

A new workerless social parasite in the ant genus *Pseudomyrmex* (Hymenoptera: Formicidae), with a discussion of the origin of social parasitism in ants

PHILIP S. WARD Department of Entomology, University of California at Davis

Abstract. The New World ant genus *Pseudomyrmex* (subfamily Pseudomyrmecinae) contains about 180 species, of which only one workerless social parasite, *P.leptosus*, from Florida, has been previously recorded. A new species discovered recently in northern Argentina, *P.inquilinus* sp. nov., is more derived morphologically and behaviourally than *P.leptosus* and has convergently developed features characteristic of the workerless inquilines known in other ant subfamilies. These features include diminutive size, reduced mouthparts, a broadened petiole and postpetiole, well-developed subpetiolar and subpostpetiolar processes, and the habit of straddling the gaster of the host queen. A cladistic analysis confirms that the new species is not closely related to its host nor to *P.leptosus*; it belongs in fact to a different species complex within the genus *Pseudomyrmex*. Two widespread Neotropical species, *P.fliformis* and *P.subater*, to which *P.inquilinus* appears to be related, show indications of being temporary social parasites on other, unrelated species of *Pseudomyrmex*. Thus, there is evidence from comparative natural history that the extreme social parasitism seen in the new species from Argentina was preceded by a period of temporary social parasitism, but 'Emery's Rule' – the claim that social parasites are close relatives of, and evolve from, their hosts – is not supported. Rather, parasitism in *Pseudomyrmex* seems to have arisen through interspecific colonization and exploitation of congeners. A review of the evidence suggests that Emery's Rule has received too uncritical an acceptance in the literature on social parasitism. Uncertainties about the generality of Emery's Rule and about the plausibility of achieving prezygotic isolation under sympatric conditions undermine the theory that social parasites evolve from within populations of their host species.

Introduction

One of the more intriguing phenomena in ants is the occurrence of species that depend upon the workers of other species for the provision of labour. Such social parasites include dulotic (slave-making) species that raid other ant nests for worker brood, and temporary social parasites whose colony-founding queens invade the nests of other species, kill the host queen, and use the workers as labourers until such time as their own worker brood has developed. In more extreme cases of permanent inquilinism, the invading queen produces sexual offspring only, typically allowing the host queen to survive and furnish a continuing supply of workers (Wilson, 1971; Buschinger, 1986; Hölldobler & Wilson, 1990). Instances of social parasitism have a patchy taxonomic and geographic occurrence, being well known among north temperate ants in the subfamilies Formicinae and Myrmicinae, but rather poorly

documented from other taxa and regions of the world (Wilson, 1984; Hölldobler & Wilson, 1990).

An important and largely unchallenged generalization about social parasitism has emerged: that there is a close phylogenetic relationship between the parasite and host species (Emery, 1909; Wasmann, 1909; Kutter, 1968; Buschinger, 1970, 1986, 1990; Heinze, 1991; Bourke & Franks, 1991). In a broad sense this is hardly disputable: most ant social parasites are either considered congeneric with their hosts or they have been artificially segregated into derivative 'satellite genera' that render the genus of the host species paraphyletic. But the close morphological resemblance between parasite and host has led to the stronger claim, known as Emery's Rule (Le Masne, 1956), that social parasites are more closely related to their hosts than to any other free-living taxa. To allow for the possibility of subsequent speciation in both the host and parasite lineages this rule can be stated as follows: for any monophyletic group of closely related social parasites the nearest non-

parasitic outgroup is a clade that includes the host species (Buschinger, 1990). This assumes, of course, that social parasitism is an irreversible trait, an assumption which appears reasonable at least for permanent social parasites.

