REL2 0.56-0.62 (n=6)); head narrower, CI 0.82-0.94, HW 0.81-0.95; lateral view of paramere as in Figs. 58a, 58b .... *peperi*
— Scape and compound eye shorter (SI 0.22-0.30, REL2 0.49-0.58); head broader, CI 0.94 and/or HW 0.96; lateral view of paramere not as in Figs. 58a, 58b 4
4. Paramere, in lateral view, with posterodorsal corner well separated from mediodorsal lobe (Figs. 59-60) 5
— Paramere, in lateral view, with posterodorsal corner bent upward and enclosing a space between itself and the mediodorsal lobe which is subequal to the area of the latter (Figs. 61-65) 6
5. Lateral view of paramere as in Figs. 59a and 59b: mediodorsal lobe relatively broad and partly enclosing a space between itself and the posterodorsal corner; larger species, HW 1.06-1.09 (n=5) .... *satanicus*
— Paramere typically as in Fig. 60a, with mediodorsal lobe more slender and more distant from posterodorsal corner (Fig. 60b depicts a less typical male, from Colombia); smaller species, HW 0.92-1.05 (n=12) .... *spinicola*
6. Mediodorsal lobe of paramere stout, directed more or less dorsally (Figs. 61, 62) 7
— Mediodorsal lobe of paramere more slender and directed posterodorsally (Figs. 63-65) 8
7. Body pubescence dense and conspicuous, suberect on dorsum of head, propodeum and petiole; smaller species, HW 0.79-0.88 (n=7) .... *veneficus*
— Body pubescence less dense and less conspicuous, predominantly appressed or decumbent on the propodeum and petiole; larger species, HW 0.88-0.97 (n=6) .... *mixtecus*
8. Smaller species, HW 0.93-0.96 (n=6) .... *janzeni*
— Larger species, HW 0.99-1.19 (n=22) .... *ferrugineus* and *flavicornis*

PSEUDOMYRMEX FERRUGINEUS GROUP

Introduction

Worker, diagnosis.—Medium sized species (HW 0.74-1.26, HL 0.86-1.42); head varying from moderately elongate to rather broad (CI 0.75-0.97), with relatively short eyes (REL 0.39-0.50, REL2 0.45-0.62) (Figs. 10-19). Masticatory margin of mandible with 6, rarely 7, teeth, MD8/MD9 0.70; mesial tooth on basal margin notably closer to apicobasal angle than to proximal tooth, MD4/MD5 0.74. Palp formula 5,3, reduced to 4,3 in two species. Anterior margin of median clypeal lobe somewhat blunt-edged, in dorsal view convex, straight or concave, laterally rounded or with sharp angles. Frontal carinae separated by about basal scape width in most species but more closely contiguous in two (FCI 0.03-0.10, FCI2 0.24-0.75, ASI 0.52-0.73), fusing anterolaterally with antennal sclerites. Funicular segments II and III about as broad as long (FLI 1.46-2.45). Profemur slender (FI 0.35-0.41). Pronotum laterally rounded. Metanotal groove well marked (MPI 0.04-0.09). Basal and declivitous faces of propodeum moderately well differentiated and subequal in length (PDI 0.94-1.30), in profile the juncture between the two subangulate or gently rounded (Figs. 20-29). Petiole relatively long (PL/HL 0.44-0.63), always much longer than high or wide (PLI 0.47-0.71, PWI 0.46-0.75), small anteroventral tooth present; in two species anterior peduncle of petiole weakly differentiated and posterolateral corners of petiolar node not expanded (these are presumably the plesiomorphic conditions in the group), in other species petiole with distinct anterior peduncle and with expanded, (sub)angulate posterolateral corners. Postpetiole broader than long (PPWI 1.03-1.85), with small anteroventral tooth. Body sculpture varying from densely punctulate or punctulate-coriarious to coriarious-imbricate, the integument sublucid to opaque; dorsum of head never with extensive smooth, shiny interspaces (punctulae usually separated by their diameters or less); propodeum of some species overlain by a coarser but weak rugulo-punctate sculpture. Standing pilosity common, present on the scapes, head, entire mesosoma dorsum (10 or more standing hairs visible in profile), petiole, postpetiole and gaster,



Figs. 54-66. *Pseudomyrmex ferrugineus* group, male terminalia. Figs. 54-55: sternite IX; Figs. 56-65: left paramere, lateral view, caudal end to right; Fig. 66: left paramere, mesial view. 54, *P. particeps* (Rincon, Costa Rica); 55, *P. mixtecus* (near Tehuantepec, Mexico); 56, *P. nigrocinctus* (10mi. NW Liberia, Costa Rica); 57, *P. particeps* (Rincon, Costa Rica); 58, *P. peperi* (58a: 3km ENE Chiapa de Corzo, Mexico; 58b: Nueva Ocotepeque, Honduras); 59, *P. satanicus* (59a: 3mi. SW Gatun Dam, Panama; 59b: Marajal, Panama); 60, *P. spinicola* (60a: Madden Dam, Panama; 60b: Aracataca, Colombia); 61, *P. mixtecus* (61a: 57.8mi. S Chilpancingo, Mexico; 61b: near Tehuantepec, Mexico); 62, *P. veneficus* (5km E Chamela, Mexico); 63, *P. flavicornis* (63a: Rio Oro, Costa Rica; 63b: 3.6mi. W Choluteca, Honduras); 64, *P. janzeni* (64a: 60mi. SE Acaponeta, Mexico; 64b: 4mi. E San Blas, Mexico); 65, *P. ferrugineus* (65a: Escuintla-Cd. Guatemala, Guatemala; 65b: 10.8mi S Pichucalco, Mexico); 66, *P. ferrugineus* (10.8mi S Pichucalco, Mexico).

absent from the extensor faces of tibiae. Appressed pubescence dense on most of body, including head and abdominal tergite IV. Color varying from light yellow- or orange-brown to black.

Queen diagnosis.—Similar to worker except for caste-specific differences. Larger in size (HW 0.76-1.36, HL 1.05-1.81), head more elongate (CI 0.60-0.80). Ocular indices differing slightly: REL 0.38-0.48, REL2 0.51-0.70. Median clypeal lobe narrower and more protruding, anterior margin convex or straight, laterally rounded or subangulate. Petiole and postpetiole generally more slender (PL/HL 0.57-0.72, PLI 0.43-0.63, PWI 0.47-0.67, PPWI 1.06-1.50). Forewing with 2 cubital cells.

Male, diagnosis.—Head varying from longer than broad to slightly broader than long (CI 0.82-1.04 in a sample of 70 males belonging to all species); compound eye large, prominent (REL2 0.49-0.62). Mandibles with 8+ teeth or denticles on masticatory margin. Palp formula as in females, but somewhat more variable (males with 5p4,3 commoner than in workers or queens). Surface of median clypeal lobe convex, its anterior margin subtriangular in shape (dorsal view) with sides converging medially to a rounded point. Petiole and postpetiole more slender than in workers (PLI 0.40-0.55, PWI 0.35-0.51) and simpler in shape. Posterolateral corners of sternites IV-VIII not notably protruding ventrally. Subgenital plate (sternite IX) with a conspicuous posteromedial concavity (Figs. 54, 55). Posterior margin of pygidium (tergite VIII) convex, directed posteroventrally. Paramere with several characteristic features: a finger-like, posterodorsally directed mediodorsal lobe; angulate or expanded posterodorsal extremity; and mesial dorsoventral ridge which joins the mediodorsal lobe posteriorly. Aedeagus with expanded posterodorsal corner, a medial protrusion on the posterior margin, numerous small teeth (15+) on the posterior margin, and on the outer face a raised ridge curving posterodorsally from a basal origin.

Comments.—Workers and queens of the *P. ferrugineus* group can be distinguished from all other *Pseudomyrmex* by their possession of the following combination of traits: mandibles with 6-7 teeth; palp formula 5,3 or 4,3; standing pilosity common on mesosoma dorsum but absent from external faces of tibiae; worker metanotal groove conspicuously impressed; and head densely punctulate, sublucid to opaque. The relatively short eyes (worker REL 0.50, queen REL 0.48) and slender petiole (worker PLI 0.71, queen PLI 0.63) are also characteristic. Among the eight other major species groups of *Pseudomyrmex* (diagnosed in Ward, 1989) only the *P. viduus* and *P. oculatus* groups have workers and queens approaching these conditions. Those of the *P. viduus* group have a shinier head, a shorter and more robust petiole (worker PLI > 0.70, worker PWI > 0.70), and standing pilosity on the tibiae (reduced in one species), while workers and queens of the *P. oculatus* group have a palp formula of 6,3 (reduced to 5,3 only in smallest species with worker and queen HW < 0.67), tectiform and sharp-edged median clypeal lobe with a broadly convex margin (dorsal view), elongate eyes (worker REL 0.48-0.61, worker REL2 0.62-0.86, queen REL 0.43-0.57, queen REL2 0.68-0.89), and short petiole (worker PLI 0.67-1.06, queen PLI 0.57-0.94). Among taxonomically isolated species not belonging to one of the major species groups, *P. fervidus* (F. Smith) bears perhaps the closest phenetic resemblance to the *P. ferrugineus* group, but its workers and queens can be distinguished by their shinier and less densely punctulate head, shorter petiole (worker PLI 0.71-0.76, worker PL/HL 0.41-0.44 (n=9); queen PLI 0.65, queen PL/HL 0.49), and standing pilosity on the outer faces of the tibiae. In addition the queens of *P. fervidus* have a distinctive, pointed median clypeal lobe not seen in *P. ferrugineus* group queens.

Males of the *Pseudomyrmex ferrugineus* group can be characterized by their palp formula, medially subangulate clypeal lobe, emarginate subgenital plate, configuration of the paramere, and shape of the aedaegus. They are approached most closely in this combination of traits by males of *P. haytianus* (Forel) and two undescribed Central American species (*P.* sp. PSW-02 and *P.* sp. PSW-54) although, curiously, the workers and queens of those species do not bear a close resemblance to those of the *P. ferrugineus* group.

All species in the *P. ferrugineus* group are obligate inhabitants of Central American swollen-thorn acacias, a biological trait not characterizing any other species group of *Pseudomyrmex*, although a few species in the otherwise quite different *P. gracilis* group and one species in the *P. subtilissimus* group have independently developed an obligate association with the acacias.

Distribution.—Members of the *P. ferrugineus* group are found from eastern (San Luis Potosi, Tamaulipas) and western (Sinaloa) Mexico south through Central America to northern Colombia (Fig. 67). Although no single species spans the entire range of the group, their collective distribution is virtually identical to that of the swollen-thorn acacias (compare Fig. 67 with Janzen 1974:3).

Synonymic List of Species

P. ferrugineus (F. Smith 1877) Mexico to Honduras
- = *P. fulvescens* (Emery 1890) (Ward 1989)
- = *P. canescens* (Wasmann 1915) (Ward 1989)
- = *P. wasmanni* (Wheeler 1921) (replacement name for *canescens*)
- = *P. bequaerti* (Wheeler 1942) (Ward 1989)
- = *P. saffordi* (Wheeler 1942) (Ward 1989)
- = *P. vesanus* (Wheeler 1942) (Ward 1989)
- = *P. bequaerti* (Enzmann 1945) (Brown 1949)
- = *P. honduranus* (Enzmann 1945) (Ward 1989)

P. flavicornis (F. Smith 1877) Guatemala to Costa Rica
- = *P. belti* (Emery 1890) (Ward 1989)
- = *P. obnubilus* (Menozzi 1927a) (Ward 1989)
- = *P. fellosus* (Wheeler 1942) (Ward 1989)

P. janzeni Ward, **sp. nov.** Mexico

P. mixtecus Ward, **sp. nov**. Mexico

P. nigrocinctus (Emery 1890) Guatemala to Costa Rica
- = *P. alfari* (Forel 1906) **syn. nov.**
- = *P. bicinctus* (Santschi 1922) **syn. nov.**
- = *P. peltatus* (Menozzi 1927) **syn. nov.**

P. particeps Ward, **sp. nov.** Costa Rica

P. peperi (Forel 1913) Mexico to Nicaragua
- = *P. convarians* (Forel 1913) (Ward 1989)
- = *P. saffordi* (Enzmann 1945) (Ward 1989)

P. spinicola (Emery 1890) Honduras to Colombia
- = *P. atrox* (Forel 1912) **syn. nov.**
- = *P. gaigei* (Forel 1914) **syn. nov.**
- = *P. infernalis* (Wheeler 1942) **syn. nov.**
- = *P. scelerosus* (Wheeler 1942) **syn. nov.**
- = *P. infernalis* (Enzmann 1945) (Brown 1949)
- = *P. scelerosus* (Enzmann 1945) (Brown 1949)

P. satanicus (Wheeler 1942) Panama

P. veneficus (Wheeler 1942) Mexico
- = *P. venificus* (Enzmann 1945) (Brown 1949)

SPECIES ACCOUNTS

Pseudomyrmex ferrugineus (F. Smith 1877)
(Figs. 18, 27, 65, 66, 70)

Pseudomyrma ferruginea F. Smith 1877:64. Lectotype worker, Mexico (BMNH) [Examined].

Pseudomyrma belti race *fulvescens* Emery 1890:64. Lectotype worker, Guatemala (Beccari) (MCSN) [Examined] [Synonymy by Ward 1989:437; see also Janzen 1967b:391].

Pseudomyrma canescens Wasmann 1915:321. Syntype workers, Tampico, Mexico (Brakhoven) (MCSN, MCZC) [Examined] [Synonymy by Ward 1989:437].

Pseudomyrma wasmanni Wheeler 1921:92. Replacement name, now unnecessary, for *P. canescens* Wasmann 1915 (nec F. Smith 1877).

Pseudomyrma belti subsp. *bequaerti* Wheeler 1942:164. Lectotype worker, Puerto Castilla, Honduras (J. Bequaert) (MCZC) [Examined] [Synonymy by Ward 1989:437].

Pseudomyrma belti subsp. *saffordi* Wheeler 1942:162. Lectotype worker, Chicoasen, Chiapas, Mexico (G. N. Collins) (MCZC) [Examined] [Synonymy by Ward 1989:437].

Pseudomyrma belti subsp. *vesana* Wheeler 1942:163. Holotype (unique syntype) worker, Cordoba, Mexico (F. Knab) (MCZC) [Examined] [Synonymy by Ward 1989:437].

Pseudomyrma belti subsp. *bequaerti* Enzmann 1945:80. Syntype workers, Puerto Castilla, Honduras (J. Bequaert) (MCZC) [Examined] [Objective synonym of *P. belti bequaerti* Wheeler; Brown 1949:42].

Pseudomyrma kuenckeli var. *hondurana* Enzmann 1945:87. Lectotype worker, Honduras (Bates) (MCZC) [Examined] [Synonymy by Ward 1989:437].

Pseudomyrmex ferruginea [sic] (F. Smith); Janzen 1966:252.

Pseudomyrmex ferrugineus (F. Smith); Kempf

Table 1. Summary of nomenclature used in the biological literature on acacia-ants, *Pseudomyrmex ferrugineus* group.* For all except some of the most recent (1979-1990) papers, the relationship between the names used in the paper and the species recognized in the current study was established by direct examination of museum specimens collected, or referred to, by the author(s). Only specific and infraspecfic epithets are listed since all species were placed in the same genus, *Pseudomyrma* Guérin, until 1952 when M. R. Smith showed that a different generic name, *Pseudomyrmex* Lund, had priority. By the rules of zoological nomenclature this necessitates a change in the ending of adjectival species names (e.g. *ferruginea* to *ferrugineus*) to agree in gender with *Pseudomyrmex* (masc.) but this convention was not followed by all authors.

	Species					
Author(s)	*ferrugineus*	*flavicornis*	*nigrocinctus*	*peperi*	*spinicola*	*veneficus*
Norton (1868a)	*flavidula* (part)	—	—	*flavidula* (part)	—	—
Belt (1874)	—	*bicolor*	—	—	—	—
Emery (1890,1891)	*belti fulvescens*	*belti*	*nigrocincta*	—	*spinicola*	—
Wheeler (1913)	*belti fulvescens* (part) *spinicola* (part)	*belti* (part)	*nigrocincta*	—	*spinicola* (part) *belti fulvescens* (part)	*belti* (part)
Wasmann (1915,1916)	*canescens*	*belti*	*nigrocincta*	—	*spinicola*	—
Safford (1922)	*belti fulvescens* (part)	*belti*	*nigrocincta*	*belti* "varieties" (part)	*spinicola* *belti fulvescens* (part)	—
Menozzi (1927a,b)	—	*belti obnubila*	*peltata*	—	—	—
Skwarra (1934a,b)	*belti wasmanni* (part)	—	—	*belti wasmanni* (part)	—	—
Wheeler (1942)	*belti fulvescens* *belti saffordi* (part) *belti vesana* *belti bequaerti* *belti wasmanni*	*belti* *belti fellosa* *belti obnubila*	*nigrocincta* *peltata*	*spinicola convarians* *belti saffordi* (part)	*spinicola* *spinicola atrox* *spinicola gaigei* *spinicola infernalis* *spinicola scelerosa*	*belti venefica* (part)
Janzen (1966,1967a)	*ferruginea* *spinicola* (part)	*belti* (part)	*nigrocincta* (part)	*nigrocincta* (part)	*spinicola* (part)	*belti* (part)
Janzen (1967b, 1969, 1973, 1974, 1975, 1983)	*ferruginea* (part)	*belti* (part)	*nigrocincta* (part)	*nigrocincta* (part) and "undescribed sp."	*ferruginea* (part)	*venefica*
Hölldobler & Engel (1979), Hölldobler & Engel-Siegel (1985)	—	—	—	—	*ferruginea*	—
Mintzer (1982), Mintzer & Vinson (1985), Mintzer *et al.* (1987)	*ferruginea*	—	—	—	—	—
Errard (1984)	*ferruginea*	—	—	—	—	—
Espelie & Hermann (1988)	*ferrugineus*	—	—	—	—	—
Ward (1989)	*ferrugineus*	*flavicornis*	*nigrocinctus*	*peperi*	*spinicola*	*veneficus*
Young *et al.* (1990)	—	*flavicornis*	*nigrocinctus*	—	*spinicola*	—

*Of the four other species in the *P. ferrugineus* group, *P. satanicus* has always been correctly identified (Wheeler, 1942; Janzen, 1969, 1973, 1974); *P. mixtecus* was mistaken for *P. veneficus* by Wheeler (1942) and for *P. flavicornis* (= *belti*) by Janzen (1966, 1973); *P. janzeni* was referred to by Janzen (1973:729) as an undescribed species derived from *P. ferrugineus*; and *P. particeps* has received no mention in the literature.

1972:218.

Worker measurements (n = 69).—HL 0.99-1.33, HW 0.92-1.15, MFC 0.054-0.108, CI 0.81-0.94, REL 0.42-0.48, REL2 0.48-0.54, OOI 1.39-3.16, VI 0.60-0.78, FCI 0.054-0.101, SI 0.41-0.46, SI2 0.79-0.91, NI 0.61-0.72, PLI 0.54-0.69, PWI 0.56-0.73, PPWI 1.34-1.70.

Worker diagnosis.—Medium-sized species (HW > 0.91; LHT 0.75-1.06) with broad head (CI > 0.80); anterior margin of median clypeal lobe straight or weakly concave, rounded laterally; palp formula 5,3; frontal carinae well separated (FCI > 0.05) and median lobe of antennal sclerite not strongly exposed (FCI2 0.45-0.69); mesosomal profile typically as in Fig. 27, with mesonotum notably inclined and with basal face of propodeum rounding gradually into declivitous face, but deviations from this pattern occur; petiole relatively short, high and wide (see relevant metrics: PLI, PWI), with a distinct anterior peduncle (PWI3 0.36-0.50); posterolateral angles of petiole moderately developed but not as pronounced as in *P. peperi* (compare Figs. 24 and 27); postpetiole broad. Head densely punctulate, predominantly opaque or subopaque but at least weakly shining on upper third of head between ocelli and compound eye; mesosoma punctulate to punctulate-coriarious, subopaque to sublucid; posterior portions of propodeum opaque to subopaque and usually overlain by larger but weak, irregular punctures or rugulae. Petiole, postpetiole and gaster with fine piligerous punctures, sublucid. Standing pilosity common; pubescence dense but fine and appressed on most surfaces. Color variable, from light reddish- or yellowish-brown to very dark brown, gaster (and usually head) somewhat darker than the mesosoma; mandibles, scapes, frontoclypeal complex, and apices of legs usually lighter.

Comments.—Workers and queens of *P. ferrugineus* can be recognized by features of head morphology (laterally rounded median clypeal lobe, well separated frontal carinae and correspondingly limited exposure of the median lobes of the antennal sclerites, and moderately broad worker head; see Fig. 18), head sculpture (densely punctulate and (sub)opaque, but weakly shining on upper third of head between the ocelli and compound eye), and coloration (variably brown, not black or orange-brown). This species is most likely to be confused with the allopatric *P. janzeni* and the partly sympatric *P. flavicornis*. See under those species for more specific discussion.

Distribution and biology.—*P. ferrugineus* is distributed from eastern and southern Mexico to El Salvador and Honduras (Fig. 70). It is a common species and colonies have been recorded from all swollen-thorn acacia species growing within its range, i.e. *Acacia chiapensis, A. collinsii, A. cookii, A. cornigera, A. gentlei, A. globulifera, A. hindsii, A. janzenii, A. mayana* and *A. sphaerocephala*. *P. ferrugineus* is usually monogynous (Janzen 1967b, 1973) but a few alcohol nest series from Guatemala, belonging to apparently mature colonies (as judged by the presence of alates), contained more than one dealate queen. Janzen (1966, 1967b) conducted a massive experimental study of the interaction between *P. ferrugineus* and *Acacia cornigera* in Mexico, and the results of these experiments, together with copious additional observations by Janzen, showed conclusively that the ants protect the acacia from herbivores and competing plants (especially vines). *P. ferrugineus* was also the subject of a study on kinship and nestmate recognition among workers (Mintzer 1982; Mintzer et al. 1985) which demonstrated a worker-based and probably inherited component to colony odor. Statements about the biology of "*P. ferruginea*" from regions south of El Salvador and Honduras (e.g. Janzen 1983) refer to a different species, *P. spinicola*.

Material examined (AMNH, BMNH, CASC, CHAH, CISC, CUIC, INHS, LACM, MCSN, MCZC, MHNG, MNHN, MZSP, NHMV, PSWC, SEMC, UCDC, USNM, WPMC).—

BELIZE *Belize*: 2.2mi W Belize, rd.to Chetumal (D.H.Janzen); 3.8mi NW Belize, rd.to Chetumal (D.H.Janzen); 4.9mi SW Belize, rd.to Cayo (D.H.Janzen); Belize (Baker; c.u.); Manatee [River] (J.D.Johnson; c.u.); nr. Belize (N.L.H.Krauss); Cayo: 36.1mi SW Belize (D.H.Janzen); 36.1mi [S]W Belize (U.Kansas Mex.Exped.); El Cayo [=San Ignacio] (N.L.H.Krauss); Pine Mtn. Ridge, Mecal R., 415m (G.D.Alpert); San Ignacio (S.E.Schoenig); *Corozal*: 13.5mi S Sta.Elena (Louisville) (D.H.Janzen); 15mi S Sta.Elena (Louisville) (D.H.Janzen); *Orange Walk*: 5mi SE Orange

Walk, rd.to Belize (D.H.Janzen); Toledo: Punta Gorda (H.Broomfield).

EL SALVADOR *Chalatenango*: 4.7mi NW La Palma, 880m (D.H.Janzen); 5.5mi SE La Palma, 1130m (D.H.Janzen).

GUATEMALA *Alta Verapaz*: San Joaquin, nr. San Cristóbal Verapaz, 1080m (D.H.Janzen); Trece Aguas (Schwarz & Barber); *Chimaltenango*: Yepocapa (H.T.Dalmat); *Coatepeque*: 2mi W Coatepeque (D.H.Janzen); *El Progreso*: 4.9mi SW Sanarate, 780m (D.H.Janzen); *Escuintla*: 1.7mi S Escuintla, 370m [on CA-2] (D.H.Janzen); 12.6mi NE Escuintla, rd. to Cd. Guatemala, 1120m (D.H.Janzen); 15km E Escuintla [on CA-9] (D.H.Janzen); 3mi N Escuintla [on CA-9] (D.H.Janzen); 3mi S Escuintla [on CA-9] (D.H.Janzen); 43km S Cd. Guatemala [=15km E Escuintla] (D.H.Janzen); 6.8mi S Escuintla, 280m [on CA-2] (D.H.Janzen); 8.3mi N Escuintla [on CA-9] (D.H.Janzen); 9.2mi N Escuintla, 900m [on CA-9] (D.H.Janzen); Escuintla (W.M.Wheeler); Pantaleon (Champion); *Guatemala*: 16.2mi NE Cd.Guatemala (D.H.Janzen); 19km S Cd.Guatemala [on CA-9] (D.H.Janzen); 20mi SE Cd.Guatemala, 1060m [on CA-1] (D.H.Janzen); 6.2mi NE Cd.Guatemala, 700m (D.H.Janzen); 7.9mi S Cd. Guatemala, 1360m [on CA-9] (D.H.Janzen); 8.1mi NE Cd. Guatemala, 850m (D.H.Janzen); Cd. Guatemala (Champion); Cd. Guatemala, 980m (D.H.Janzen); Escuintla-Cd.Guatemala [=19km S Cd. Guatemala] (D.H.Janzen); *Huehuetenango*: 12.4mi SE Mex.border at Cd. Cuauhtemoc (D.H.Janzen); 12.5mi SE Mex.border at Cd. Cuauhtemoc (D.H.Janzen); 37.6mi NW Huehuetenango, 900m (D.H.Janzen); 7.1mi SE Mex.border at Cd. Cuauhtemoc (D.H.Janzen); 9.3mi SE Mex.border at Cd. Cuauhtemoc (D.H.Janzen); *Izabal*: 1.1mi NE Quiriguá, 120m (D.H.Janzen); 2.1mi SW Morales, 50m (D.H.Janzen); Lago Izabal, 1km NE El Estor [=1.5km NE El Estor] (D.H.Janzen); Los Amates (Kellerman); Murciellago (D.H.Janzen); Quiriguá (W.M.Wheeler); *Jutiapa*: 6.7mi N San Cristóbal, 280m (D.H.Janzen); 6.9mi N San Cristóbal, 290m (D.H.Janzen); 9mi SW Jutiapa, 950m (D.H.Janzen); *Petén*: 70km NW Tikal (W.R.Tschinkel); Tikal (T.H.Hubbell; N.L.H.Krauss; W.R.Tschinkel); *Quezaltenango*: 7.2mi NE San Felipe, on Retalhuleu-Quezaltenango Rd. (D.H.Janzen); 7.5mi NE San Felipe, on Retalhuleu-Quezaltenango Rd. (D.H.Janzen); *Retalhuleu*: 1.3mi E Champerico (D.H.Janzen); 2mi NE Champerico (D.H.Janzen); 5mi W Retalhuleu (D.H.Janzen); 5mi W Retalhuleu, Hwy. CA-2, at Rio Nil (D.H.Janzen); Champerico (Baker; F.Knab); Puenta Samala, 3.8mi NE San Felipe (D.H.Janzen); Retalhuleu (Stoll); *SantaRosa*: 25mi SE Escuintla, 200m [on CA-2] (D.H.Janzen); *Solola*: "Pacific slope", 3000ft. (c.u.); *Suchitepéquez*: Patulul (W.M.Wheeler); *Zacapa*: 10mi SW El Lobo, 170m [on CA-9] [=9.2mi NE Piedras de Afilar] (D.H.Janzen); 2.6mi SW El Lobo, 100m [on CA-9] [=16.6mi NE Piedras de Afilar] (D.H.Janzen); 8.1mi SW Los Amates, 160m [on CA-9] [=8.0mi NE El Lobo] (D.H.Janzen); 8.2mi NE Piedras de Afilar, 160m [on CA-9] [=12.2mi NE Rio Hondo] (D.H.Janzen); *dept.unknown*: "Guatemala" (Beccari); Concepcion, 1400ft. (C.N.Ainslie); Mimosa, "Cocepcion" [Concepcion] (C.N.Ainslie).

HONDURAS *Atlántida*: Tela (quarantine New Orleans, U.S.A.) (T.J.Baker); *Colón*: Puerto Castilla (J.Bequaert); *Comayagua*: "Comayaena" (S. Passoa); 11.7mi S San Antonio, 830m (D.H.Janzen); 15.7mi N Siguatepeque, 530m (D.H.Janzen); Minas de Oro (J.B.Edwards); *Copán*: 10.4mi S Sta. Rosa de Copán, 980m (D.H.Janzen); 11.9mi S Sta. Rosa de Copán, 1130m (D.H.Janzen); 17.3mi N Sta. Rosa de Copán, 780m (D.H.Janzen); *Cortés*: 24.6mi SW San Pedro Sula, 240m (D.H.Janzen); 6.8mi S San Pedro Sula, 480m [=20.9mi SW Quimistán] (D.H.Janzen); San Pedro Sula (S.C.Bruner; W.M.Mann); *Ocotepeque*: 4.4mi E [Nueva] Ocotepeque, 1310m (D.H.Janzen); *Santa Bárbara*: 7.3mi E Quimistán (D.H.Janzen); 13.7mi SW Quimistán, 320m (D.H.Janzen); *Yoro*: Coyoles, W of Olanchito (Echternacht); *dept.unknown*: "Honduras" (Bates).

MEXICO *Camp.*: 0.1mi S Tenabo (D.H.Janzen); 0.8mi E Campeche (D.H.Janzen); 10.6mi E Campeche (D.H.Janzen) ; 20mi E Campeche, Hwy.180 (D.H.Janzen); 29mi E & 12mi S Campeche (Ruinas Edzna)(D.H.Janzen); 48mi NE Puerto Real (Isla Aguada), Hwy. 180 (D.H.Janzen); Ruinas Edzna (U.Kansas Mex.Exped.); *Chis.*: 10 mi NE [NW?] Tapachula [on Hwy. 200?] (D.H.Janzen);

10.8mi S Pichucalco (D.H.Janzen); 11km SE Pichucalco, 400m (P.S.Ward); 11mi E Arriaga (D.H.Janzen); 1km WSW Palenque, 80m (P.S.Ward); 26km E Cintalpa (W.MacKay); 2mi S Pichucalco (D.H.Janzen); 32mi W [San] Cristóbal de las Casas, Hwy.190 (D.H.Janzen); 3km ENE Chiapa de Corzo, 500m (P.S.Ward); 3mi N Soyalo [on Hwy.195] (D.H.Janzen); 4mi NW Ocosingo (R.C.Bechtel & E.I.Schlinger; R.F.Smith); 4mi S Simojovel(R.C.Bechtel & E.I.Schlinger; E.I.Schlinger); 56.9mi NE [NW?] Tapachula [on Hwy.200?] (D.H.Janzen); 5mi SE Tapilula [on Hwy.195] (D.H.Janzen); 6.9mi N Tapilula (D.H.Janzen); 7mi SW Teapa [on Hwy.195] (D.H.Janzen); 8.5mi S La Trinitaria, 1160m (U.Kansas Mex.Exped.); 8.5mi S La Trinitaria, Hwy.190 (D.H.Janzen); 8mi W Las Cruces, Hwy.190, 660m (D.H.Janzen); 96km S Tuxtla Gutiérrez, 732m (D.E. & J.A.Breedlove); Acapetahua Las Bugamvillas (F.Diaz); Arriaga (D.H.Janzen); Cd. Cuauhtemoc (D.H.Janzen); Chicoasen (G.N.Collins); El Real (Goodnight & Stannard); Ixtacomitan (R.Andrews); Llano Grande (G.N.Collins); Palenque (c.u.); Pichucalco (G.N.Collins); Rio Huixtla, Huixtla (J.G.Pereira); Ruinas Palenque (E.M.Fisher); San Sebastian [near Tuxtla Gutierrez; see Safford 1922:393] (G.N.Collins); Santo Domingo, 15mi SE [SW?] Simojovel (R.F.Smith); Tapilula (D.H.Janzen); Tonalá, 40m (D.H.Janzen); Tonola [prob.=Tonalá] (A.Petrunkewitch); Tuxtla Gutierrez (N.L.H.Krauss; W.P.Stoutamize); Yaxoquintela (J.E.Rawlins); Yerba Santa (G.N.Collins); *Gro.*:10mi NE Acapulco (D.H.Janzen); 15.8mi S Chilpancingo (D.H.Janzen); 18mi S Chilpancingo (F.D.Parker;F.D.Parker & L.A.Stange); 25.4mi S Chilpancingo (D.H.Janzen); 55mi N Acapulco, Hwy.95 (Cornell Univ.Mex.Field Party; c.u.); 57.8mi S Chilpancingo (D.H.Janzen); 59.9mi N Acapulco (D.H.Janzen); 62.4mi N Acapulco (D.H.Janzen); 74km N Acapulco (W.MacKay); Acapulco (L.J.Lipovsky); Revolcadero (N.L.H.Krauss); San Geronimo de Juarez (W.von Hagen); *Hgo.*: 2km W Orizatlán, 245m (W.MacKay); *Mor.*: 15mi S Cuernavaca (E.S.Ross; W.S.Ross); Cuernavaca (W.M.Wheeler); *Oax.*: 11.4-17.0mi W Tehuantepec (D.H.Janzen); 1mi W Temascal (D.H.Janzen); 22.2mi N Puerto Escondido, 700m (D.H.Janzen); 25mi W Tehuantepec (D.H.Janzen); 3.2mi NE Tehuantepec (D.H.Janzen); 42km N San Pedro Pochutla, 850m (W.MacKay); 44mi W Tehuantepec (E.E.Gilbert & C.D.MacNeil); 5mi E Temascal (D.H.Janzen); 9.6km E Santiago Astata, 10m (W.MacKay); Bahias de Huatulco (W.MacKay); Pinotepa Nacional (S.W.T.Batra); Salina Cruz (D.H.Janzen); Tehuantepec (F.Knab; W.P.Stoutamize); Temascal (H.V.Daly; D.H.Janzen); Temascal, 25m (D.H.Janzen); Tuxtepec (J.Camela G.; W.M.Mann); Valle Nacional (G.V.Halffter); *Q.Roo:* 12.2mi S Peto, Q.Roo-Yucatan border (D.H.Janzen); 16.9mi W Cd. Chetumal, rd. to Peto (D.H.Janzen); 22.5mi S Felipe Carillo Puerto (D.H.Janzen); 6.4mi E Polyuc (D.H.Janzen); 7mi W Felipe Carillo Puerto (D.H.Janzen); 8.1mi S Felipe Carillo Puerto (D.H.Janzen); 8mi S Felipe Carillo Puerto (D.H.Janzen); Sian Ka'an (A.Dejean); Sian Ka'an Reserve, nr. Felipe Carillo Puerto (A.Dejean); Vallarta (A.Dejean); *S.L.P.*: 27mi N Tamazunchale (D.H.Janzen); 40-50mi NW Cd. del Maiz (W.S.Ross); 4mi N Valles, 300ft. (W.S.Creighton); Cd. Valles (D.H.Janzen); El Bonito, 7mi S Cd. Valles, 300ft. (P.H. & M.Arnaud); El Salto (A.Mintzer; c.u.); Huichihuayan (L.J.Lipovsky); Rio Amahac, Tamazunchale, 300ft. (W. S. Creighton); Tamazunchale (D. H. Janzen; W. S. Ross); locality not specified, prob. Tanquian [see Safford 1923:390] (Safford); *Tab.*: 0.6mi S Paraíso on rd. to Cárdenas (D.H.Janzen); 0.9mi S Chontalpa (D.H.Janzen); 12.8mi S Chontalpa (D.H.Janzen); 2.1mi E Frontera (D.H.Janzen); 3 mi W Cárdenas (D.H.Janzen); 30.2mi W Cd. El Carmen (D.H.Janzen); 37.8mi E Coatzacoalcos, Hwy.180 (D.H.Janzen); 6.6mi S Chontalpa (D.H.Janzen); Chontalpa, 26mi S Cárdenas (D.H.Janzen); Cárdenas (D.H.Janzen); Teapa (J.C. & D.Pallister; H.H.Smith; W.P.Stoutamize); *Tamps.*: 22.7mi S Cd. Victoria (D.H.Janzen); 41mi S Cd. Victoria (C.W.Obrien); 50mi N Valles (G.E.Bohart); 5mi N Cd. Mante (A.Mintzer); 7km WSW El Encino, 140m (P.S.Ward); Antiguo Morelos (c.u.); Cd. Madero (F.Infante M.); Ciudad Mante (N.E. & M.A.Evans; N.L.H.Krauss); El Limon (H.E.Evans); Forlon (L.J.Lipovsky); Gonzales (c.u.); Llera (W.E.LaBerge); Mesa de Llera (A.Mintzer); N of Antiguo Morelos (A.Mintzer); Rio Guayalejo at

Hwy.85 (A.S.Menke & L.A.Stange); S of Cd. Mante (A.Mintzer); Tampico (Brakhoven; D.L.Crawford; H.Jourdan; N.L.H.Krauss; Locke; E.Palmer; E.A.Schwarz; W.P.Stephen; c.u.); Tampico, dunes at Cd. Madero (D.H.Janzen); Xicotencatl (H.C.Millender); *Ver.:* "N.M.,Vera Cruz" (Townsend); "Vera Cruz" (G.Seurat; H.H.Smith); 10mi W Veracruz (G.E.Bohart); 14km ENE La Tinaja, 50m (P.S.Ward); 15mi W Veracruz (U.Kansas Mex.Exped.); 16km E Cuilahuac [=Cuitláhuac] (W.MacKay); 24.9mi NW Acayucan (D.H.Janzen); 28km N Cardel, Morro de la Mancha (V.Rico-Gray); 30mi S Acayucan (F.D.Parker); 3mi N Sayula (R.C.Bechtel; R.C.Bechtel & E.I.Schlinger); 4mi NE Minatitlan (R.C.Bechtel & E.I.Schlinger); 4mi NW Rinconada Antigua, 1350ft. (U.KansasMex.Exped.); 4mi W Puente Nacional, 900ft. (U.Kansas Mex.Exped.); 6.5km N Tierra Blanca, 50m (W.MacKay); 7mi S Cardel, 600ft. (c.u.); 9km NNW Sontecomapan, 20m (P.S.Ward); Boca del Rio (U.Kansas Mex.Exped.); Buen Pais (R.C.Bechtel & E.I.Schlinger); Camaron (E.Skwarra); Cordoba (F.Knab; R.R.Snelling; c.u.); Cotaxtla Exp. Sta., Cotaxtla (D.H.Janzen); Est. Biol. Los Tuxtlas (H.A.Hespenheide); Est. Biol. "Los Tuxtlas", nr. San Andres Tuxtla (G.Ibarra M.); Fortin (c.u.); Jalapa (Rangel; W.M.Wheeler; c.u.); Jalapilla, mun. Jilotepec (G.Alemán); Los Cocos (A.Petrunkewitch); Los Tuxtlas, 10km NNW Sontecomapan, 200m (P.S.Ward); Mirador (E.Skwarra); Mocambo (D.H.Janzen); Orizaba (c.u.); Palma Sola (Halffter & Reyes); Panuco (F.Parker & D.Miller); Playa Azul, Catemaco (W.P.Stoutamize); Pueblo Nuevo, nr. Tezonapa (Cornell Univ. Mex. Field Party); Remutadero (E.Skwarra); Santa Lucrecia [=Jesus Carranza] (F.Knab; P.Knab); Tamarindo (E.Skwarra); Tamos (F.C.Bishop); Tinajas [presumably La Tinaja, on Hwy.150] (F.D.Parker & L.A.Stange); Tlacocintla (E.Skwarra); Veracruz (G.E.Bohart; N.L.H.Krauss; E.Skwarra; L.A.Stange); *Yuc.:* 14.8mi S Ticul, "Hwy.180" [prob.Hwy.261] (D.H.Janzen); 8mi E Merida (rd. to Pto. Juarez) (D.H.Janzen); Merida (D.H.Janzen; N.L.H.Krauss); Merida (S margin of town) (D.H.Janzen); Tekax, 33mi W Peto (D.H.Janzen); Temax (Gaumer); *state unknown*: "Mex"("Norton").