The apparent veracity of Emery's Rule has in turn inspired the hypothesis that social parasites originate from their hosts by sympatric speciation (Buschinger, 1970, 1990; Bourke & Franks, 1991). This has been argued most cogently for workerless inquilines. Bourke & Franks (1991) present a model that posits a facultatively polygynous ancestral species exhibiting variation in queen size. Small queens (microgynes) come to specialize in the production of sexual offspring (i.e. they become intraspecific social parasites), and size-based assortative mating leads eventually to reproductive isolation between parasite and host. Apart from raising questions about the efficacy of disruptive selection in producing prezygotic isolation (cf. Rice & Hostert, 1994), this model and others like it (e.g. Buschinger, 1990) rest on the assumption that Emery's Rule is generally valid. Yet, there have been surprisingly few explicit phylogenetic tests of this assumption (Ward, 1989; Agosti, 1994).

This paper describes a new workerless social parasite in the Neotropical ant genus *Pseudomyrmex*. It is the second known example in its subfamily (Pseudomyrmecinae), and it is considerably more modified in appearance than the only other workerless inquiline heretofore recorded in the group. At the same time it provides an opportunity to determine whether Emery's Rule applies in this case, and to reexamine the applicability of the 'rule' to other taxa. The results caution against the uncritical acceptance of Emery's Rule and suggest the need to reevaluate the theory that social parasites evolve sympatrically from their hosts.

Materials and Methods

The new species described herein was discovered during fieldwork in northern Argentina, in late January and early February, 1995. Other species examined in this study were collected at various times during a long-term investigation of the genus *Pseudomyrmex* in the Neotropics. Material in museum collections has also been studied. The abbreviations for museum collections cited here are listed in Arnett *et al.* (1993) and Ward (1993).

Metric measurements were carried out as described in Ward (1989a, 1993). The following measurements and indices are used here: HW (head width), HL (head length), EL (eye length), EW (eye width), MFC (minimum distance between the frontal carinae), MD1 (basal width of the mandible), MD2 (width of mandible at the juncture of the basal and masticatory margins), MD3 (mandible length), EW (eye width), SL (scape length), FL (profemur length), FW (profemur width), PL (petiole length), PH (petiole height), DPW (dorsal petiolar width), MPW (minimum petiolar width), PPL (postpetiole length), PPW (postpetiole width), LHT (length of metatibia), CI (cephalic index: HW/HL), OI (ocular index: EW/EL), REL (relative eye length: EL/HL), REL2 (relative eye length, using HW: EL/HW), FCI (frontal carinal index: MFC/HW), SI (scape

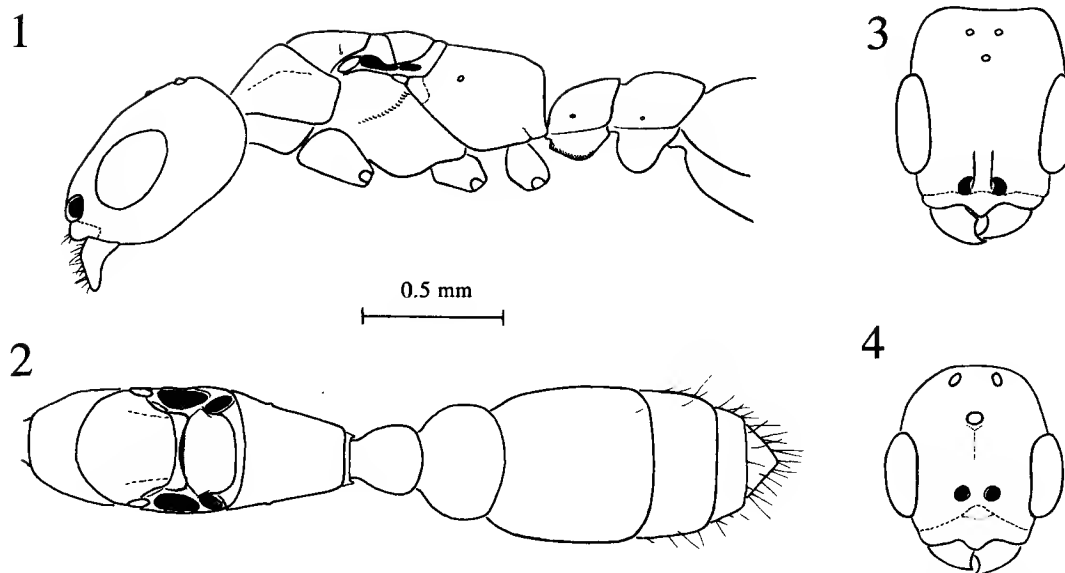
Table 1. Data set used for cladistic analysis of *Pseudomyrmex inquilinus* and other taxa. '?' signifies unknown, polymorphic or inapplicable. See text for description of character states.

| | 00000 12345 | 00001 67890 | 11111 12345 | 1111 6789 897 |
|------------------------------------|----------------|----------------|----------------|---------------------|
| <i>Tetraponera</i> | 0000? | 0000? | 00000 | 00?0 |
| <i>Pseudomyrmex inquilinus</i> | 1100? | ?2011 | 00001 | 0100 |
| <i>Pseudomyrmex subater</i> | 01100 | 12011 | 00001 | 1201 |
| <i>Pseudomyrmex duckei</i> | 01100 | 10010 | 00001 | 1201 |
| <i>Pseudomyrmex filiformis</i> | 01100 | 01010 | 00001 | 0000 |
| <i>Pseudomyrmex oki</i> | 01110 | 00010 | 11100 | 0010 |
| <i>Pseudomyrmex gebelli</i> | 01111 | 01010 | 11100 | 0010 |
| <i>Pseudomyrmex pallidus</i> group | 01111 | 01010 | 12110 | 0010 |
| <i>Pseudomyrmex viduus</i> group | 01100 | ?011? | 00000 | 0000 |

index: SL/HW), FI (profemur index: FW/FL), PLI (petiole length index: PH/PL), PWI (petiole width index: DPW/PL), and PPWI (postpetiolar width index: PPW/PPL). For further details see Ward (1989a).

The procedure used for cladistic analysis was as follows. A data set of nineteen characters was developed for the social parasite, its host species, and allied taxa. Further discussion of the choice of terminal taxa, including the outgroup, appears later in this paper (under 'Phylogenetic affinities of *Pseudomyrmex inquilinus*'). Emphasis was placed on features previously found to be useful at the species and species group level in *Pseudomyrmex* (Ward, 1989a, 1991, 1993). The characters and character states used for cladistic analysis are listed below, and the data matrix is given in Table 1. The data set was analysed using HENNIG86, version 1.5 (Farris, 1988).

1. Queen and male: mandible, masticatory margin (0) straight, dentate, (1) concave, edentate (Figs 3 and 4).
2. Queen and worker: mandible, ventral ridge (0) absent, (1) present.
3. Queen and worker: basal margin of mandible, proximal tooth (0) absent, (1) present.
4. Queen and worker: median clypeal lobe, laterally (0) rounded, (1) angulate.
5. Worker: standing pilosity on mesosoma dorsum (0) common (> 11 setae visible in profile), (1) sparse (< 9 setae visible in profile).
6. Worker: standing pilosity on mesosoma (0) sparse to common, not underlain by dense subdecumbent pilosity, (1) abundant, and underlain by dense subdecumbent pilosity, which gives worker a 'scruffy' appearance.
7. Queen: standing pilosity on dorsum of body (0) common, conspicuous in profile on head, mesosoma, petiole and postpetiole, (1) sparse: 2–3 pairs of setae on pronotum, none visible in profile on propodeum, 1–3 pairs on petiole and postpetiole, (2) very sparse, absent from pronotum, propodeum, petiole and postpetiole.
8. Queen and worker: standing pilosity on extensor faces of mid- and hind-tibiae (0) sparse (fewer than 8 standing hairs), (1) common (> 10 hairs).
9. Queen and worker: hind basitarsal sulcus (0) present, (1) absent.



Figs 1–4. *Pseudomyrmex inquilinus*, sp. nov. Fig. 1, lateral view of holotype queen (excluding appendages and most of gaster); Fig. 2, dorsal view of holotype queen, excluding head; Fig. 3, full-face, dorsal view of head, excluding antennae, holotype queen; Fig. 4, same, paratype male.

10. Queen: profemur (0) relatively broad ($FI \geq 0.42$), (1) slender ($FI < 0.42$).

11. Male: posterolateral corners of sterna VI, VII and VIII (0) rounded, not produced, (1) angulate and produced ventrally.