Pseudomyrmex flavicornis (F. Smith 1877)
(Figs. 16, 25, 63, 69)

Pseudomyrma flavicornis F. Smith 1877:67. Lectotype worker, Nicaragua (BMNH) [Examined].
Pseudomyrma belti Emery 1890:63. Syntype workers, Alajuela, Costa Rica (BMNH, MCSN) [Examined] [Synonymy by Ward 1989:438].
Pseudomyrma belti var. *obnubila* Menozzi 1927a:273. Syntype worker, San José, Costa Rica (H. Schmidt) (NHMB) [Examined] [Synonymy by Ward 1989:438].
Pseudomyrma belti subsp. *fellosa* Wheeler 1942:160. Syntype workers, Nicaragua (W. Fluck); Granada, Nicaragua (C. F. Baker) (AMNH, LACM, MCZC) [Examined] [Synonymy by Ward 1989:439].
Pseudomyrmex flavicornis (F. Smith); Kempf 1972:218.

Worker measurements (n = 29).—HL 1.06-1.42, HW 0.99-1.21, MFC 0.075-0.114, CI 0.83-0.94, REL 0.39-0.45, REL2 0.45-0.51, OOI 1.28-2.71, VI 0.59-0.73, FCI 0.068-0.098, SI 0.40-0.46, SI2 0.82-0.97, NI 0.61-0.68, PLI 0.57-0.67, PWI 0.60-0.72, PPWI 1.36-1.80.

Worker diagnosis.—Similar to *P. ferrugineus* (q.v.) except as follows. Larger, with shorter eyes, on average (Figs. 16, 50). Head densely punctulate, opaque; overlying rugulo-punctate sculpture on propodeum tending to be better developed than in *P. ferrugineus*. Pilosity and pubescence denser on average. Head black, gaster and postpetiole dark brown to black, mesosoma and petiole varying from black to a contrasting lighter brown or reddish-brown; mandibles, scapes, fronto-clypeal complex, and apices of legs brown.

Comments.—Key traits of this species are the laterally rounded median clypeal lobe, large size (worker HW > 0.98; queen HW 1.12-1.19, n=13), broad opaque head (worker CI > 0.82; queen CI 0.73-0.76) and dark color. *P. flavicornis* is one of three species in the *P. ferrugineus* group whose workers and queens have a black or very dark brown body (mesosoma sometimes contrastingly lighter). The other two, *P. mixtecus* and *P. veneficus*, are allopatric to *P. flavicornis* and smaller in size;

other distinguishing features are mentioned in the key and discussed under those species. A tendency towards lighter coloration of the mesosoma in northern populations of *P. flavicornis* sometimes makes it difficult to distinguish this species from sympatric dark-colored *P. ferrugineus*. Even the darkest workers and queens of the latter species are, however, smaller (an average difference in workers, almost absolute in *P. ferrugineus* queens which have HW 0.96-1.12 (n = 37)) with longer eyes (Fig. 50) and shorter scapes for a given relative head breadth (Fig. 51); and they show some reflectance of light on the upper third of the head between the ocelli and compound eye in contrast to the more or less opaque-headed *P. flavicornis*. In addition, *P. ferrugineus* queens have more elongate heads (CI 0.68-0.73) than those of *P. flavicornis*.

Distribution and biology.—This is a monogynous species ranging from Guatemala to Costa Rica (Fig. 69), which inhabits *Acacia collinsii* and, less frequently, *A. cornigera* and *A. hindsii*. It was one of the first acacia-ants to be brought to the attention of naturalists, thanks to an early account of its biology by Thomas Belt (1874) (under the name *Pseudomyrma bicolor*). In the more recent literature *P. flavicornis* has usually been referred to as "*P. belti*", but note that there is not a perfect correspondence in name usage (Table 1).

Material examined (AMNH, ANSP, BMNH, CASC, CUIC, INBC, LACM, MCSN, MCZC, MZSP, NHBM, NHMV, PSWC, SEMC, UCDC, USNM).—

COSTA RICA *Alajuela*: Alajuela (A.Alfaro); Atenas (A.Alfaro); Ojo de Agua (A.Alfaro); Tacares (A.Alfaro); Turrúcares (A.Alfaro); *Guanacaste*: 1.4mi N La Cruz, 200m (D.H.Janzen); 10.7mi NW Liberia (D.H.Janzen); 1km S Cañas (D.H.Janzen); 2mi E Playa Coco (D.H.Janzen); 2mi SE Cañas [=2mi S Cañas] (D.H.Janzen); 4km S Cañas(D.H.Janzen); 5km S Liberia (D.H.Janzen); 6mi E, 6mi S Cañas (D.H.Janzen); 6mi W Liberia (D.H.Janzen); 7km N Cañas (D.H.Janzen); Bahia del Coco (A.Alfaro); Ballena, Rio Tempisque (A.Alfaro); El Coco (R.J.Hampton); Finca Taboga, 6mi S, 6mi W Cañas (D.H.Janzen); Hda. La Pacifica, 5km NW Cañas (E.R.Heithaus); Hda. La Pacifica, nr. Cañas, 50m (P.S.Ward); La Cueva, 12km N Liberia (D.H.Janzen); Liberia (A.Alfaro; M.G.Naumann); Palo Verde (D.E.Gill; H.A.Hespenheide; D.H.Janzen; D.Whitacre); Palo Verde, 50m (D.M.Olson); Palo Verde, <100m (J.Longino); Rio Corobici, nr.Cañas (R.M.Bohart); Santa Cruz (P.P.Calvert); Santa Rosa Natl. Pk. (F.Joyce); Santa Rosa Natl. Pk., 300m (J.Longino; P.S.Ward); Santa Rosa Natl. Pk., 5m (P.S.Ward); Santa Rosa Natl. Pk., <5m (P.S.Ward); Tempisque (A.Alfaro); *Heredia:* Lagunilla (C.H.Ballow); *Puntarenas*: 1km NE Tárcoles, 20m (P.S.Ward); 4km E Tivives, 5m (L.S.Farley); Barranca,near Puntarenas (A.Alfaro); *San José*: Bebedero (A.Alfaro); Rio Oro (D.H.Janzen); San José (Nauck;H.Schmidt); Villa Colon (A.Alfaro); Villa Colon, 600-700m (J.Longino); *prov.unknown*: "Costa Rica"(c.u.); Ciruela(J.F.Tristan).

EL SALVADOR *Ahuachapan*: 7.8mi S Hachadura, 50m (D.H.Janzen); *Chalatenango*: 5.4mi N La Palma, 850m (D.H.Janzen); *La Libertad*: 2.6mi S Santa Tecla, 1010m [=11.8mi N La Libertad] (D.H.Janzen); 2mi E La Libertad (D.H.Janzen); La Libertad (E.S.Ross); Quezaltepeque (D.Cavagnaro & M.E.Irwin); *La Union*: 7.1mi W Amatillo, 190m (D.H.Janzen); *Lapaz*: 11.6mi W Zacatecoluca, 0m (D.H.Janzen); *San Miguel*: 0.4mi W San Miguel (D.H.Janzen); betw. La Unión & San Miguel, 110m (D.H.Janzen); *San Salvador*: San Salvador (O.L.Cartwright; N.L.H.Krauss); *Sonsonate*: 34.4mi W La Libertad (D.H.Janzen); 6.6mi S Sonsonate [=43.6mi W La Libertad] (D.H.Janzen); *Usulutan*: E slope Cerro Verde, 3800ft. (D.Q.Cavagnaro & M.E.Irwin); *dept.unknown*: Los Chorros (D.Q.Cavagnaro & M.E.Irwin); Los Chorros Natl. Pk. (M.E.Irwin).

GUATEMALA *Escuintla*: 12.6mi NE Escuintla, rd. to Cd. Guatemala, 1120m (D.H.Janzen); 15km E Escuintla [on CA-9] (D.H.Janzen); 43km S Cd. Guatemala [=15km E Escuintla] (D.H.Janzen); *Guatemala*: 19km S Cd. Guatemala [on CA-9] (D.H.Janzen); 7.9mi S Cd. Guatemala [on CA-9] (D.H.Janzen); Amatitlan (Bates); Escuintla-Cd.Guatemala [=19km S Cd. Guatemala] (D.H.Janzen); Lake Amatitlan (c.u.); *Jutiapa*: 47mi S Escuintla, 250m [=47mi SE Escuintla] (D.H.Janzen); 7.7mi E Jutiapa, Hwy.1, 900m (D.H.Janzen); 9.7mi E Jutiapa, 750m (hwy.to San Cristóbal) [=9.3mi NE Jutiapa] (D.H.Janzen); *Santa Rosa*: 12.2mi W Taxisco (D.H.Janzen); 3.8mi S

Guazacapán (D.H.Janzen); Guazacapán (R.H.Painter); *Zacapa*: 10mi SW El Lobo, 170m [on CA-9] [=9.2mi NE Piedras de Afilar] (D.H.Janzen); 2.6mi SW Rio Hondo, 200m [on CA-9] (D.H.Janzen); 22.3mi SW Quiriguá [on CA-9] (D.H.Janzen); 22.3mi SW Quiriguá [on CA-9] (D.H.Janzen); 8.2mi NE Piedras de Afilar, 160m [on CA-9] [=12.2mi NE Rio Hondo] (D.H.Janzen); km142 on Guatemala-Pto. Barrios Rd. nr. Los Amates (D.H.Janzen).

HONDURAS *Choluteca*: 19mi NE Choluteca (D.H.Janzen); 3.6mi W Choluteca, 200m (D.H.Janzen); 4.5mi W Choluteca (D.H.Janzen); *Colón*: Puerto Castilla (J.Bequaert); Valle: 4.6mi E Jicaro Galan, 190m (D.H.Janzen); La Union, 28.4mi E El Amatillo (frontera) (D.H.Janzen).

NICARAGUA *Chontales:* no specific locality (T.Belt); *Estelí*: 2mi N Condega, 500m (D.H.Janzen); *Granada:* 2.2mi W Nandaime (D.H.Janzen); 2mi N Nandaime, 160m (D.H.Janzen); Granada (C.F.Baker); *León*: 28.1mi SE León (D.H.Janzen); *Managua:* 8.1mi E San Benito (D.H.Janzen); 8.8mi N Tipitapa (D.H.Janzen); 9.9mi NE Masachapa, Hwy.8, 180m (D.H.Janzen); 9mi N Tipitapa, 50m (D.H.Janzen); *Matagalpa*: 15.8mi NW Sebaco [=15.8mi W Sebaco] (D.H.Janzen); 2.6mi N Dario (D.H.Janzen); 4.1mi S Matagalpa, 650m (D.H.Janzen); 4.5mi SE Dario (D.H.Janzen); *Rivas:* 1mi N San Juan del Sur (D.H.Janzen); 1mi NW Peñas Blancas [=1mi N Peñas Blancas] (D.H.Janzen); 20.5mi NW Peñas Blancas (D.H.Janzen); 4.4mi SE La Virgen [=4.4mi S La Virgen] (D.H.Janzen); Isla Ometepe (F.Joyce); La Virgen [on Hwy.1] (D.H.Janzen); San Juan del Sur, 10m (D.H.Janzen); *Zelaya*: Wounta Hanlover (Fluck); *dept.unknown*: "Nicaragua" (W.Fluck; c.u.).

Pseudomyrmex janzeni Ward, **sp. nov.**
(Figs. 19, 29, 64, 70)

Holotype worker.—MEXICO, Nayarit: 60 mi. SE Acaponeta, Hwy. 15, 15.ix.1963, D. H. Janzen (LACM). HW 1.00, HL 1.08, EL 0.51, PL 0.55, PH 0.36.

Paratypes.—Same data as holotype: series of 166 workers, 62 queens and 45 males (AMNH, BMNH, CASC, EBCC, GBFM, INBC, LACM, MCZC, MZSP, PSWC, UCDC, USNM). Additional non-type material is listed below.

Worker measurements (n = 12).—HL 1.00-1.18, HW 0.93-1.03, MFC 0.063-0.096, CI 0.88-0.94, REL 0.45-0.47, REL2 0.49-0.52, OOI 1.45-2.29, VI 0.58-0.68, FCI 0.068-0.098, SI 0.42-0.45, SI2 0.84-0.91, NI 0.62-0.69, PLI 0.59-0.71, PWI 0.63-0.73, PPWI 1.37-1.73.

Worker diagnosis.—Very similar to *P. ferrugineus* (q.v.) except as follows. Size smaller, on average. In lateral view mesonotum less steeply inclined; basal and declivitous faces of propodeum forming a less obtuse angle (compare Figs. 27 and 29). Petiole shorter and higher, on average (Fig. 48). Weak rugulo-punctate sculpture on propodeum even less evident than in *P. ferrugineus*. Pubescence denser, becoming decumbent to suberect on parts of body, most notably the gula (Fig. 19). Head and mesosoma rather light orange-brown, gaster the same or a slightly darker brown.

Comments.—Within the *P. ferrugineus* group *P. janzeni* can be characterized by its relatively small size (worker and queen HW < 1.04), broad head (worker CI > 0.86), laterally rounded median clypeal lobe, and uniform orange-brown color. *P. janzeni* is evidently closely related to *P. ferrugineus* (as surmised by Janzen 1973); all of the metric measurements and indices of these two species overlap, although there is a tendency for *P. janzeni* workers to have shorter, higher petioles (Fig. 48). Workers and queens of *P. janzeni* are perhaps best distinguished from those of *P. ferrugineus* by the combination of lighter orange-brown color, suberect gular pubescence (best seen in a backlit lateral view of the head), and the flatter profile of the worker mesosoma (see description above and Fig. 29). While some individuals of the highly variable *P. ferrugineus* approach these conditions there is no indication of a convergence towards this morphology in western Mexico (Guerrero) where populations of *P. ferrugineus* come closest to those of *P. janzeni*.

Distribution and biology.—First recognized by Janzen (1967a, 1969, 1973) as a distinct but undescribed species, *P. janzeni* is confined to a limited area in western Mexico (Fig. 70) where it is sympatric with the much darker colored and commoner *P. veneficus*. Colonies occupy *Acacia hindsii* and are polygynous; additional details of the life history can be found in Janzen's (1973) paper on polygynous acacia-ants.

Material examined. Type material listed above, plus the following (LACM, MCZC, PSWC, UCRC, USNM).—

MEXICO *Jal.:* Puerto Vallarta (J.A.Comstock); *Nay.:* 14.5mi E San Blas (D.H.Janzen); 2mi E San Blas (R.van den Bosch); 31mi N Tepic (D.H.Janzen); 36mi N Tepic (D.H.Janzen); 4mi E San Blas (M.Irwin; M.Irwin & E.I.Schlinger; E.I.Schlinger); 5mi E San Blas (F.Parker & D.Miller); Compostela (c.u.); Rio Palillo, 14mi E San Blas (D.H.Janzen); Tepic (H.A.Scullen); *Sin.*: 20mi E Villa Union (E.I.Schlinger).

Pseudomyrmex mixtecus Ward, **sp. nov.**
(Figs. 15, 26, 55, 61, 69)

Holotype worker.—MEXICO, Guerrero: 25.4 mi. S. Chilpancingo, 10.viii.1966, D. H. Janzen #M008810966 (LACM). HW 0.97, HL 1.07, EL 0.48, PL 0.55, PH 0.35.

Paratypes.—Same data as holotype, and three other accession numbers (M007810966, M009810966, M010810966) with same locality, date, and collector: series of 43 workers, 34 queens and 17 males (AMNH, BMNH, CASC, EBCC, GBFM, INBC, LACM, MCZC, MZSP, PSWC, UCDC, USNM). Additional non-type material is listed below.

Worker measurements (n = 13).—HL 0.94-1.19, HW 0.89-1.03, MFC 0.054-0.073, CI 0.86-0.95, REL 0.42-0.47, REL2 0.46-0.52 OOI 1.22-2.28, VI 0.61-0.73, FCI 0.056-0.073, SI 0.43-0.45, SI2 0.86-0.97, NI 0.60-0.65, PLI 0.60-0.68, PWI 0.60-0.68, PPWI 1.40-1.73.

Worker diagnosis.—Similar to *P. ferrugineus* (q.v.) except as follows. Size smaller (HW < 1.04, LHT < 0.90), head broad (CI > 0.85); frontal carinae separated by about basal scape width or less (FCI2 0.45-0.54). Basal and declivitous faces of propodeum forming a less obtuse angle in profile than typical for *P. ferrugineus* (compare Figs. 26 and 27). Head densely punctulate, opaque. Standing pilosity rather common, usually some setae exceeding 0.12 mm and 0.20 mm in length on mesosoma dorsum and petiole, respectively. Pubescence dense but appressed. Very dark brown to black, appendages lighter.

Comments.—*P. mixtecus* is distinguished from all other species, except *P. veneficus* and *P. flavicornis*, by its laterally rounded median clypeal lobe, broad head, and black (or very dark brown) body. It differs from *P. veneficus* by the fully opaque head, absence of conspicuous suberect pubescence on the petiole, and larger size. *P. mixtecus* is evidently closely related to *P. flavicornis* but averages smaller in size (compare worker HW and LHT values), a difference which is absolute in queens (queen HW 0.96-1.01 (n=8), whereas queen HW > 1.11 in *P. flavicornis*). In addition the petiole is relatively longer and higher, for a given head width, in both workers and queens of *P. mixtecus* (Figs. 44-47).

Distribution and biology.—*P. mixtecus* is known only from the Mexican states of Guerrero and Oaxaca (Fig. 69). Colonies have been collected from *Acacia hindsii* and *A. collinsii*, but little more has been recorded about their biology. Janzen's field notes indicate that this species is monogynous.

Material examined. Type material listed above, plus the following (CUIC, LACM, MCZC, MZSP, PSWC, SEMC, USNM, WPMC).—

MEXICO *Gro.*: 10mi NE Acapulco (D.H.Janzen); 29.6mi N Acapulco, 1400ft. (D.H.Janzen); 30mi N Acapulco, Hwy.95 (Cornell Univ. Mex. Field Party); 57.8mi S Chilpancingo, Hwy.95 (D.H.Janzen); 74km N Acapulco (W.MacKay); Acapulco (Baker; F.Knab; N.L.H.Krauss; L.J.Lipovsky); Puerto Marques (N.L.H.Krauss); San Geronimo de Juarez (W.von Hagen); *Oax.:* 11.4-17.0mi W Tehuantepec (D.H.Janzen); 13.8mi W Tehuantepec, 1500ft. (D.H.Janzen); 19km N San Pedro Pochutla, 200m (W.MacKay); 6.0mi E Niltepec, Hwy.190, 100m (D.H.Janzen).