12. Male: pygidium, posterior margin (0) directed posteroventrally, not notably recurved, (1) recurved, directed ventrally, (2) strongly recurved, forming an anteroventrally directed pocket.

13. Male: paramere, mesal dorsoventral lobe (0) attached continuously to inner wall of paramere, (1) in the form of an isolated digitiform structure attached to inner wall of paramere at base only (Fig. 14).

14. Male: paramere, large thin posterodorsal lobe (0) absent, (1) present (Figs 13 and 14).

15. Male: paramere, distal end, inner face (0) without a dorsomesally or posterodorsomesally directed, irregular concavity, bordered anteriorly by a mesal dorsoventral lobe which is connected by a low saddle to the highest point of the posterodorsal ridge, (1) of such a form (Figs 15, 17, 19, 21).

16. Male: paramere, distal end (0) highest point of posterodorsal ridge not developed as truncate, subconical protrusion (as seen in lateral profile), (1) so developed (Figs 7, 9).

17. Male: paramere, distal end (0) without broadly rounded (semicircular) distal extremity, (1) of such a form (Figs 7, 9).

18. Male: aedeagus, outer face (0) without an anterodorsal to posteroventral impression, bordered anteriorly by an oblique ridge and posteriorly by a carina or lamella that terminates near a small incision or tooth on the posterior margin of the aedeagus, (1) of such a form, the posterior border a denticulate carina which does not cover most of the posterior margin, in lateral view, (2) of such a form, the posterior border a lamella which forms most of the posterior margin.

19. Male: aedeagus, posterior margin, (0) entire or with at

most a single distinct tooth, (1) with several (six) to many teeth (Fig. 24).

Where characters varied within one of the supraspecific taxa (*P. pallidus* group, *P. viduus* group and genus *Tetraponera*) they were coded as unknown, except for character 4 (the shape of the median clypeal lobe). For this character the groundplan of the *P. viduus* group was inferred to be state 0, and the angulate condition seen in one derivative and nonbasal species, *P. tachigaliae*, is presumed to be derived within the group.

Descriptive taxonomy

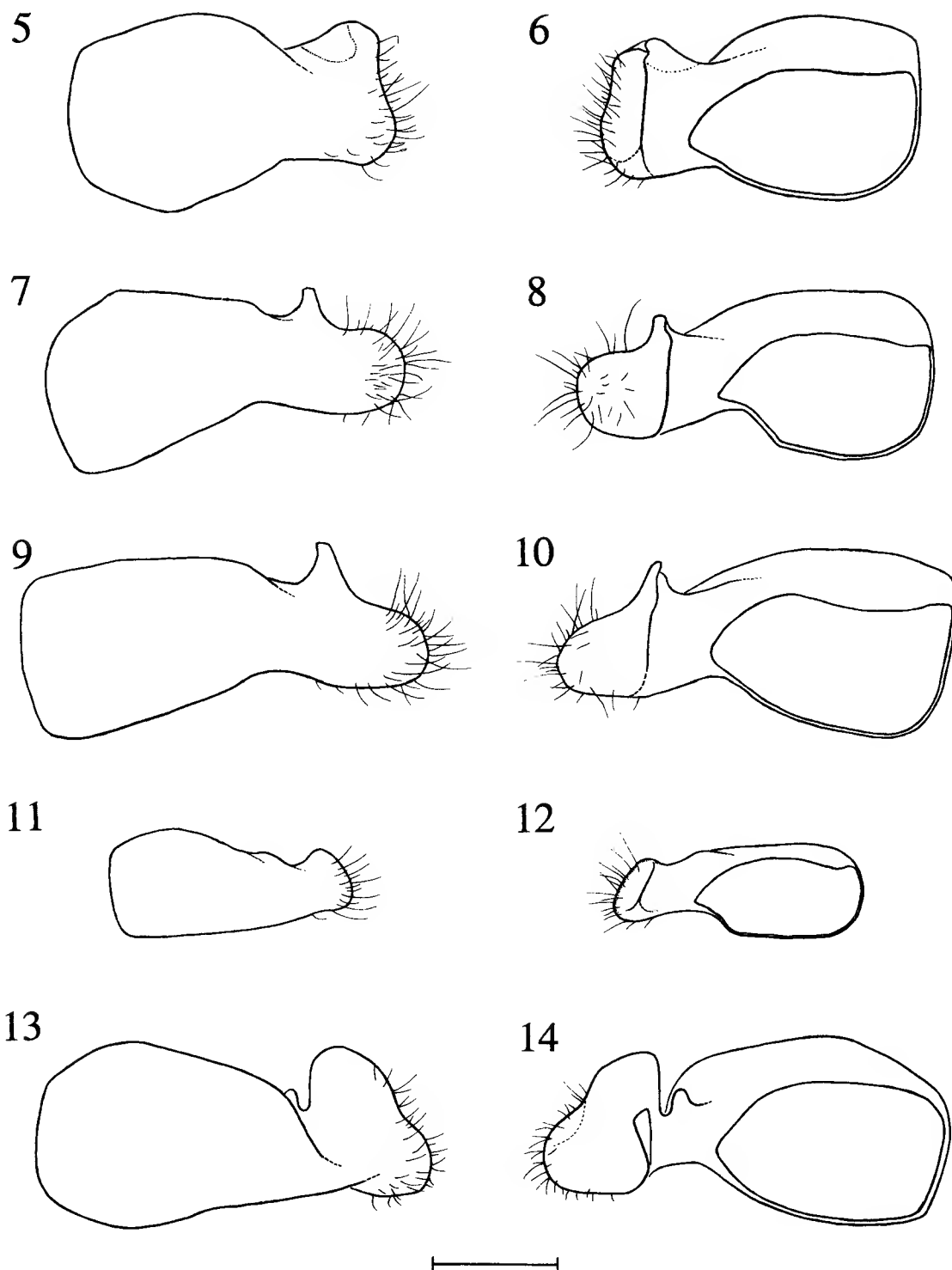
Pseudomyrmex inquilinus, sp. n. (Figs 1–4, 11, 12, 21, 22)

Holotype queen. ARGENTINA, Catamarca: Santa Maria, 2000 m, 26°42'S, 66°03'W, 2 February 1995; P. S. Ward acc. no. 12845; in nest of host species, *Pseudomyrmex* sp. PSW-64 (Ward acc. no. 12844), in dead twig of *Baccharis* sp. HW 0.63, HL 0.74, EL 0.36, LHT 0.48. (MCZC)