Pseudomyrmex nigrocinctus (Emery 1890)
(Figs. 13, 22, 56, 72)

Pseudomyrma nigrocincta Emery 1890:64. Syntype workers, queens, males, Alajuela, Costa Rica (A. Alfaro) (BMNH, MCSN, MCZC, MHNG) [Examined]. One syntype worker from MCSN here designated LECTOTYPE.

Pseudomyrma alfari Forel 1906:228. Two syntype workers, Tivives, embouchure de Jesus-Maria, Costa Rica (A. Alfaro) (MHNG) [Examined]. One syntype here designated LECTOTYPE. **Syn. nov.**

Pseudomyrma nigrocinta var. *bicincta* Santschi 1922:347. Syntype workers, Costa Rica (MHNG, NHMB) [Examined]. One syntype from NHMB here designated LECTOTYPE. **Syn. nov.**

Pseudomyrma peltata Menozzi 1927a:273. Three syntype workers, SanJosé, Costa Rica (H. Schmidt) (NHMB) [Examined]. **Syn. nov.**

Pseudomyrmex nigrocincta [sic] (Emery); Janzen 1966:252.

Pseudomyrmex nigrocinctus (Emery); Kempf, 1972:221.

Worker measurements (n = 21).—HL 0.89-1.08, HW 0.74-0.85, MFC 0.035-0.051, CI 0.75-0.84, REL 0.40-0.45, REL2 0.51-0.56, OOI 1.39-2.76, VI 0.62-0.78, FCI 0.044-0.065, SI 0.44-0.48, SI2 0.81-0.89, NI 0.58-0.64, PLI 0.59-0.68, PWI 0.49-0.61, PPWI 1.10-1.30.

Worker diagnosis.—Small species with elongate head and short eyes (REL 0.45, REL2 0.56, EL/LHT 0.61). Palp formula 5,3. Median clypeal lobe rather narrow, its surface and anterior margin convex. Frontal carinae separated by about basal scape width (FCI 0.055). Metanotal groove well marked; basal and declivitous faces of propodeum subequal (Fig. 22). Petiole short (PLI > 0.57), its anterior peduncle broad in dorsal view (PWI3 0.50-0.61) and not well differentiated from the node (Fig. 22). Petiole lacking expanded posterolateral corners. Postpetiole less broad than in most other species in the *P. ferrugineus* group (see PPWI values). Head densely punctulate and subopaque, becoming sublucid posteriorly where the punctulae are separated by shiny interspaces. Mesosoma punctulate to (laterally) coriarious-imbricate, sublucid, becoming subopaque on the propodeum. Standing pilosity moderately common (as in Fig. 22); pubescence dense and closely appressed. Orange-brown, often with anterolateral fuscous patches on abdominal tergite IV (these form a distinct transverse black band in queens).

Comments.—Workers and queens of *P. nigrocinctus* are easily distinguished from all other acacia ants, except *P. particeps* (see below), by their small size (HW < 0.86 in both castes), elongate head in the worker (worker CI < 0.85), and narrow petiole and postpetiole (worker PWI3 0.50, worker PPWI 1.30, queen PWI2 0.57-0.63). The orange color and short eyes are also characteristic.

Distribution and biology.—*P. nigrocinctus* is found from Guatemala to Costa Rica, with most records coming from the southern end of its range (Fig. 72). Colonies are monogynous, and have been collected from *Acacia collinsii*, *A. cornigera* and *A. hindsii*. Records from *Acacia gentlei* and A. *globulifera* (Beulig & Janzen 1969:59) need to be confirmed because of possible confusion with *P. peperi*. Janzen's (1967b) observations on "*P. nigrocincta*" in Mexico refer to *P. peperi*. On the other hand descriptions of the biology and behavior of *P. nigrocinctus* in Costa Rica (Janzen 1973, 1974, 1975, 1983; Beulig & Janzen 1969) are reliably attributed to *P. nigrocinctus*.

Material examined (AMNH, ANSP, INBC, LACM, MCSN, MCZC, MHNG, MZSP, NHMB, PSWC, USNM, WPMC).—

COSTA RICA *Alajuela*: Alajuela (A.Alfaro); Atenas (A.Alfaro); Cascajal (A.Alfaro); Escobal (A.Alfaro); Ojo de Agua (A.Alfaro); Turrúcares (P.P.Calvert); *Guanacaste*: 1.4mi N La Cruz (D.H.Janzen); 10.7mi NW Liberia (D.H.Janzen); 10mi NW Liberia, 70m (D.H.Janzen); 10mi NW Liberia, 70m [=10.7mi NW Liberia] (D.H.Janzen); 2mi S Cañas (D.H.Janzen); 4km N Cañas (D.H.Janzen); 5km S Liberia (D.H.Janzen); 7km N Cañas (D.H.Janzen); El Coco (R.J.Hampton); Finca Taboga, 6mi S, 6mi W Cañas (D.H.Janzen); Garita (A.Alfaro); Hda. La Pacifica, nr. Cañas, 50m (P.S.Ward); La Cueva, 12km N Liberia (D.H.Janzen); Palo Verde (D.E.Gill; D.H.Janzen); Palo Verde, 50m (D.M.Olson); Santa Cruz (P.P.Calvert); Santa Rosa Natl. Pk., 290m (P.S.Ward); Santa Rosa Natl. Pk., 300m (J.Longino; P.S.Ward); Santa Rosa Natl. Pk., 5m (P.S.Ward); Santa Rosa Natl. Pk., <5m (P.S.Ward); Tempisque (A.Alfaro); *Puntarenas*: 2km E Tivives, <5m (L.S.Farley); Tivives (A.Alfaro); *San José*: 3.5km NE Santiago de Pur (D.H.Janzen); San José

(H.Schmidt; c.u.); *prov.unknown*: "Costa Rica" (c.u.).

GUATEMALA *Zacapa*: 2.0mi NE Rio Hondo, 190m [on CA-9] (D.H.Janzen); 22.3mi SW Quiriguá [on CA-9] (D.H.Janzen).

HONDURAS *Choluteca*: 7.4mi NE Choluteca, 150m (D.H.Janzen).

NICARAGUA *Boaco:* 11.7mi E San Benito (D.H.Janzen); *Estelí:* 13.1mi N San Isidro (D.H.Janzen); 2.5mi N Condega, 620m (D.H.Janzen); 6.8mi N San Isidro, 780m (D.H.Janzen); 7.5mi NW San Isidro, 550m (D.H.Janzen); *León*: Izapa (J.M.Maes); *Madriz:* 3mi W Somoto, 650m (D.H.Janzen); *Matagalpa:* 15.8mi NW Sebaco (D.H.Janzen); 2.6mi N Dario (D.H.Janzen); 4.5mi SE Dario (D.H.Janzen); 4mi S Dario, 350m (D.H.Janzen); *Rivas:* 1km W Peñas Blancas (D.H.Janzen); C.R. border, 1mi N Peñas Blancas, <5m [=1mi NW Peñas Blancas] (D.H.Janzen); Isla Ometepe (F.Joyce).

Pseudomyrmex particeps Ward, sp. nov.
(Figs. 14, 23, 54, 57, 72)

Holotype worker.—COSTA RICA, *Puntarenas*: Rincon, Peninsula Osa, 3.iii.1965, D.H. Janzen #III (LACM). HW 0.83, HL 1.10, EL 0.50, PL 0.50, PH 0.31.

Paratypes.—Same data as holotype: series of 82 workers, 14 males, one queen (AMNH, BMNH, CASC, GBFM, INBC, JTLC, LACM, MCZC, MZSP, PSWC, UCDC, USNM). Additional non-type material listed below.

Worker measurements (n = 12).—HL 0.93-1.10, HW 0.77-0.83, MFC 0.037-0.050, CI 0.75-0.84, REL 0.44-0.48, REL2 0.55-0.60, OOI 1.47-1.96, VI 0.65-0.75, FCI 0.048-0.062, SI 0.45-0.49, SI2 0.78-0.83, NI 0.53-0.62, PLI 0.58-0.66, PWI 0.55-0.60, PPWI 1.03-1.26.

Worker diagnosis.—Very similar to *P. nigrocinctus* (q.v.) except as follows. Eyes longer (REL2 0.55-0.60, EL/LHT 0.59-0.64) (Figs. 14, 42, 43). Front of head more strongly shining. Medium to dark brown; gaster uniformly dark brown or black; mandibles, fronto-clypeal complex, and appendages lighter brown.

Comments.—*P. particeps* is obviously a very close relative of the allopatric *P. nigrocinctus*, but there are consistent differences between the two in eye size and color which exceed the limits of variation seen throughout the much wider range of *P. nigrocinctus*. Workers in the type series of *P. particeps* also have more elongate heads than those of *P. nigrocinctus* but this distinction is not seen in other samples. Differences between queens of the two species are more striking with the two known queens of *P. particeps* having more elongate heads (CI 0.61, compared with 0.67-0.72 in a sample of 13 *P. nigrocinctus* queens) and longer metatibiae relative to head width (LHT/HW 1.12 versus 0.97-1.07 in *P. nigrocinctus*). Additional alates of *P. particeps* are needed to confirm these differences and the apparent distinctions in male genitalia (see male key).

Distribution and biology.—*P. particeps* is a rare species known only from the Osa Peninsula and one adjacent locality, in Costa Rica (Fig. 72). It appears to be associated exclusively with *Acacia allenii,* a forest species (see Janzen, 1974 for more information about the host plant). In contrast, *P. nigrocinctus* is found farther north in more open habitats where it typically inhabits *Acacia collinsii.* The differences in worker morphology between *P. particeps* and *P. nigrocinctus* (darker color and more elongate head and/or eyes in the former) parallel those observed between populations of *P. spinicola* from the same areas (see below under *P. spinicola*), suggesting similar selection pressures associated with more forested habitats and partial (*P. spinicola*) or exclusive (*P. particeps*) occupancy of a different *Acacia* species.

Material examined. Type material listed above, plus the following (JTLC, LACM, PSWC).—

COSTA RICA *Puntarenas*: 4mi S Rincón (D.H.Janzen); Bahia Drake, Osa Penin. (F.Joyce); Corcovado Natl. Pk., Sirena, 50m (J.T.Longino); Rincón (A.R.Moldenke); *San José*: 16.7mi SW San Isidro on Hwy.22, 160m (D.H.Janzen).

Pseudomyrmex peperi (Forel 1913)
(Figs. 12, 24, 58, 71)

Pseudomyrma peperi Forel 1913:213. Syntype workers, Patulul, Guatemala (Peper) (MHNG) [Examined]. One syntype here designated LECOTYPE.

Pseudomyrma spinicola race *convarians* Forel 1913:214. Syntype worker, Patulul, Guatemala (Peper) (MHNG) [Examined] [Synonymy by Ward 1989:452].

Pseudomyrma sabanica [sic] var. *saffordi* Enzmann 1945:89. Syntype workers, Yerba Santa, Chiapas, Mexico (G. N. Collins) (MCZC) [Examined] One syntype here designated LECTOTYPE. [Synonymy by Ward 1989:452].

Pseudomyrmex peperi (Forel); Kempf 1972:222.

Worker measurements (n = 53).—HL 0.86-1.13, HW 0.76-0.90, MFC 0.034-0.064, CI 0.76-0.89, REL 0.45-0.50, REL2 0.54-0.62, OOI 1.15-2.06, VI 0.59-0.79, FCI 0.042-0.071, SI 0.44-0.49, SI2 0.76-0.88, NI 0.62-0.71, PLI 0.54-0.65, PWI 0.63-0.75, PPWI 1.41-1.83.

Worker diagnosis.—Small species (HW < 0.92) with moderately elongate head (Fig. 12); anterior margin of median clypeal lobe straight or slightly produced medially, laterally rounded or subangulate (never sharply angulate as in *P. spinicola* and *P. satanicus*). Palp formula 4,3, rarely 5p4,3. Frontal carinae separated by about basal scape width. Mesosomal and petiolar profile typically as in Fig. 24, but in some workers basal and declivitous faces of propodeum less well differentiated and/or anteroventral tooth of petiole more prominent. Petiole and postpetiole broad, the former subtriangular in dorsal view with well developed posterolateral angles (Fig. 24). Dorsum of head obscurely punctulate-coriarious, matte. Remainder of body with finely punctulate to punctulate-coriarious sculpture, opaque to sublucid; propodeum lacking overlying rugulo-punctate sculpture seen in *P. ferrugineus*. Standing pilosity not especially abundant, sometimes lacking (worn?) on mesonotum. Appressed pubescence abundant but very fine. Light to medium brown, rarely dark brown, the gaster sometimes darker than the rest of body; appendages lighter.

Comments.—*P. peperi* is recognized by the features mentioned above and in the key. The combination of small elongate head, broad posterolaterally angulate petiole, and matte head surface is found in no other acacia ant workers or queens.

Distribution and biology.—This species has a rather wide distribution, from eastern Mexico to Nicaragua (Fig. 71). It has been collected from *Acacia chiapensis*, *A. collinsii*, *A. cornigera*, *A. gentlei*, *A. globulifera* and *A. hindsii*. *P. peperi* is apparently polygynous over much of its range, and often occurs sympatrically with the commoner *P. ferrugineus*. Some aspects of its biology in Mexico are discussed by Janzen (1967b) under the name "*P. nigrocincta*".

Material examined (AMNH, BMNH, CASC, INHS, LACM, MCZC, MNHG, MZSP, NHMV, PSWC, SEMC, UCDC, USNM).—

BELIZE *Belize*: 16mi SW Belize, rd. to Cayo (D.H.Janzen); 5.5mi NW Belize, rd. to Chetumal (D.H.Janzen); *Cayo*: 20km S Augustine, 300m (G.D.Alpert); San Ignacio (S.E.Schoenig); *Corozal*: 15mi S Sta.Elena (Louisville) (D.H.Janzen).

EL SALVADOR *Ahuachapan*: 7.8mi S Hachadura (D.H.Janzen); *Chalatenango*: 2.5mi N Tejutla, rd. to La Palma, 580m (D.H.Janzen); 4.7mi NW La Palma, 880m (D.H.Janzen); 5.5mi SE La Palma, 1130m (D.H.Janzen); 7.5mi SE Tejutla, 320m (D.H.Janzen); *La Libertad*: 2-4km S Quezaltepeque (W.L.Brown); 2mi E La Libertad (D.H.Janzen); 5mi N Quezaltepeque (M.E.Irwin); 7.4mi N La Libertad (D.H.Janzen); Hda. Capolinas, 5kmNW Quezaltepeque, 450m (M.E.Irwin); Quezaltepeque (M.E.Irwin); Santa Tecla [=Nueva San Salvador] (P.Berry); *La Union*: 7.1mi W Amatillo, 190m (D.H.Janzen); between La Unión & San Miguel, 100m [=22.3mi S Sirama] (D.H.Janzen); between La Unión & Usulatán, 150m [=2.6mi S Sirama] (D.H.Janzen); *Lapaz*: 11.6mi W Zacatecoluca, 0m (D.H.Janzen); *San Miguel*: between La Unión & San Miguel, 110m [=22.3mi E Usulutan] (D.H.Janzen); *Santa Ana*: 5.3mi NW Santa Ana, 660m (on Hwy.1) (D.H.Janzen); *Sonsonate*: 24.2mi SE Hachadura (D.H.Janzen); 4.5mi S Sonsonate (D.H.Janzen); 41.4mi NW La Libertad, 10m (D.H.Janzen).

GUATEMALA *Alta Verapaz*: San Joaquin, nr. San Cristóbal Verapaz, 1080m (D.H.Janzen); *El Progreso*: 24.5mi NE Cd. Guatemala [on CA-9] (D.H.Janzen); *Escuintla*: 1.7mi S Escuintla, 370m [on CA-2] (D.H.Janzen); 43km S Cd. Guatemala [=15km E Escuintla] (D.H.Janzen); Escuintla (W.M.Wheeler); San José (E.S.Ross; E.I.Schlinger & E.S.Ross); *Guatemala*: 19km S Cd. Guatemala [on CA-9] (D.H.Janzen); 20mi SE Cd. Guatemala, 1060m [on CA-1] (D.H.Janzen); 7.9mi S Cd. Guatemala, 1360m [on CA-9] (D.H.Janzen); Escuintla-Cd.Guatemala [=19km S Cd. Guatemala] (D.H.Janzen); *Izabal*: 9.9mi SW Quiriguá (D.H.Janzen); Lago Izabal, 1.5km NE El Estor (D.H.Janzen); Quiriguá (D.H.Janzen; W.M.Wheeler); nr. Mariscos (D.H.Janzen); *Jutiapa*: 11.5mi W Jutiapa, 900m (D.H.Janzen); 12.3mi E Guazacapán (D.H.Janzen); 2.3mi NW Pijiji [=Pijije] (D.H.Janzen); 23mi E Taxisco (G.F. & S.Hevel); 3.4mi N San Cristóbal, rd. to Jutiapa, 400m (D.H.Janzen); 47mi SE Escuintla, 250m [=47mi S Escuintla] (D.H.Janzen); 6.9mi N San Cristóbal, 290m (D.H.Janzen); 8.4mi N San Cristóbal, 280m (D.H.Janzen); 9.7mi E Jutiapa, 750m (hwy.to San Cristóbal) [=9.3mi NE Jutiapa] (D.H.Janzen); *Petén*: 70km NW Tikal (W.R.Tschinkel); Tikal (D.H.Janzen; W.R.Tschinkel); *Retalhuleu*: 2mi NE Champerico (D.H.Janzen); 5mi W Retalhuleu (D.H.Janzen); 5mi W Retalhuleu, Hwy.CA-2, at Rio Nil (D.H.Janzen); *Santa Rosa*: 6mi S Guazacapán (D.H.Janzen); *Suchitepéquez*: Patulul (Peper); *Zacapa*: 10mi SW El Lobo, 170m [on CA-9] [=9.2mi NE Piedras de Afilar] (D.H.Janzen); 2.0mi NE Rio Hondo, 190m [on CA-9] (D.H.Janzen); 2.6mi SW El Lobo, 100m [on CA-9] [=16.6mi NE Piedras de Afilar] (D.H.Janzen); 5.6mi NE Rio Hondo, 250m [on CA-9] (D.H.Janzen); 8.1mi SW Los Amates, 160m [on CA-9] [=8.0mi NE El Lobo] (D.H.Janzen); 9.7mi NE Piedras de Afilar, 150m [on CA-9] [=9.5mi SW El Lobo] (D.H.Janzen); Zacapa (W.M.Wheeler); km142 on Guatemala-Pto.Barrios Rd. nr. Los Amates (D.H.Janzen).

HONDURAS *Choluteca:* 19.3mi SW San Marcos de Colón, on Hwy.1 (D.H.Janzen); 19mi NE Choluteca (D.H.Janzen); 20.4mi SW San Marcos de Colón, 490m (D.H.Janzen); 3.6mi W Choluteca, 200m (D.H.Janzen); 7.4mi NE Choluteca, 150m (D.H.Janzen); *Colón*: Trujillo, 80m (Echternacht); *Comayagua*: 11.7mi S San Antonio, 830m (D.H.Janzen); 4mi N Comayagua, 500m (D.H.Janzen); *Cortés*: 24.6mi SW San Pedro Sula, 240m (D.H.Janzen); *Francisco Morazán*: 24.3mi S Camayagüela (=Tegucigalpa), 1000m (D.H.Janzen); 30.4mi S Camayagüela (D.H.Janzen); 30.5mi S Camayagüela, 930m (D.H.Janzen); *Ocotepeque*: 2.3mi E [Nueva] Ocotepeque, 1090m (D.H.Janzen); Nueva Ocotepeque, 910m (D.H.Janzen); *Santa Bárbara*: 13.7mi SW Quimistán, 320m (D.H.Janzen); *Valle*: 18.5mi W Jicaro Galan (D.H.Janzen); 4.6mi E Jicaro Galan, 190m (D.H.Janzen).

MEXICO *Camp.*: 0.1mi S Tenabo, rd. to Becal (D.H.Janzen); 0.8mi E Campeche (D.H.Janzen); 29mi E & 12mi S Campeche (Ruinas Edzna) (D.H.Janzen); 29mi E Campeche (D.H.Janzen); 48mi NE Puerto Real (Isla Aguada), Hwy.180 (D.H.Janzen); 5mi S Tenabo (Campeche-Becal Rd.) (D.H.Janzen); Campeche (N.L.H.Krauss); *Chis.:* 2.4mi E Chiapa de Corzo, Hwy.190, 580m (D.H.Janzen); 2km N Yxhuatan [Ixhuatán], "2mi N Tapilula" (D.H.Janzen); 32mi W [San] Cristóbal de las Casas, Hwy.190 (D.H.Janzen); 3km ENE Chiapa de Corzo, 500m (P.S.Ward); 3mi N Soyalo [on Hwy.195] (D.H.Janzen); 42.5mi S Comitán, Hwy.190, 680m(D.H.Janzen); 5.4mi E Chiapa de Corzo, Hwy.190, 770m (D.H.Janzen); 56.9mi NE [NW?] Tapachula [on Hwy.200?] (D.H.Janzen); 7.0mi NE [NW?] Tapachula [on Hwy. 200?] (D.H.Janzen); 7.5mi NW Cd.Cuauhtemoc, Hwy.190 (D.H.Janzen); 8.5mi S La Trinitaria, Hwy.190 (D.H.Janzen); Finca Esmeralda (R.Nettel F.); Puerto de San Benito [=Puerto Madero] (R.Nettel F.); Tonalá, 40m (D.H.Janzen); Yerba Santa (G.N.Collins); *Hgo.:* 2km W Orizatlán, 245m (W.MacKay); *Oax.:* 11.4-17.0mi W Tehuantepec (D.H.Janzen); 19km N San Pedro Pochutla, 200m (W.MacKay); 3.9mi E Tehuantepec (D.H.Janzen); 5.7mi W "Tapanapec" [=Tapanatepec] (D.H.Janzen); 6.0mi E Niltepec ,Hwy.190, 100m (D.H.Janzen); 8.1mi W Niltepec, Hwy.190, 60m (D.H.Janzen); Temascal (D.H.Janzen); Temascal, 25m (D.H.Janzen); *Q.Roo:* 12.2mi S Peto, Q.Roo-Yucatan border (D.H.Janzen); 26.6mi S Felipe Carillo Puerto (D.H.Janzen); 5.4mi E Polyuc (D.H.Janzen); Cancun (A.Dejean); Cenote de Las Ruinas, 8km NW Polyuc (J.Red et al.); Chetumal (J.C. & D.Pallister); San Miguel, Cozumel I. (N.L.H.Krauss); Sian Ka'an (A.Dejean); Sian Ka'an Reserve, nr. Felipe Carillo Puerto (A.Dejean); *S.L.P.*: 2mi N Rio Amahac, Tamazunchale, 400ft. (W.S.Creighton); 6mi NW Tamazunchale, 600ft.(Univ.Kansas Mex.Exped.); 8mi W San Joachin (W.J.Gertsch); El Bonito, 7mi S Cd. Valles, 300ft. (P.H. & M.Arnaud); El Salto (W.E.LaBerge); Tamazunchale (D.H.Janzen); Tamazunchale, 600ft. (W.S.Creighton); *Ver.:* 29.5mi NW Tuxpan, Hwy.122 [actually Hwy.127] (D.H.Janzen); Alazan (F.Parker & D.Miller); Cordoba (W.M.Mann); Cotaxtla Exp. Sta., Cotaxtla (D.H.Janzen); Mirador (E.Skwarra); Veracruz (E.Skwarra); *Yuc.:* 30mi S Merida (P.J.Spangler); 8mi E Merida (rd. to Pto. Juarez) (D.H.Janzen); Itzimna (J.C. & D.Pallister);Merida (D.H.Janzen; N.L.H.Krauss); Oxkutzcab (D.H.Janzen); Sta. Elena, S of Ticul, "Hwy.180" [prob.Hwy.261] (D.H.Janzen); *state unknown*: "Mex"("Norton").

NICARAGUA *Estelí:* 1mi N Condega, 500m (D.H.Janzen); 2.5mi N Condega, 620m (D.H.Janzen); *León*: San Jacinto (J.M.Maes); *Madriz:* 3mi W Somoto, 650m [=2.5mi W Somoto] (D.H.Janzen); *Nueva Segovia*: 7.1mi W Amatillo (D.H.Janzen).

Pseudomyrmex satanicus (Wheeler 1942)
(Figs. 10, 20, 59, 68)

Pseudomyrma satanica Wheeler 1942:174. Syntype workers, queen, male, Rio Agua Salud, Canal Zone, Panama (W. M. Wheeler) (AMNH, LACM, MCZC) [Examined]. One MCZC syntype worker here designated LECTOTYPE.
Pseudomyrmex satanica [sic] (Wheeler); Janzen 1966:252.
Pseudomyrmex satanicus (Wheeler); Kempf 1972:223.

Worker measurements (n = 15).—HL 1.16-1.36, HW 1.10-1.26, MFC 0.035-0.057, CI 0.90-0.97, REL 0.45-0.50, REL2 0.48-0.52, OOI 0.92-1.67, VI 0.69-0.78, FCI 0.030-0.049, SI 0.45-0.49, SI2 0.88-1.00, NI 0.63-0.68, PLI 0.47-0.54, PWI 0.46-0.63, PPWI 1.35-1.54.

Worker diagnosis.—Similar to *P. spinicola* (q.v.) except as follows. Larger (HW > 1.09), head broader (CI > 0.88) (Fig. 34) with straight or slightly concave posterior margin and subangulate posterolateral corners (Fig. 10). (The posterior margin of the head approaches this condition in some *P. spinicola* workers but these have much smaller, more elongate heads, HW < 1.10, CI < 0.90.) Median clypeal lobe narrower (CLW/HW 0.20-0.22; see Fig. 33). Palp formula 4,3. Head with pronounced pit-like impression below the median ocellus (absent or poorly developed in *P. spinicola*). Metanotal groove better developed, longer. Petiole tending to be more slender, with less distinct posterolateral corners (this characteristic seen in some workers of *P. spinicola*, especially individuals from Panama). Body pubescence averaging thicker than in *P. spinicola*. Dark brown in color, mandibles and appendages lighter.

Comments.—The foregoing diagnosis will allow discrimination of *P. satanicus* workers from those of the closely related *P. spinicola*; queens can be recognized by size alone (HL > 1.65, HW > 1.20). *P. satanicus* can be distinguished from the remaining members of the *P. ferrugineus* group by the emarginate, laterally angulate median clypeal lobe of the worker and the large size of the queen.

Distribution and biology.—*P. satanicus* is a forest species restricted to a few localities in central Panama where its host plant, *Acacia melanoceras,* grows (Fig. 68). Both the ant and plant are intolerant of forest clearance and are considered vulnerable to extinction (Janzen 1974). The ant is polygynous, with 5-20 or more queens per colony, and the workers are particularly aggressive, even for acacia-ants (Wheeler 1942; Janzen 1974). See Janzen (1974:43-53) for additional details on *P. satanicus* and its host plant.

Material examined (AMNH, LACM, MCZC, PSWC, USNM).—

PANAMA *Canal Zone:* "Canal Zone" (A.H.Jennings); 3mi SW Gatún Dam (D.H.Janzen); Barro Colorado Island (D.H.Janzen); France Field (G.C.Wheeler); Marajal [Majagual] nr. Colon (W.M.Wheeler); Red Tank (W.M.Wheeler); Rio Agua Salud (W.M.Wheeler); Zorra Island (D.H.Janzen); *Panamá*: Rio Piedras (D.H.Janzen); *prov.unknown*: "Panama"(c.u.).

Pseudomyrmex spinicola (Emery 1890)
(Figs. 11, 21, 60, 68)

Pseudomyrma spinicola Emery 1890:64. Lectotype worker, Alajuela, Costa Rica (Alfaro) (MCSN) [Examined].
Pseudomyrma spinicola race *atrox* Forel 1912:24.

Syntype workers, Panama (Christophersen) (MHNG, NHMB) [Examined]. **Syn. nov.** One syntype from MHNG here designated LECTOTYPE.

Pseudomyrma spinicola race *Gaigei* Forel 1914:615. Syntype workers, Columbien (Gaige) (MHNG), Fundacion, Colombia (F. M. Gaige) (LACM, MCZC) [Examined]. **Syn. nov**.

Pseudomyrma spinicola subsp. *infernalis* Wheeler 1942:180. Syntype workers, queens, males, Venado, Canal Zone, Panama (W. M. Wheeler), Red Tank, Canal Zone, Panama (W. M. Wheeler), and Las Sabanas, Panama (W. M. Wheeler) (AMNH, MCZC) [Examined]. One MCZC worker, from Red Tank, here designed LECTOTYPE. **Syn. nov.**

Pseudomyrma spinicola subsp. *scelerosa* Wheeler 1942:181. Syntype workers, Granada, Nicaragua (C. F. Baker) (AMNH, MCZC) [Examined]. One MCZC worker here designated LECTOTYPE. **Syn. nov.**

Pseudomyrma spinolae [sic] var. *infernalis* Enzmann 1945:91. Syntype workers, queens, Red Tank, Canal Zone, Panama (W. M. Wheeler) (MCZC) [Examined] [Objective synonym of *P. spinicola* subsp. *infernalis* Wheeler; Brown 1949:43].

Pseudomyrma spinolae [sic] var. *scelerosa* Enzmann 1945:91. Syntype workers, Granada, Nicaragua (C. F. Baker) (MCZC) [Examined] [Objective synonym of *P. spinicola* subsp. scelerosa, Wheeler; Brown 1949:43].

Pseudomyrmex spinicola (Emery); Wheeler and Wheeler 1956:386.

Worker measurements (n = 41).—HL 0.99-1.28, HW 0.94-1.15, MFC 0.032-0.067, CI 0.84-0.97, REL 0.42-0.47, REL2 0.45-0.54, OOI 1.22-2.77, VI 0.64-0.83, FCI 0.032-0.061, SI 0.45-0.50, SI2 0.88-1.05, NI 0.61-0.69, PLI 0.47-0.64, PWI 0.49-0.71, PPWI 1.32-1.85.

Worker diagnosis.—Median clypeal lobe emarginate, laterally angulate (Fig. 11), relatively broad (CLW/HW 0.21-0.25). Palp formula 5,3 (rarely 5p4,3). Frontal carinae relatively close, and median lobes of antennal sclerites rather exposed (FCI2 0.24-0.42). Head longer than broad but variably so (see range of CI values). Posterior margin of head ranging from broadly convex (Fig. 11) to straight or even weakly concave, usually rounding gently into the sides of head. Basal face of propodeum subequal to declivitous face, rounding into latter; in dorsal view propodeal spiracles salient,protruding laterally. Petiole generally slender (PLI <0.65) with a well developed anterior peduncle; in dorsal view posterolateral angles typically prominent. Head densely punctulate, sublucid, interspaces small (punctulae essentially contiguous on most of head) but shiny. Mesosoma finely punctulate dorsally becoming punctulate-coriarious laterally, sublucid; propodeum lacking overlying, coarser rugulo-punctate sculpture. Standing pilosity usually moderately common on body dorsum and including some hairs > 0.20 mm. Appressed pubescence common on most surfaces. Varying from light orange-brown to dark brown in color.

Comments.—The short, broad, emarginate and laterally angulate median clypeal lobe (Fig. 11) distinguishes the worker of this species. The sublucid integument, elongate petiole, prominent propodeal spiracles, and somewhat angulate posterolateral corners of the petiole are also characteristic. In addition, queens and workers of *P. spinicola* have more elongate scapes and legs than those of all other species except *P. satanicus* (Figs. 30, 31). For differences between *P. spinicola* and the closely related *P. satanicus* see under the latter species.

P. spinicola is a variable taxon and has received several infraspecific names, here considered junior synonyms. Southeastern populations (from the Río Grande de Tàrcoles in Costa Rica east through Panama to northern Colombia) are somewhat differentiated from the others, with the workers and queens tending to have more elongate heads, darker color, and more slender petioles with less pronounced posterolateral angles (see Figs. 34, 35). In Costa Rica the contrasts between the two sets of populations are rather striking, and are perhaps accentuated by habitat differences since some (but not all) the southeastern populations are associated with *Acacia allenii* growing in forested situations, while the northern populations are primarily from *Acacia collinsii* in open habitats. Samples from Panama (all associated with *A. collinsii*) are more variable and partly bridge the phenotypic gap. It is possible that more than one species is masquerading in this variation but the evidence remains ambiguous.

Distribution and biology.—*P. spinicola* is a monogynous species, distributed from Honduras to northern Colombia (Fig. 68), which is associated with *Acacia collinsii* and, less frequently, *Acacia allenii* and *A. cornigera*. Janzen (1983) provides a good summary of its biology in Costa Rica, under the name "*P. ferruginea*". Observations on "*P. ferruginea*" in Costa Rica, Nicaragua, Panama and Isla Providencia (Janzen 1969, 1974, 1975, 1983) refer to *P. spinicola*; true *P. ferrugineus* does not occur south of Honduras and El Salvador.

Material examined (AMNH, ANSP, BMNH, CUIC, FFIC, GBFM, GCWC, INBC, JTLC, KSUC, LACM, MCSN, MCZC, MHNG, MZSP, NHMB, PSWC, UCDC, USNM).—

COLOMBIA *Atlantico:* Cuatro Bocas, 200m (J.F.G.Clarke); *Bolívar*: Hda. Monterey, 50m (G.Fagua; F.Fernández); *Magdalena*: Aracataca (P.J.Darlington); Fundacion (F.M.Gaige); Fundacion, Santa Marta Mts.,300ft. (F.M.Gaige); *San Andrés y Providencia:* "Old Providence Isl." (D.Fairchild); Isla Providencia, 300ft.(D.H.Janzen); *dept. unknown:* "Columbien" (Gaige).

COSTA RICA *Alajuela*: Alajuela (A.Alfaro); San Mateo (P.Biolley); Surubres, nr. San Mateo (P.Biolley); Turrúcares (A.Alfaro); *Cartago*: Turrialba (c.u.); *Guanacaste*: 10.7mi NW Liberia (D.H.Janzen); 2mi S Cañas (D.H.Janzen); 5km S Liberia (D.H.Janzen); 6mi W Liberia (D.H.Janzen); 7km N Cañas (D.H.Janzen); Cañas, "La Pacifica" (R.L.Jeanne); Finca La Pacifica (D.W.Davidson); Garita (A.Alfaro); Hda. Comelco, 24km NW Cañas (InterAm Hwy) (E.R.Heithaus); Hda. La Pacifica, nr. Cañas, 50m (P.S.Ward); Palo Verde (D.E.Gill; E.Guerrant & P.Fiedler; H.A.Hespenheide; D.H.Janzen);Palo Verde, 50m (D.M.Olson); Palo Verde, <100m (J.Longino); Rio Corobici, nr. Cañas (R.M.Bohart); Santa Rosa Natl. Pk.(E.M.Barrows); Santa Rosa Natl. Pk., 300m (J.Longino; P.S.Ward); Santa Rosa Natl. Pk., 5m (P.S.Ward); Santa Rosa Natl. Pk., <5m (P.S.Ward); *Heredia:* "15mi SE Pto.Viejo" [15km SW Pto.Viejo] (D.H.Janzen); *Puntarenas*: 1-5mi NW Rincón (D.H.Janzen); 14.1mi N Golfito (D.H.Janzen); 14km E Palmar Norte, 70m (P.S.Ward); 1km NE Tárcoles, 20m (P.S.Ward); 21.6 rd.mi NE Palmar Norte, 90m (D.H.Janzen); 3.4mi SE Golfito, 30m (D.H.Janzen); 4mi SW Rincón (D.H.Janzen); Corcovado Natl. Pk. (D.W.Davidson; J.T.Longino); Corcovado Natl. Pk., Llorona (J.T.Longino); Corcovado Natl. Pk., Sirena, 100m (P.S.Ward); Corcovado Natl. Pk., Sirena, 10m (P.S.Ward); Entrada Boruca, 20km NE Palmar Sur (D.H.Janzen); Osa Penin., nr. Rincón (D.H.Janzen); Reserva Biol. Carara, 30m (P.S.Ward);Rincón (D.H.Janzen); Rio Terraba, nr. Palmar Sur (D.H.Janzen); *San José*: 16.4mi SW San Isidro, 160m (D.H.Janzen); 3.5km NE Santiago de Pur (D.H.Janzen); Santa Ana (D.H.Janzen); Tarrazu [Rio?] (A.Alfaro); Villa Colón (A.Alfaro; D.H.Janzen); Villa Colón, 880m (A.Alfaro).

HONDURAS *Choluteca:* 11.1mi NE Choluteca, 450m (D.H.Janzen); 3.6mi W Choluteca, 200m (D.H.Janzen); *Colón*: El Canal, Puerto Castilla (W.M.Mann); Roetan Isl. [Isla de Roatán] (M.Bates); Trujillo, 80m (Echternacht).

NICARAGUA *Boaco:* Empalme do Boaco [=El Empalme?] (Echternacht); *Chontales:* no specific locality (Janson); *Estelí:* 7.5mi NW San Isidro, 550m (D.H.Janzen); *Granada:* Granada (C.F.Baker); *León*: 19mi SE León [=3.5mi N Pto.Somoza (Sandino)] (D.H.Janzen); 28.1mi SE León (D.H.Janzen); *Madriz:* 13.9mi from Honduras, on Nic.border, Hwy.1 (D.H.Janzen); 2.5mi W Somoto (D.H.Janzen); *Managua:* 20mi N Tipitapa, 90m [=19.4mi N Tipitapa] (D.H.Janzen); 8.1mi E San Benito (D.H.Janzen); 9mi N Tipitapa, 50m [=8.8mi N Tipitapa] (D.H.Janzen); *Matagalpa:* 15.8mi NW Sebaco (D.H.Janzen); 2.6mi N Dario (D.H.Janzen); 4.1mi S Matagalpa, 650m (D.H.Janzen); 4mi S Dario, 350m [=4.5mi SE Dario] (D.H.Janzen); 4mi S Darío, 350m (D.H.Janzen); *Rivas:* C.R. border, 1mi N Peñas Blancas, <5m [=1mi NW Peñas Blancas] (D.H.Janzen); Isla Ometepe (F.Joyce); San Juan del Sur, 10m [=1mi N San Juan del Sur] (D.H.Janzen).