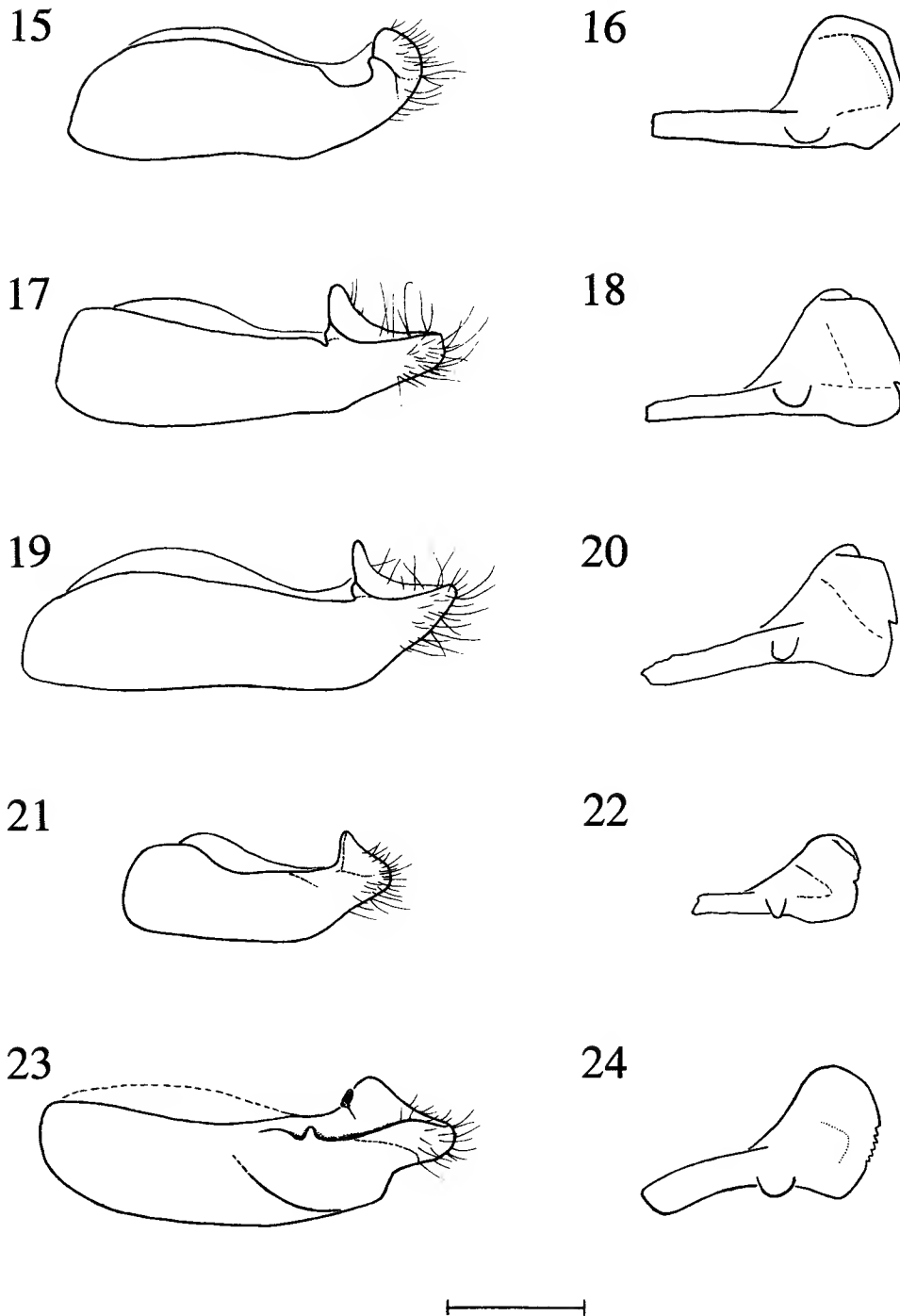
Paratypes. Series of (i) eight queens and one male from same host nest as the holotype (ii) two queens from a second nest, same host species, locality and date. (BMNH, IMLA, LACM, MZSP, PSWC)

Queen measurements ($n = 7$). HW 0.63–0.65, HL 0.74–0.78, EL 0.36–0.38, DPW 0.29–0.33, PPW 0.41–0.46, LHT 0.47–0.50, CI 0.83–0.87, OI 0.60–0.62, REL 0.49–0.50, REL2 0.57–0.59, FCI 0.091–0.115, SI 0.40–0.45, FI 0.37–0.40, PLI 1.12–1.27, PWI 1.08–1.20, PPWI 1.65–1.83.

Description, queen. Of diminutive size for the genus *Pseudomyrmex* (HW < 0.68, LHT < 0.52). Mandible relatively broad (MD2/MD3 ≈ 0.55), with basal and external margins subparallel (MD1/MD2 ≈ 0.96); basal and masticatory margins distinctly differentiated, the former lacking teeth or denticles,



Figs 5–14. *Pseudomyrmex* males, left parameres, lateral (left) and mesal (right) views. Figs 5–6, *P. filiformis* (Peru); Figs 7–8, *P. duckei* (Panama); Figs 9–10, *P. subater* (Panama); Figs 11–12, *P. inquilinus* (Argentina); Figs 13–14, *P. sp.* PSW-64 (Argentina). Scale line equals 0.25 mm for Figs 5–8, 13–14, and 0.20 mm for Figs 9–12.