PANAMA *Canal Zone:* 7.5mi NW Balboa (between Summit Gdn. &Paraiso) (D.H.Janzen); Ancon (S.F.Blake); Barro Colorado Island (Weber); Cerro Galera (P.S.Ward); Chivachiva trail (W.M.Wheeler); Chivachiva trail, nr. Red Tank (W.M.Wheeler); Culebra [presumably Culebra Cut] (D.D.Gaillard); E end of Madden Dam (D.H.Janzen); Gamboa (N.Banks); Howard AFB, W of Panama City, 50m (W.L.Brown et al.); Madden Dam (D.Quintero et al.); Paraiso (A.Busck); Red Tank (W.M.Wheeler); Ruta 1, 14km W Panama City, 100m (W.L.Brown et al.); Venado (W.M.Wheeler); W end Madden Dam (D.H.Janzen); *Chiriquí:* 10.7mi ESE Concepción (D.H.Janzen); 12.9mi E Remedios (D.H.Janzen); 19.6mi E Sapotilla, 50m (D.H.Janzen); 7.2mi W Remedios (D.H.Janzen); 9.5mi S Boquete, 620m (D.H.Janzen); *Coclé:* 0.3mi W Agua Dulce, 50m (D.H.Janzen); 10.4mi NE Santa Maria, 60m [=1.9mi W Agua Dulce, Hwy. 1] (D.H.Janzen); 2.7mi SW Penonome (D.H.Janzen); *Herrera:* Cerro Guacamaya, Albina al N. de Monagrillo (D.Quintero et al.); *Los Santos:* 3.1mi N Pedasi (D.H.Janzen); Azuero Penin., 5.4mi SE Los Santos, <5m (D.H.Janzen); *Panamá*: 18.6mi SW Chepo (D.H.Janzen); Bella Vista (N.Banks); Las Sabanas (G.C.Wheeler; W.M.Wheeler); Las Sabanas, Panama City (H.F.Dietz); Rio Corona, S of El Valle, 2000ft. (C.W.Rettenmeyer); Rio Tetita, San Carlos (F.D.Rattinibane); savannah nr. Juan Diaz (Weber); *Veraguas*(?): Las Palmas (c.u.); *Veraguas:* 4km NW Santiago (D.Quintero); *prov. unknown*: "Panama" (Christophersen).

Pseudomyrmex veneficus (Wheeler 1942)
(Figs. 17, 28, 62, 69)

Pseudomyrma belti subsp. *venefica* Wheeler 1942:162. Syntype workers, males, queens, Escuinapa, Sinaloa, Mexico (J. H. Batty) (AMNH, MCZC) [Examined]. One MCZC syntype worker here designed LECTOTYPE.

Pseudomyrma belti subsp. *venifica* Enzmann 1945:81. Syntype workers, queens, Manzanillo, Colima, Mexico (C. H. T. Townsend) (MCZC) [Examined] [Synonymy by Brown 1949:42].

Pseudomyrmex venefica [sic] (Wheeler); Janzen 1969:241.

Pseudomyrmex belti veneficus (Wheeler); Kempf 1972:216.

Pseudomyrmex veneficus (Wheeler); Ward 1989:439.

Worker measurements (n = 12).—HL 0.95-1.04, HW 0.85-0.95, MFC 0.045-0.073, CI 0.88-0.95, REL 0.44-0.47, REL2 0.47-0.52, OOI 1.26-2.30, VI 0.66-0.75, FCI 0.051-0.081, SI 0.43-0.46, SI2 0.85-0.94, NI 0.58-0.65, PLI 0.60-0.67, PWI 0.58-0.67, PPWI 1.35-1.73.

Worker diagnosis.—Similar to P. *ferrugineus* (q.v.) except as follows. Smaller (LHT 0.69-0.80), with broad head (CI > 0.87); frontal carinae separated by basal scape width or less (FCI2 0.40-0.60); petiole short (PL 0.43-0.54) and relatively narrow (see PWI values) with somewhat rounded posterolateral angles (Fig. 28). Head densely punctulate, subopaque to sublucid, with weak silvery reflectance. Overlying rugulo-punctate sculpture on propodeum weak and ill-defined. Standing pilosity variable in abundance, becoming rather short (0.10 mm) and sparse in southern populations. Pubescence thick and conspicuous, suberect on some surfaces especially the propodeum and petiole; suberect pubescence on petiolar dorsum contrasting with the appressed pubescence on the postpetiole (Fig. 28). Very dark greyish-brown to black, parts of the mesosoma and petiole sometimes with lighter yellowish brown (more consistently so in the queen).

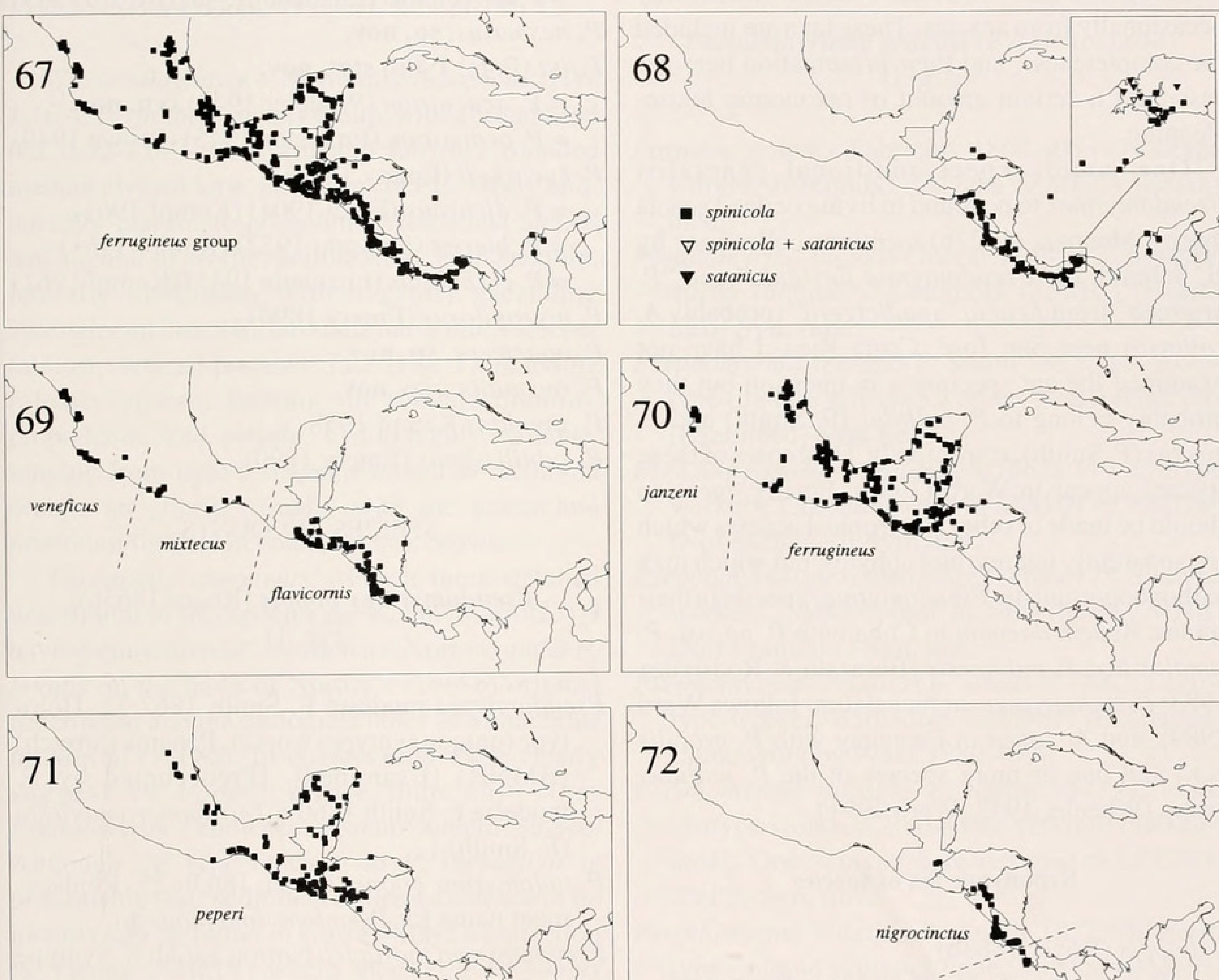
Comments.—The small size (worker HW < 0.96; queen HW 0.84-0.96, n=12), conspicuous suberect pubescence on the propodeum and petiole, and black coloration of the head and gaster distinguish workers and queens of *P. veneficus*. The related species, *P. flavicornis*, is larger (worker HW > 0.98, queen HW 1.12-1.19) with a broader and more robust petiole (Figs. 25, 28). Workers and queens of *P. flavicornis* also lack the sublucid head and conspicuous suberect pubescence characteristic of *P. veneficus*. *P. mixtecus* is somewhat intermediate between these two - it has the head sculpture and pubescence typical of *P. flavicornis* but approaches *P. veneficus* in size (worker and queen head widths overlapping, although only slighter in the queens where HW 0.96-1.01 (n=8) in *P. mixtecus*) and petiolar dimensions (Figs. 44-47).

Distribution and biology.—*P. veneficus* has a limited distribution in western Mexico (Sinaloa to Michoacan) (Fig. 69) where colonies occupy *Acacia hindsii* and, at one locality, *A. collinsii*. Janzen (1973) gives a detailed description of the ecology and behavior of this highly polygynous, effectively unicolonial, species whose colonies are among the largest of all social insects (containing millions of workers and several hundred thousand queens).

Material examined (AMNH, CASC, EBCC, INHS, LACM, MCSN, MCZC, MZSP, PSWC, UCDC, UCRC, USNM).—

MEXICO *Col.*: 9.4mi NW Manzanillo (D.H.Janzen); Manzanillo (C.H.T.Townsend; W.M.Wheeler); Paso del Rio, 200ft. (I.J.Cantrall); *Jal.:* 2km E Chamela, 20m (P.S.Ward); 5km E Chamela, 50m (P.S.Ward); 6mi NE El Rincon, 1600ft. (R.J.Hamton); Barra de Navidad (N.L.H.Krauss); Chamela (R.J.McGinley; J.F.Watkins); *Mich.*: 1.1mi N Gabriel Zamora, 820m (D.H.Janzen); 1.5mi N La Mira (D.H.Janzen); 15km WNW Playa Azul, 50m (P.S.Ward); *Nay.:* 12mi NE San Blas (W.J.Gertsch & W.Ivie); 16mi NW Tepic (W.E.LaBerge); 31mi N Tepic (D.H.Janzen); 37mi N Tepic (D.H.Janzen); 4mi E San Blas (M.E.Irwin); Rio Palillo, 14mi E San Blas (D.H.Janzen); *Sin.*: 14.6mi S Mazatlan (D.H.Janzen); 20mi E Villa Union (E.I.Schlinger); 20mi E Villa Union, 235m (M.E.Irwin; E.Schlinger et al.); 20mi S Villa Union (E.I.Schlinger); 5mi E Concordia (W.J.Gertsch & J.A.Woods); Escuinapa (J.H.Batty); Palmito (L.de Mauzo); Piedra Blanca (R.M.Bohart); *state unknown*: "Mexico"(c.u.).

OTHER ACACIA-ASSOCIATED



Figs. 67- 72. Distributions of species in the *Pseudomyrmex ferrugineus* group.

PSEUDOMYRMEX FROM CENTRAL AMERICA

Introduction

Three of the species discussed below (*Pseudomyrmex nigropilosus*, *P. simulans* and *P. subtilissimus*) are obligate inhabitants of Central American swollen-thorn acacias, although they are not closely related to the *P. ferrugineus* group (Ward 1991). A fourth species, *P. reconditus*, is known only from a single collection, made in association with *Acacia collinsii*. The remaining six species (*P. boopis*, *P. gracilis*, *P. hesperius*, *P. ita*, *P. kuenckeli* and *P. opaciceps*) are non-specialist *Pseudomyrmex* which have been collected only occasionally from acacias. These taxa are included for completeness, and their presentation here necessitates a certain amount of taxonomic housecleaning.

One could expect additional generalist *Pseudomyrmex* to be found in living or dead acacia thorns. Menozzi (1927b) mentions collections by H. Schmidt of "*Pseudomyrma flavidula*" and "*P. brunnea*" from *Acacia* "*spadicigera*" (probably *A. collinsii*) near San José, Costa Rica. I have not examined the ant specimens in question but they probably belong to *P. pallidus* (F. Smith) and *P. ejectus* (F. Smith), respectively. Diagnoses of these species appear in Ward (1985). Finally, mention should be made of other Neotropical acacias which are apparently not myrmecophytes, but which may harbor opportunistic *Pseudomyrmex* species in their spines: *Acacia daemon* in Cuba with *P. pazosi*, *P. simplex* and *P. cubaensis* (Berazaín & Rodriguez 1983; *Pseudomyrmex* nomenclature follows Ward 1989), and *A. caven* in Paraguay with *P. gracilis* (s.l.) and one or more species in the *P. pallidus* group (Wheeler 1942; Ward 1991).

Synonymic list of species

P. boopis (Roger 1863b)
= *P. modestus* (F. Smith 1862) (preoccupied)
= *P. thoracicus* (Norton 1868b) **syn. nov.**
= *P. excavatus* (Mayr 1870) (Kempf 1967)
= *P. flaviventris* (Emery 1896) (Kempf 1960)
= *P. fusciceps* (Santschi 1931) (Kempf 1960)
= *P. guatemalensis* (Enzmann 1945) (Kempf 1960)
P. gracilis (Fabricius 1804)
= *P. bicolor* (Guérin 1844) **syn. nov.**
= *P. sericatus* (F. Smith 1855) **syn. nov.**
= *P. dimidiatus* (Roger 1863a) **syn. nov.**
= *P. mexicanus* (Roger 1863a) **syn. nov.**
= *P. variabilis* (F. Smith 1877) (Ward 1989)
= *P. pilosulus* (F. Smith 1877) **syn. nov.**
= *P. volatilis* (F. Smith 1877) **syn. nov.**
= *P. canescens* (F. Smith 1877) **syn. nov.**
= *P. guayaquilensis* (Forel 1907) (unavailable name)
= *P. glabriventris* (Santschi 1922) **syn. nov.**
= *P. veliferus* (Stitz 1933) **syn. nov.**
= *P. longinodus* (Enzmann 1945) (Brown 1949)
P. hesperius, **sp. nov.**
P. ita (Forel 1906) **stat. nov.**
= *P. acaciarum* (Wheeler 1942) **syn. nov.**
= *P. acaciorum* (Enzmann 1945) (Brown 1949)
P. kuenckeli (Emery 1890)
= *P. dichrous* (Forel 1904) (Kempf 1961)
= *P. bierigi* (Santschi 1932) (Kempf 1961)
= *P. crenulatus* (Enzmann 1945) (Kempf 1961)
P. nigropilosus (Emery 1890)
P. opaciceps, **sp. nov.**
P. reconditus, **sp. nov.**
P. simulans Kempf 1958
P. subtilissimus (Emery 1890)

SPECIES ACCOUNTS

Pseudomyrmex boopis (Roger 1863b) (Fig. 1)

Pseudomyrma modesta F. Smith 1862:32. Holotype (unique syntype) worker, Panama (Stretch) (BMNH) [Examined]. [Preoccupied by *P.* modesta F. Smith 1860 = *Tetraponera modesta* (F. Smith).]

Pseudomyrma boopis Roger 1863b:25. Replacement name for *Pseudomyrma modesta*.

Pseudomyrma thoracica Norton 1868b:8. Syntype workers, Cordova, Mexico (Sumichrast) [Not examined; see comments below]. Syn. nov.

Pseudomyrma excavata Mayr 1870:410. Syntype workers, "N. Granada" (BMNH, MHNG, NHMV) [Examined] [Synonymy by Kempf

1967:2].

Pseudomyrma excavata var. *flaviventris* Emery 1896:2. Syntype workers, Darien, Panama (Festa) (MCSN, MHNG) [Examined] [Synonymy by Kempf 1960:22].

Pseudomyrma excavata var. *fusciceps* Santschi 1931:271. Two syntype workers, France Field, Panama (A. Bierig) (NHMB) [Examined] [Synonymy by Kempf 1960:22].

Pseudomyrma spinicola subsp. *modesta* F. Smith; Wheeler 1942:105.

Pseudomyrma tenuis var. *guatemalensis* Enzmann 1945:92. Holotype worker, Escuintla, Guatemala [Not examined] [Synonymy by Kempf 1960:22].

Pseudomyrmex boopis (Roger); Kempf 1967:2.

Worker diagnosis.—Medium-sized species (HW 1.16-1.29) in the *P. tenuis* group, with a broad head (CI 0.92-1.02), tectiform and laterally rounded median clypeal lobe, large eyes (REL 0.66), and laterally marginate pronotum. Mesosoma arched and angular in profile; petiole short, high and thin, laterally marginate, with a gently ascending anterodorsal face which rounds into a much steeper (almost vertical) posterior face (Fig. 1). Standing pilosity sparse, lacking on the mesonotum, propodeum, and petiole. Color highly variable, ranging from light testaceous brown to bicolored orange and black (usually with the gaster and pronotum lightest in color) to dark brown.

Taxonomic comments.—For a more detailed description of this species see Kempf (1960:23). I have synonymized *P. thoracicus* (Norton) under *P. boopis* on the basis of Norton's (1868b) original description and the biological notes of Sumichrast in Norton (1868a). In combination these clearly suggest *P. boopis* rather than any other *Pseudomyrmex* known to occur in southern Mexico. Although the type material of *P. thoracicus* is presumably lost, additional indirect evidence of its identity can be found in Gustav Mayr's collection in Vienna (NHMV) where there is a *P. boopis* worker from Colombia ("Neugranada") identified by Mayr as "*P. thoracica* Norton". This take son added significance when it is realized that Mayr was apparently the recipient of some of Norton's material. During a brief visit to NHMV I noted specimens of several species, including *P. ferrugineus*, *P. peperi*, *P. elongatulus* (Dalla Torre) and *P. brunneus* (F. Smith) (although unfortunately not *P. boopis*), labelled "Mex. Norton" or "N.Am./Norton".

Distribution and biology.—*P. boopis* occurs in rainforest and tropical moist forest from southern Mexico to Ecuador, Venezuela and northern Brazil. This species is less arboreal than most *Pseudomyrmex*, and nests typically in rotten wood on or near the ground. The type specimen of *P. boopis* came from a nest in a swollen-thorn acacia (Smith 1862:33), however, and Janzen found colonies in thorns of *Acacia melanoceras* seedlings in Panama.

Pseudomyrmex gracilis (Fabricius 1804) (Fig. 6)

Formica gracilis Fabricius 1804:405. Lectotype worker, Essequibo, Guyana (ZMUC) [Examined].

Pseudomyrma bicolor Guérin 1844:427. Syntype queen (unique?), Colombia (ZSMC) [Examined] **Syn. nov.**

Pseudomyrma sericata F. Smith 1855:159. Holotype (unique syntype) worker, Brazil (BMNH) [Examined] **Syn. nov.**

Pseudomyrma dimidiata Roger 1863a:177. Syntype workers, Colombia (not in MNHN or ZMHB) [Not examined] **Syn. nov.**

Pseudomyrma mexicana Roger 1863a:178. Syntype workers, Mexico (not in MNHN or ZMHB) [Not examined] **Syn. nov.**

Pseudomyrma variabilis F. Smith 1877:62. Lectotype worker, Barbadoes (BMNH) [Examined] [Synonymy by Ward 1989:439].

Pseudomyrma pilosula F. Smith 1877:62. Two syntype workers, Barbadoes (BMNH) [Examined]. One syntype here designated LECTOTYPE. **Syn. nov.**

Pseudomyrma volatilis F. Smith 1877:65. Holotype (unique syntype) male, Mexico (BMNH) [Examined] **Syn. nov.**

Pseudomyrma canescens F. Smith 1877:66. Holotype (unique syntype) queen, Abydos, Brazil (BMNH) [Examined] **Syn. nov.**

Pseudomyrma gracilis var. *glabriventris* Santschi 1922:345. Syntype workers, Izozo, Bolivia (Lizer & Delétang) (NHMB) [Examined] **Syn. nov.**

Pseudomyrma gracilis mexicana var. *guayaquilensis* Forel 1907:7. Worker, Guayaquil, Ecuador (Buchwald) (MHNG) [Examined] Unavailable infrasubspecific name.

Pseudomyrma gracilis var. *velifera* Stitz 1933:68. Holotype queen, Champerico, Guatemala (Paessler) (not in ZMUH; Weidner 1972) [Not examined] **Syn. nov.**

Pseudomyrma gracilis var. *longinoda* Enzmann 1945:87. Syntype worker, Peru (MCZC) [Examined] [Synonymy by Brown 1949:43].

Pseudomyrmex gracilis (Fabricius); Kusnezov 1953:214.

Worker diagnosis.—With the traits of the *gracilis* group (see couplet 6 of the key; p. 130) 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, rounded laterally; pronotum dorsolaterally marginate but not sharply so; in lateral view mesonotum more steeply inclined than basal face of propodeum; petiole long and slender (PLI 0.46-0.57) with a distinct anterior peduncle (Figs. 6, 53); head densely punctulate with a subopaque to sublucid (not matte) appearance; standing pilosity abundant, fine, predominantly pale silvery-white (not black).

Size and color extremely variable (HW 1.39-2.07), varying from unicolorous black (appendages lighter) to unicolorous orange-brown, with many intermediate and bicolored combinations. In populations from Mesoamerica the gaster is typically black, or if paler (orange-brown) then it is usually accompanied by a similar light coloration of the mesosoma (and sometimes also the head).

Taxonomic comments.—The *P. gracilis* complex presents one of the more taxonomically challenging problems in the genus *Pseudomyrmex* and the above treatment is by no means a final solution. The worker- and queen-based forms, newly synonymized under *P. gracilis*, fall within the bounds of the preceding diagnosis, but it is quite possible that my concept of this species will prove to be too broad. The types of *P. dimidiatus*, *P. mexicanus* and *P. veliferus* could not be located. They are judged to be junior synonyms on the basis of the original descriptions. The unique male holotype of *P. volatilis* is clearly a member of the *P. gracilis* group based on size (HW 1.48), mandibular dentition, pilosity, petiole shape, and shape of the parameres. In comparison with males of *gracilis* group species known to occur in Mexico, namely *P. gracilis*, *P. major* (see below), *P. nigropilosus* and *P. opaciceps*, the type specimen agrees best with *P. gracilis*.

The concept of *P. gracilis* adopted above encompasses an impressive amount of phenotypic variability. Collections from single regions often give the impression that this variation is distributed bimodally or multimodally, as more or less discrete morphs. For example, nest samples from Costa Rica can be segregated on the basis of worker morphology into (i) a large (HW > 1.80), usually lighter-colored form (with orange mesosoma, petiole, and postpetiole, and black head and gaster), (ii) a smaller, bicolored, usually more heavily infuscated form, and (iii) an all-black form of variable size. The first two are typically found in open or xeric habitats while the third is more common in closed forest, suggesting some ecotypic differentiation. Yet when large enough sample sizes are obtained all degrees of intermediacy in size and color are encountered, and the variation in color (less so size) can be seen among individuals (workers and alate queens) from the same nest. Thus, if there are ecotypes they do not appear to be reproductively isolated.

Left unresolved after the establishment of the above synonymy is the relationship of *P. gracilis* to the following nominal taxa: *P. alternans* (Santschi), *P. gracilis atrinodus* (Santschi), *P. gracilis argentinus* (Santschi) and *P. santschii* (Enzmann). But the following deserves recognition as a distinct species: *Pseudomyrmex major* (Forel 1899:91), **stat. nov.** (syntype worker, Pinos Altos, Chihuahua, Mexico (Buchan-Hepburn) (BMNH) (examined); original combination: *Pseudomyrma gracilis* var. *major*). Workers of *P. major* can be distinguished from those of *P. gracilis* by their emarginate median clypeal lobe, less distinct anterior peduncle of the petiole, and larger average size. Males of *P. major* have broadened fore-tarsal segments. *P. major* is confined to western Mexico, where it occurs sympatrically with *P. gracilis* without show-ing signs of intergradation.

Distribution and biology.—Befitting its wide distribution (southern United States to Argentina and Brazil) and variable phenotype, *P. gracilis* can be found in a variety of habitats from mangroves and thorn scrub to rainforest. It is often particularly common in disturbed situations such as old fields, roadsides, and secondary forest. Nests are usually located in dead twigs or small branches, but there are a substantial number of records of colonies occupying swollen-thorn acacias in Central America (Mexico to Panama). In a few localities *P. gracilis* is a common acacia inhabitant and under these circumstances it may exhibit local adaptation and phenotypic differentiation (see also Wheeler 1942:107). For example, Janzen collected a series of specimens from *Acacia gentlei* in Belize (15 mi. S Santa Elena) which have somewhat distinctive morphology: the workers are large, dark, abundantly hairy, and possess rather short petioles (PLI 0.55), although none of these features is outside the total range of variation for the species. Janzen (1974:98) notes that the workers of this large black morph have atypically aggressive behavior. Given the kind of ecotypic variation to which *P. gracilis* is prone, it is not surprising to find a tendency of some populations to specialize on acacias. The ecology of this species is reminiscent of other animal species which show broad ecophenotypic variation, e.g. fish with trophic polymorphisms (Kornfield et al. 1982; Grudzien and Turner 1984; Sandlund et al. 1992).

Pseudomyrmex hesperius Ward, **sp. nov.**
(Fig. 4)

Holotype worker.—MEXICO Sinaloa: 15.9 mi. NE Concordia, Hwy. 40, 600m, 9.vi.1967, D. H. Janzen XVIII, ex *Acacia hindsii* (LACM). HW 0.66, HL 0.83, EL 0.36, PL 0.34, PH 0.26.

Paratypes.—Same data as holotype: series of 11 workers (BMNH, LACM, MCZC, MZSP, PSWC, USNM).

Additional non-type material.—MEXICO Sinaloa: 14 km. S Mazatlán, 18.vii.1965, R. R. Snelling, 15 workers (LACM, MCZC, PSWC).

Worker measurements (n=6).—HL 0.78-0.85, HW 0.65-0.69, MFC 0.028-0.043, CI 0.79-0.83, REL 0.43-0.46, REL2 0.54-0.57, OOI 0.86-1.15, VI 0.75-0.82, FCI 0.043-0.062, SI 0.48-0.51, SI2 0.87-0.93, FI 0.41-0.45, PDI 0.84-0.95, MPI 0.053-0.066, NI 0.54-0.59, PLI 0.73-0.77, PWI 0.63-0.70, PPWI 1.41-1.56.

Worker diagnosis.—Small species (see above measurements) with elongate, subrectangular head and short eyes (REL 0.43-0.46, OI 0.61-0.65). Masticatory margin of mandible with five teeth, the fourth tooth (counting from the apex) separated by a gap of ca. 0.05 mm from the apicobasal tooth; MD8/MD9 0.70; third and fourth teeth small, contrasting with the large subapical and apical teeth (the latter ca. 0.032 and 0.055 mm in length, respectively); mesial tooth on basal margin situated slightly closer to apicobasal tooth than to proximal tooth (MD4/MD5 0.65); palp formula 5,3; median clypeal lobe short, its anterior margin straight to weakly convex, sharply rounded laterally; minimum distance between frontal carinae subequal to or less than basal scape width; frontal carinae diverging anteriorly and fusing with the antennal sclerites; pronotum laterally rounded, without humeral angles; in lateral profile the mesonotum and basal face of propodeum slightly inclined anteriorly, separated by a well developed metanotal groove (Fig. 4); basal face of propodeum rounding into the longer declivitous face, the latter somewhat concave in profile; petiole short, apedunculate, shaped as in Fig. 4, with a prominent triangular anteroventral tooth; in dorsal view petiole very broad anteriorly (PWI3 0.59-0.62); postpetiole broader than long, its anteroventral process small and inconspicuous. Mandibles finely striate; head punctulate on a smooth shining background, punctulae separated by one to several diameters on upper half of head, becoming denser towards the clypeus; mesosoma sublucid, with weak punctulate-coriarious sculpture; petiole, postpetiole and gaster shining, with very fine piligerous punctures. Standing pilosity common but short (< 0.10 mm) on most parts of body, lacking on outer faces of tibiae. Appressed pubescence widely distributed, moderately dense on abdominal tergite IV. Dark brown; mandibles, appendages and fronto-clypeal complex tending towards a lighter brown.

Taxonomic comments.—This is a taxonomically isolated species, not belonging to any of the nine major species groups of *Pseudomyrmex* (see Ward 1989). The salient features of *P. hesperius* are small size (HW < 0.72), reduced mandibular dentition and palp formula, short truncate median clypeal lobe, short eyes (especially obvious in lateral view, such that OI > 0.60), short apedunculate petiole with a broad attachment to the propodeum (PWI3 0.60), punctulate head sculpture, sublucid integument, and short standing pilosity. Some of these traits are shared with two other Mesoamerican *Pseudomyrmex*, *P. fervidus* (F. Smith) and a related undescribed species, but both of these are larger (HW > 0.70), with standing pilosity which is longer and more extensive (present on the outer faces of the tibiae).

Biology.—Although the type specimens of *P. hesperius* were collected from *Acacia hindsii* this species is not an obligate acacia inhabitant. The series from 14 km. south of Mazatlán was collected from dead branches of a woody plant, not *Acacia* (R. R. Snelling, pers. comm.).

Pseudomyrmex ita (Forel 1906) **stat. nov.** (Fig. 2)

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

Pseudomyrma sericea var. *acaciarum* Wheeler 1942:176. Syntype workers, Tumba Muerta Road, Panama (W. M. Wheeler) (LACM, MCZC) [Examined] **Syn. nov.**

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.

Worker diagnosis.—A medium-sized member (HW ca. 0.75-0.98) of the *P. sericeus* group, with large elongate eyes (REL 0.65), convex median clypeal lobe, subcontiguous frontal carinae (MFC 0.02), and palp formula of 6,4. Head longer than broad (CI 0.85). Basal face of propodeum shorter than declivitous face and meeting the latter at an angle. Petiole short, high (PLI > 1.00), with sharp dorsolateral margins; in profile anterior and dorsal faces of petiole weakly differentiated, rounding sharply into the vertical posterior face (Fig. 2). Body with fine punctulate-coriarious sculpture, opaque. Standing pilosity very sparse; a pair of stout setae present on the pronotal humeri, petiole, and postpetiole. Dark brown-black, with lighter brown maculation variably present on the pronotum, petiole, postpetiole, fronto-clypeal complex, and appendages.

Taxonomic comments.—This is one of several species originally described as "varieties" of *P. sericeus* (Mayr). Workers of *P. ita* can be distinguished from those of *P. sericeus* by the angulate shape of their petiole, especially in lateral view (Fig. 2); the petiole of *P. sericeus* is subtriangular in profile, with more gently rounded edges.

Distribution and biology.—*P. ita* occurs from Mexico to Colombia, and typically inhabits dead twigs or branches of various woody plants. It has been collected from thorns of *Acacia cornigera* in Mexico and *A. collinsii* in Costa Rica and Panama.

Pseudomyrmex kuenckeli (Emery 1890) (Fig. 3)

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

Pseudomyrma kuenckeli var. *dichroa* Forel 1904:41. 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 1945:84. Holotype worker, "Guernavaca", Mexico (not in MCZC) [Not examined; but other *P. kuenckeli* workers in the MCZC from Cuernavaca, Mexico (Wheeler) evidently represent the source series] [Synonymy by Kempf 1961:402].

Pseudomyrmex kuenckeli (Emery); Kusnezov 1953:214.

Worker diagnosis.—A member of the *P. viduus* group, easily recognized by the shiny broad head (CI 1.12), short eyes (REL 0.46), flattened mesosoma, blocky petiole, and abundant pilosity (Fig. 3). For further description see Kempf (1961:402).

Distribution and biology.—This is a widely distributed but generally uncommon species, found from Mexico to Argentina and Brazil. *P. kuenckeli* appears to have a preference for nesting in large dead branches, in somewhat open or seasonally dry forest. Its association with ant **acacias** is sporadic at best and based upon two records from Costa Rica: Emery (1891:168) reported a single specimen collected by Alfaro from a swollen-thorn **acacia**, and Menozzi (1927b) recorded a collection by H. Schmidt from *Acacia* "*spadicigera*" (probably a misidentification of *A. collinsii*) near San José.

Pseudomyrmex nigropilosus (Emery 1890)
(Fig. 7)

Pseudomyrma nigropilosa Emery 1890:62. Syntype workers, Liberia, Costa Rica (A. Alfaro) (MCSN, MHNG) [Examined].

Pseudomyrmex nigropilosus (Emery); Kempf 1958:453.

Worker diagnosis. With the traits of the *P. gracilis* group (see couplet 6 of key) and the following more specific features. Head longer than broad (CI 0.84-0.90); anterior margin of median clypeal lobe convex, conspicuously protruding; dorsolateral margination of pronotum usually blunt; mesonotum more steeply inclined than basal face of propodeum; petiole relatively robust (PLI 0.69-0.77) with a short anterior peduncle (Fig. 7, 53); head and mesosoma densely punctulate to coriarious-imbricate, and subopaque; standing pilosity conspicuous on most of the body including the outer faces of the tibiae, consisting largely of black hairs, those on the petiole and propodeum long (> 0.20 mm) and curved. Color varying from concolorous orange-brown to bicolored orange and black to (western Mexico) predominantly black with orange mottling on the head, mesosoma, and appendages.

Taxonomic comments.—Among the *Pseudomyrmex* species recorded from swollen-thorn acacias, *P. nigropilosus* is easily identified by its elongate eyes and head (REL 0.55-0.59, CI 0.84-0.90), short petiole (PLI 0.69-0.77), and conspicuous black pilosity (Fig. 7). Kempf (1958) provides further descriptive details.

Distribution and biology.—*P. nigropilosus* is found from Nayarit, western Mexico to Guanacaste Province, Costa Rica, and is restricted to nesting in swollen-thorn acacias (including *Acacia collinsii*, *A. cornigera* and *A. hindsii*). It is a member of the *P. gracilis* group and therefore not closely related to the principal group of acacia-ants (*P. ferrugineus* group). Janzen (1975) points out that *P. nigropilosus* is essentially a parasite of the *Pseudomyrmex*/*Acacia* mutualism. It occupies abandoned or otherwise uninhabited plants and reaps the benefits of this association without protecting the acacia from herbivores or competing plants. Additional information about the ecology of this species is given in Janzen (1975).

Pseudomyrmex opaciceps Ward, sp. nov.
(Fig. 5)

Holotype worker.—GUATEMALA *Retalhuleu:* Puente Samala, 3.8 mi. NE San Felipe, 24.vii.1966, D. H. Janzen W006724966 (LACM). HW 1.43, HL 1.42, EL 0.85, PL 0.89, PH 0.39.

Paratypes.—Series of 11 workers with same data as holotype; large series of ca. 60 workers and 10 males with the same locality and collector as holotype but the following dates and collection numbers: 18.vii.1966 M002718966 (possibly mis-labelled - see below), 18.vii.1966 W002718966, 18.vii.1966 W004718966, 18.vii.1966 W005718966 (possibly mis-labelled - see below), 23.vii.1966 W002723966, 24.vii.1966 W001724966, 24.vii.1966 W003724966 (BMNH, LACM, MCZC, MZSP, PSWC, UCDC, USNM).

Additional non-type material.—Series of workers, queens, and males from six additional localities. MEXICO *Chiapas*: 94.5 mi. SE Tonola (D. H. Janzen). GUATEMALA *Retalhuleu*: 2 mi. N Puente Samala, 3.8 mi. NE San Felipe (D. H. Janzen); 3 mi. N Puente Samala, 3.8 mi. NE San Felipe (D. H. Janzen); 5 mi. W Retalhuleu, Hwy. CA-2 at Rio Nil

(D. H. Janzen); *Guatemala*: Ciudad de Guatemala (D. H. Janzen). EL SALVADOR *La Libertad*: Quezaltepeque (M. Irwin & D. Cavagnaro) (LACM, MCZC, PSWC).

Worker measurements (n=14).—HL 1.30-1.42, HW 1.33-1.43, MFC 0.040-0.058, CI 0.99-1.04, REL 0.57-0.61, REL2 0.56-0.61, OOI 0.14-0.68, VI 0.65-0.71, FCI 0.029-0.042, SI 0.46-0.50, SI2 0.77-0.88, FI 0.36-0.39, PDI 1.12-1.37, MPI 0.059-0.076, NI 0.65-0.70, PLI 0.42-0.47, PWI 0.38-0.43, PPWI 0.92-1.16.

Worker diagnosis.—With the traits of the *P. gracilis* group (see couplet 6 of key) and the following more specific features. Head about as broad as long; anterior margin of median clypeal lobe straight to weakly convex; pronotum with blunt dorsolateral margination; mesonotum more steeply inclined than basal face of propodeum; petiole long and slender (see PLI and PWI values) with a distinct anterior peduncle (Fig. 6); head densely punctulate-coriarious and matte; standing pilosity abundant, pale silvery-white, not black. Color: head and mesosoma dark brown to black, mandibles and appendages lighter brown; petiole, postpetiole and gaster a contrasting pale luteous brown or orange-brown. Portions of the fronto-clypeal complex, malar area, and mandibles may also be luteous brown.

Taxonomic comments.—This species is distinguished from the closely related and sympatric *P. gracilis* by a modest but consistent difference in head sculpture. In workers and queens of *P. opaciceps* the punctulate-coriarious sculpture and associated dense pubescence obscure the sheen of the head, producing a matte appearance under soft light, while in *P. gracilis* the head remains at least weakly shining. In addition the workers and queens of *P. opaciceps* average smaller in size than those of *P. gracilis* and they have a more slender petiole (PLI < 0.48; see Figs. 5, 6, 53). Finally, *P. opaciceps* has a distinctive and largely invariant color pattern: the pale yellow or orange-brown petiole, postpetiole and gaster contrast with the much darker head and mesosoma. This is not observed in Central American *P. gracilis*, although a similar color pattern occurs in some Colombian populations of *P. gracilis*, and it also seen in some individuals of the more distantly related South American species *P. venustus* (F. Smith).

Among the *P. opaciceps* paratypes in LACM, the pinned specimens with Janzen collection numbers M002718966 and W005718966 appear to have been mis-labelled. In the Janzen alcohol collection samples M002718966 and W005718966 contain colony series of two quite different species (in the *P. ferrugineus* and *P. pallidus* groups, respectively); but there are two other alcohol samples from the same date and locality (W002718966 and W004718966) which are of *P. opaciceps*. I conclude that a frame-shift occurred in the process of labelling the pinned series of specimens, producing the labelling error (this has happened to a substantial number of *P. ferrugineus* group collections - see "Materials and Methods" section). The remaining paratype (and non-type) material of *P. opaciceps* appears to be correctly labelled.

Biology.—*P. opaciceps* is evidently a generalist twig-nesting *Pseudomyrmex*, but Janzen also collected it from an *Acacia cornigera* tree overgrown by vines and unoccupied by the *P. ferrugineus* group (5 mi. W Retalhuleu, Guatemala, collection numbers M010714966-A and M010716966-D).

Pseudomyrmex reconditus Ward, sp. nov.
(Fig. 8)

Holotype worker.—NICARAGUA, *Madriz*: 2.0 mi. S Honduran border, Hwy 1, 840m, 29.vii.1967, mi. 8207.2, D. H. Janzen, ex *Acacia collinsii* (LACM).