Figs 15–24. *Pseudomyrmex* males, dorsal views of left paramere (left) paired with left lateral views of the aedeagus (right). Figs 15–16, *P. filiformis*; Figs 17–18, *P. duckei*; Figs 19–20, *P. subater*; Figs 21–22, *P. inquilinus*; Figs 23–24, *P. sp.* PSW-64. These are the same males depicted in Figs 5–14. Scale line equals 0.25 mm for Figs 15–18, 23–24 and 0.20 mm for Figs 19–22.

except for an acute apicobasal tooth; masticatory margin strongly concave and essentially edentate (Fig. 3), at best very weakly crenulate, with a small denticle, discernable only at high magnification, at about two thirds of the distance between the apicobasal tooth and the apical tooth. Closed mandibles

with a gap (0.03–0.04 mm wide) between the midpoints of their masticatory margins as a consequence of the aforementioned concavity. Palp formula 3,2. Median clypeal lobe broadly rounded, and lacking a distinctive transverse truncation on the upper surface (typical of nearly all other *Pseudomyrmex* – see

Ward, 1990). Frontal carinae well separated, the distance between them subequal to the maximum scape width (FCI ≈ 0.10). Head moderately elongate (CI 0.83–0.87), with weakly convex sides and a straight to shallowly concave posterior margin, in frontal view (Fig. 3). Evidently fully winged: all known specimens dealate, with a full complement of thoracic sclerites (and queen pupa seen to have wings). Metapleural gland opening and bulla reduced, inconspicuous. Legs relatively short, the profemur in particular small and slender (FL 0.44–0.46, FI 0.37–0.40). Meso- and metatibiae each with a pair of apical spurs, the posterior one of each pair conspicuously pectinate. In dorsal view propodeum subtrapezoidal, the sides converging posteriorly; in lateral view, the basal (dorsal) face of propodeum with a long weakly declining surface, followed by a shorter steeper portion, which is nevertheless well differentiated from the short, vertical declivitous face of the propodeum (Fig. 1). Petiole short, broad, apedunculate, submarginate laterally, and with a large conspicuous ventral keel that protrudes posteroventrally (Fig. 1). Dorsal face of petiole flat, with a slight median depression; posterior face absent, owing to an expanded helcium. Postpetiole short and broad, with a bulging ventral protrusion that is thick and wide, not keel-like. Remainder of gaster about the same length as the mesosoma.

Mandible sublucid, with very weak, almost obsolete, transverse striolae. Head moderately shiny, with numerous punctulae, about 0.01 mm in diameter or less, separated by one to several diameters, on a finely coriaceous background sculpture. Mesoscutum and mesoscutellum similarly sculptured, punctures more scattered; in contrast, pronotum, propodeum and petiole densely coriaceous-reticulate, and subopaque, especially the propodeum; episternum and sides of pronotum less strongly sculptured. Postpetiole and gaster sublucid, with scattered, very fine punctures on a weakly coriaceous background.

Standing pilosity very scarce, essentially absent from the scapes (except apex), head capsule (above the clypeus), mesosoma, legs, petiole, postpetiole and fourth abdominal (first gastric) tergite. A single short seta present consistently on each side of the mesoscutum, near the lateral margin. Gastric pilosity beginning on the fifth abdominal tergite (or on the posterior margin of the fourth), and becoming long and dense near the apex (Fig. 2). Very fine, short, submicroscopic pubescence present on much of the body but scarcely visible at normal magnification (50–100 \times). Body orange–brown, mesoscutellum and metanotum with variable darker infuscation; mandibles, clypeus and gula pale yellow–brown.