Paratypes.—One worker, one dealate queen, same data as holotype (LACM).

Holotype and paratype worker measurements.—HL 1.54, 1.44, HW 1.54, 1.47, MFC 0.071, 0.056, EL 0.93, 0.86, PL 0.88, 0.78, PH 0.57, 0.47, CI 1.00, 1.02, OI 0.52, 0.52, REL 0.61, 0.59, REL2 0.61, 0.58, OOI -0.01, -0.01, VI 0.73, 0.71, FCI 0.046, 0.038, SI 0.47, 0.47, FI 0.44, 0.39, PDI 1.21, 1.12, MPI 0.067, 0.061, NI 0.62, 0.64, PLI 0.64, 0.60, PWI 0.57, 0.53, PPWI 1.40, 1.25.

Paratype queen measurements.—HL 1.79, HW 1.66, MFC 0.065, EL 1.02, PL 1.21, PH 0.75, CI 0.92, OI 0.51, REL 0.57, REL2 0.62, OOI 0.22, VI 0.79, FCI 0.039, SI 0.45, FI 0.46, NI 0.61, PLI 0.62, PWI 0.61, PPWI 1.53.

Worker diagnosis.—With the traits of the *P.*

gracilis group (see couplet 6 of key) and the following more specific features. Head as broad as long; anterior margin of median clypeal lobe slightly convex, rounded laterally; pronotum with blunt dorsolateral margination; mesonotum more steeply inclined than basal face of propodeum; petiole of moderate length, high (PLI 0.60-0.64), with a distinct anterior peduncle but without a well developed anteroventral tooth (Figs. 8, 53), and lacking sharp dorsolateral margination; postpetiole notably broader than long. Mandibles weakly striolate, sublucid, becoming shagreened basally; head and mesosoma densely but finely punctulate-coriarious to coriarious-imbricate, subopaque; petiole, postpetiole, and gaster with fine piligerous punctures, obscured from view by the associated pubescence. Standing pilosity only moderately dense but with some apparent loss due to abrasion of the type specimens; hairs mostly black, not silvery-white, present on the head, mesosoma dorsum, petiole, and postpetiole; at least some moderately long (0.23-0.27 mm) hairs on the propodeum and petiole; one or two short hairs present on the outer faces of the meso- and meta-tibiae, the others possibly worn off; fine appressed golden pubescence present on most of the body. Head and mesosoma black, gaster dark brown, petiole and postpetiole orange; appendages brown, with orange flecking on the legs.

Taxonomic comments. This species is known only from the types. It is readily distinguished from all other acacia-associated species in the *P. gracilis* group by the combination of broad head (see CI values), robust petiole (PLI 0.60-0.64), and black pilosity. *P. reconditus* is similar to an undescribed *Pseudomyrmex* species collected from *Tachigali* in northern Peru (P. sp. PSW-35) but the latter has a shorter petiole, more extensive silvery-white pilosity and pubescence, and is all black in color.

Biology.—The type collection from *Acacia collinsii* is the only record. A single worker of *P. nigropilosus* occurred in the same alcohol vial as the workers and queen of *P. reconditus*. It remains to be confirmed that *P. reconditus* is confined to nesting in swollen-thorn acacias.

Pseudomyrmex simulans Kempf 1958 (Fig. 9)

Pseudomyrmex simulans Kempf 1958:459. Holotype worker, Tumba Muerta Road, Panama (W. M. Wheeler) (MCZC) [Examined].

Worker diagnosis.—With the traits of the *P. gracilis* group (see couplet 6 of key) and the following more specific features. Head longer than broad (CI 0.86-0.90); anterior margin of median clypeal lobe straight to broadly convex, rounded laterally; pronotum with sharp dorsolateral margination; mesonotum more steeply inclined than basal face of propodeum; petiole relatively short and high (PLI 0.61-0.66), with a distinct anterior peduncle (Figs. 9, 53), and with moderate dorsolateral margination; head and mesosoma finely punctulate-coriarious to coriarious-imbricate, subopaque; standing pilosity rather short, pale and inconspicuous, present on the mesosoma dorsum and (usually) outer surfaces of the tibiae, but sometimes lacking or worn off on the latter; fine appressed pubescence on most of body; dark brown-black in color, distal portions of appendages lighter; mandibles luteous.

Taxonomic comments.—This curious species bears a superficial resemblance to the obligate acacia-ants (*P. ferrugineus* group), although its affinities to other *P. gracilis* group species are clear from eye size, pilosity, palp formula, mesosomal structure, and male genitalia. *P. simulans* can be recognized by the combination of elongate eyes (REL 0.52-0.55), short petiole (PLI 0.61-0.66), short inconspicuous pilosity, and black color.

Distribution and biology.—*P. simulans* is known only from a few collections, all from swollen-thorn acacias (*A. collinsii*), in Panama (Canal Zone and the provinces of Veraguas, Los Santos and Panamá). Nothing has been published about its nesting biology or behavior, but Janzen's field notes indicate that the workers are more timid than those of the *P. ferrugineus* group. One might surmise that its habits are similar to those of *P. nigropilosus*, although the two species do not appear to be one another's closest relatives (Ward 1991).

Pseudomyrmex subtilissimus (Emery 1890)

Pseudomyrma subtilissima Emery 1890:65. Lectotype worker, Alajuela, Costa Rica (Alfaro)

(MCSN) [Examined].
Pseudomyrmex subtilissimus (Emery 1890); Kempf 1972:224.

Worker diagnosis.—A member of the *P. subtilissimus* group, and immediately distinguishable from all other acacia-associated *Pseudomyrmex* by its small size (HW < 0.60), elongate head (CI < 0.66), apedunculate petiole, and scarcity of standing pilosity. See Ward (1989:432) for further discussion of this species.

Distribution and biology.—*P. subtilissimus* has been collected only in Nicaragua and Costa Rica. What little is known about its biology suggests that it is a timid, non-protective species living in the thorns of *Acacia* plants occupied by (declining?) colonies of *P. flavicornis*.

PHYLOGENY AND BIOGEOGRAPHY OF THE OBLIGATE ACACIA-ANTS

The 47-character data set used for cladistic analysis of the *P. ferrugineus* group is given in Table 2. Implicit enumeration by Hennig86, using the ie* command, yielded a single most parsimonious tree of length 73, consistency index 0.86 (0.84 excluding autapomorphies of ingroup species) (Fig. 73). This tree has an unresolved trifurcation involving five *Pseudomyrmex* species: *ferrugineus*, *janzeni*, and (*flavicornis* + (*mixtecus* + *veneficus*)). These five species together constitute what may be termed the *P. ferrugineus* complex. It is allied to the pair of sister species, *P. spinicola* and *P. satanicus*. The sister group of these seven species is the isolated and autapomorphous *P. peperi*. Finally, *P. nigrocinctus* and *P. particeps* make up a basal pair of species with relatively unspecialized morphology.

Separate analyses of worker-, queen-, and male-based data sets produced trees in substantial agreement with these findings and largely congruent with one another (Figs. 74-76). This indicates that some confidence can be attached to the main features of the cladogram, and that homoplasy in worker and queen morphology — possibly due to parallel selection pressures during diffuse coevolution of the ant/acacia interaction (see below) — has not been so rampant as to obscure all evidence of relationship, since both castes point to a cladistic pattern similar to that derived from male morphology (primarily male genital characters). Disagreement revolves around the position of taxa within the *P. ferrugineus* complex. Worker morphology suggests that *P. mixtecus* is more closely related to *P. flavicornis* than to *P. veneficus*. The male character set supports a (*P. mixtecus* + *P. veneficus*) pairing and is uninformative about other relationships within the *P. ferrugineus complex*. The queen-based tree is identical in topology to that based on all characters, i.e. it supports (*P. flavicornis* + (*P. mixtecus* + *P. veneficus*)) but does not resolve relationships among *P. ferrugineus*, *P. janzeni*, and the foregoing trio.

The inferred phylogeny of the *P. ferrugineus* group (Fig. 73) suggests that speciation has occurred primarily as a consequence of geographical isolation. Of the three pairs of sister species, two (*P. nigrocinctus* + *P. particeps*, *P. mixtecus* + *P. veneficus*) are composed of allopatric species (Figs. 69, 72), while the ranges of the third pair (*P. spinicola* and *P. satanicus*) are more or less contiguous (Fig. 68). The trio of species comprising (*P. flavicornis* + (*P. mixtecus* + *P. veneficus*)) also have entirely non-overlapping distributions, and they point to the importance of geographical barriers in southwestern Mexico to speciation in this complex (Fig. 69). This is also indicated by the distributions of *P. ferrugineus* and *P. janzeni*, the latter an allopatric isolate in western Mexico (Fig. 70), although it should be noted that the cladistic analysis did not confirm a sister group relationship between these two phenetically similar species. At higher levels in the cladogram there is some geographical overlap between taxa, but dispersal has not been so extensive as to obliterate all evidence of vicariance. Within the *P. ferrugineus* complex, for example, *P. flavicornis* and relatives are largely confined to the Pacific slopes of Mesoamerica in contrast to the more eastern distribution of *P. ferrugineus* (Figs. 69-70). The *P. ferrugineus* complex itself is centred in northern Central America, with only one species (*P. flavicornis*) occurring south of Honduras, as far as Costa Rica in this case, while its sister group (*P. spinicola* and *P. satanicus*) occurs primarily south of Honduras and extends all the way to northern Colombia (Fig. 68). This suggests an historical barrier somewhere in the region of present day

Honduras or Nicaragua which split these two clades. The most basal divisions within the *P. ferrugineus* group involve much more extensive geographical overlap, making any historical inferences difficult. The distributions of the species *P. peperi* and *P. nigrocinctus* are consistent with an origin and early diversification of the *P. ferrugineus* group in either northern or central Mesoamerica. The timeframe for this is unknown but presumably occurred prior to the formation of the Panamanian land bridge (i.e. before early Pliocene or late Miocene). Early diversification in the group may have been encouraged by the presence of an island archipelago in the region (Donnelly 1992).

Finally, we come to the question of whether the phylogenies of the acacia-ants and their host acacias are congruent. A phylogeny of the swollen-thorn acacias is not available but Janzen's (1974) revision contains some relevant information. Janzen (1974) concluded that the Central American swollen-thorn acacias are polyphyletic, i.e. that myrmecophytism arose more than once or that non-myrmecophytic acacia species independently acquired myrmecophytic traits through hybridization. He also noted (Janzen 1966) that individual species of acacia can be associated with more than one *Pseudomyrmex* species and vice versa. None of this leads one to expect a pattern of co-speciation, and mapping known host associations on the *Pseudomyrmex* cladogram (Fig. 73) confirms the opportunistic nature of the interaction. It seems that most species in the *Pseudomyrmex ferrugineus* group occupy any swollen-thorn acacia species available to them. On the other hand, the possibility of locally non-random associations between ants and available plants, perhaps mediated by competition, deserves investigation.

Three species of acacia-ants, *P. janzeni*, *P. particeps* and *P. satanicus*, are confined to a single acacia species (*A. hindsii*, *A. allenii* and *A. melanoceras*, respectively), the former (*P. janzeni*) almost certainly because of its limited geographical distribution but the last two because of their apparent specialization on the acacia or the forest habitat to which it is restricted. Populations of other swollen-thorn acacia species occur within the probable dispersal ranges of alate queens of *P. particeps* and *P. satanicus* but are apparently not colonized. These two host-specific *Pseudomyrmex* have the smallest ranges of any members of the *P. ferrugineus* group and are clearly the most endangered.

CONCLUDING REMARKS

Table 2. Data set used for cladistic analysis of the *Pseudomyrmex ferrugineus* group. *P. fervidus* served as outgroup (see text). "?" signifies polymorphism or ambiguity in expression of the character state. Characters 12, 13 and 16 were considered unordered.

	1	11	21	31	41
fervidus	0000000000	??00000001	?000?00000	0000000000	0000?0
nigrocinctus	0001000001	1021000010	0011001000	0001110010	1001101
particeps	0001000001	1021000011	0010001100	0001110010	1001101
peperi	0011001121	2210020011	0011011001	0002100111	1112212
spinicola	1100101111	010010001?	1110?01110	0112100011	1212221
satanicus	1110111111	0100100011	1210201110	0112100011	1212221
ferrugineus	0000001111	0100001011	1110201010	0102101111	1222221
janzeni	0000001111	0100001010	1110201010	0102101111	1222221
flavicornis	0000001111	0100011012	1110201010	0102101111	1222221
mixtecus	0000001111	0100011012	1111111010	0102101121	1222221
veneficus	0000001111	0100001112	1111111010	0102101121	1222221

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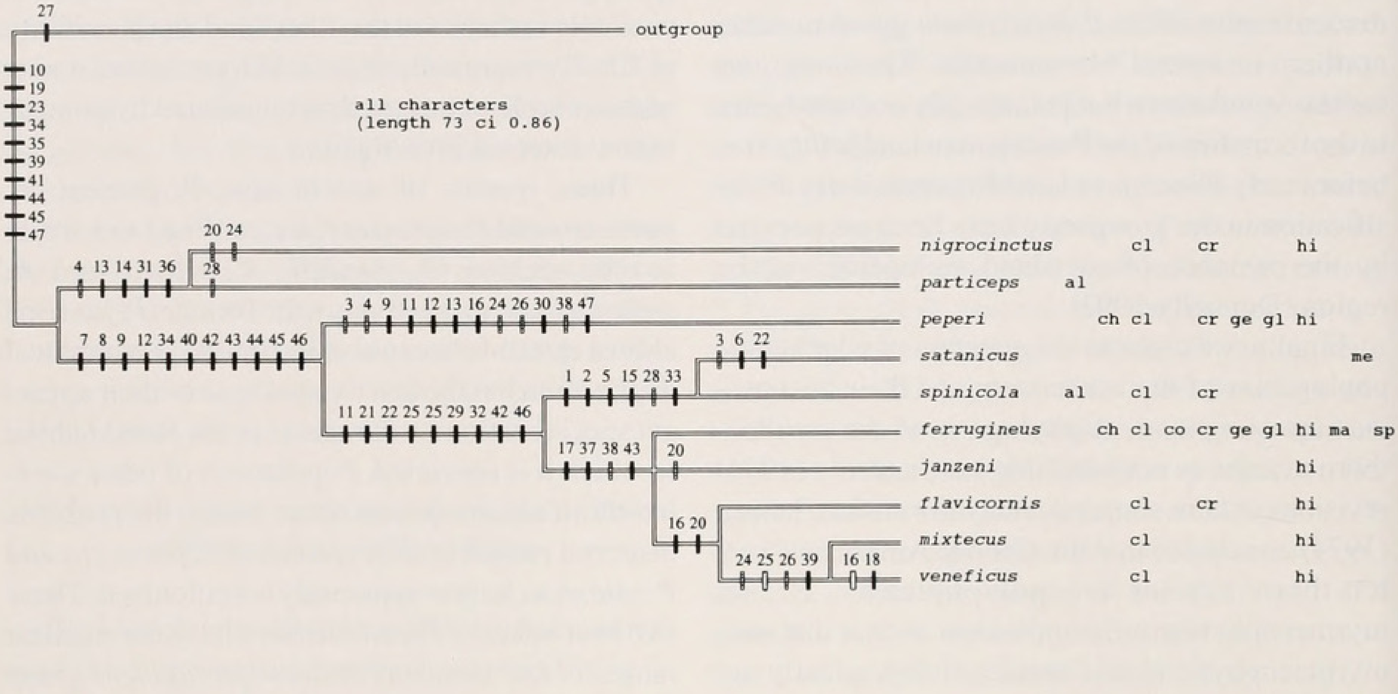

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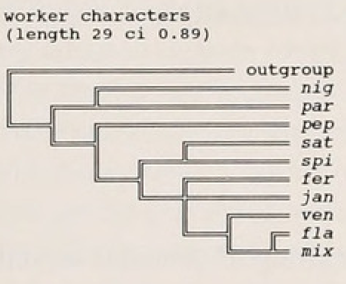
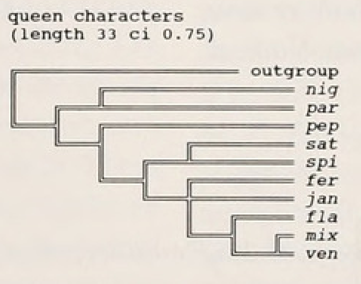
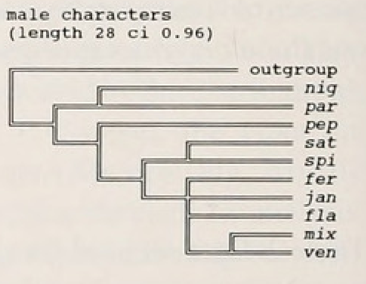


75



76



Figs 73-76. Phylogenetic relationships of the obligate acacia-ants, *Pseudomyrmex ferrugineus* group. 73: cladogram based on the entire 47-character data set (Table 2), with character state changes indicated and with host plant associations listed for each species. Solid bars: unique forward changes; hatched bars: homoplasious forward changes; open bars: reversals. There are alternative, equally parsimonious reconstructions of character state change for characters 4, 12, 16, 38 and 46. By reference to other *Pseudomyrmex* species, most changes occurring between the outgroup (*P. fervidus*) and the ingroup (i.e. changes in characters 10, 19, 23...47) are probably synapomorphies of the latter, but one character state (27.0) appears to be a derived feature of *P. fervidus*. The following abbreviations are used for host plants: al = *Acacia allenii*, ch = *A. chiapensis*, cl = *Acacia collinsii*, co = *A. cooki* and *A. janzenii*, cr = *A. cornigera*, ge = *A. gentlei*, gl = *A. globulifera*, hi = *A.hindsii*, ma = *A. mayana*, me = *A. melanoceras*, sp = *A. sphaerocephala*. 74-76: cladograms based on the worker, queen and male character sets, respectively.

This systematic study of *Pseudomyrmex* ants associated with swollen-thorn acacias in Central America demonstrates that the primary group of obligate acacia-ants (the *P. ferrugineus* group) is monophyletic and comprises 10 species. Four additional unrelated *Pseudomyrmex* species, from two other species groups, have become secondary specialists on the acacias. These latter species appear to be parasites or commensals but little is known about their biology (except *P. nigropilosus*). These 14 specialists are joined by at least six generalist twig-nesting *Pseudomyrmex* which occasionally colonize acacia thorns.

The well known mutualism between ants and Central American acacias applies with certainty only to members of the *P. ferrugineus* group and their associated plants. Within this group experimental evidence of a mutualism is available only for the *P. ferrugineus* x *A. cornigera* interaction (Janzen 1966, 1967b), although the biology and behavior of the other nine species of ants suggest that they also provide important protection to their host acacias under most conditions. Cladistic analysis of the *P. ferrugineus* group, coupled with a consideration of host plant associations, indicates a pattern of diffuse coevolution, not one-on-one cospeciation (see also Janzen 1966). It seems likely that the original obligate acacia-ant (the common ancestor of the *P. ferrugineus* group) underwent coevolution with its acacia host, but since then speciation and diversification of the two groups have been decoupled — the swollen-thorn acacias are apparently even polyphyletic (Janzen 1974) — and there has been much opportunistic pairing of ants and plants. Such liberal sharing of partners has presumably made the association susceptible to invasion by other *Pseudomyrmex* and *Acacia* lineages.

At the same time the key features of the system — absolute dependence of ants in the *P. ferrugineus* group on acacia plants, the reliance of at least some (probably most) of the swollen-thorn acacia species on ants for normal growth and reproduction, and the suite of mutually beneficial traits exhibited by both partners — mark this as one of the more impressive insect/plant mutualisms known.

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