Description, male. Mandibles similar to those of queen; masticatory margin edentate and with same peculiar concave edge, although not as pronounced (Fig. 4). Palp formula 3,2 as in queen. Head broad (HW 0.65, CI 0.96), and posterior margin very rounded (Fig. 4). Eyes and ocelli not strongly protruding from head capsule. Scape short, subequal in length to second funicular segment. Total length of antenna about 1.4 mm. Propodeum, petiole and postpetiole similar to those of queen, but less extreme in shape: propodeal faces less distinct, petiole and postpetiole less broad, and petiole less strongly margined. Subgenital plate much wider than long, its

posterior margin shallowly and broadly concave. Pygidium with a truncate posterior margin, not recurved anteroventrally. Paramere as in Figs 11, 12, 21; mesal dorsoventral lobe developed as an oblique, rounded, dorsomesal protrusion, joined through a low saddle to a posterodorsal ridge, the surface between the two concave and directed posterodorsomesally (Fig. 21). Aedeagal plate simple, somewhat circular in outline, outer margin entire except for a weak medial incision and one or two adjacent, very small denticulae. Outer surface of aedeagus with a broad oblique impression (anterodorsal to posteroventral), bordered on either side by corresponding weak ridges, the anterior ridge situated about midway between the posterior margin and the lateral apodeme, the posterior ridge merging with the posterior margin above the level of the aforementioned incision (Fig. 22). Body sculpture paralleling that of queen, but integument a little less shiny; subopaque, shagreened areas on the head between the antennal insertions and in the ocellar triangle; mesoscutum and mesoscutellum with coarser sculpture than in queen. Standing pilosity very scarce, distributed as in the queen. Pubescence slightly more noticeable than in queen, but still rather inconspicuous. Dark brown, with paler, transverse yellow–brown bands on the posterior margins of the gastric segments; mandibles, fronto-clypeal complex, gula and forecoxa contrastingly pale, almost white; antennae and legs light brown.

Worker. The worker caste is unknown and probably non-existent.

Comments. The queen of this species is immediately distinguishable from all known congeners by any one of the following features: the concave and edentate masticatory margin of the mandibles, the reduced palp formula (3,2), the shape of the petiole (especially the lack of a posterior face), shape of the postpetiole (short, broad and deep), and the lack of standing pilosity on nearly all parts of the body except the mouthparts and apex. Also distinctive are the edentate basal margin of the mandible, the lack of a transverse truncation on the median clypeal lobe, the well separated frontal carinae, the slender forefemur, the short legs, and the long basal face of the propodeum. The male is diagnosable by the mandible shape, palp formula, lack of a posterior face on the petiole, highly reduced standing pilosity, and the male genitalia (see description above).

Host species. Based on worker and queen morphology, as well as male genitalia, the host species is easily recognizable as a member of the *P. pallidus* group (diagnosis in Ward, 1989a). Within this group it belongs to a taxonomically vexing assemblage of species that may be termed the *P. flavidulus* complex. Members of this complex are characterized by the following combination of character states: male paramere with large posterodorsal lobe preceded anteriorly by a much smaller finger-like lobe (Figs 13 and 14); abdominal tergite IV of worker and queen densely pubescent; head relatively elongate (worker CI ≤ 0.90); worker profemur relatively slender (worker FI ≤ 0.47); and worker and queen predominantly orange or orange–brown in colour. There are several species within the *P. flavidulus* complex, but the limits of intra- and interspecific variation are not yet clear. For the moment the host species is referred to using a code number, *Pseudomyrmex* sp. PSW-64.

Table 2. Contents of two nests of *Pseudomyrmex* sp. PSW-64 occupied by the parasitic species, *P.inquilinus*.

| | Nest no. 12841 | Nest no. 12844 |
|----------------|----------------|----------------|
| Host species | | |
| Dealate queens | 1 | 1 |
| Workers | 19 | 22 |
| Alate queens | 5 | 0 |
| Alate males | 3 | 6 |
| Worker pupae | 2 | present |
| Queen pupae | 8 | 0 |
| Male pupae | present | 24 |
| Parasite | | |
| Dealate queens | 2 | 9 |
| Alate males | 0 | 1 |
| Queen pupae | 1 | 0 |
| Queen prepupae | 4 | 0 |
| Indeterminate | | |
| Eggs, larvae | present | present |

As currently interpreted this species is known only from Catamarca and Tucumán provinces in Argentina, although a related (and possibly conspecific) form occurs in Bolivia. The *flavidulus* complex as a whole is widely distributed and common in the Neotropics, from Costa Rica to Argentina.

Biology, behaviour. The host species was found nesting in dead stems of *Baccharis salicifolia* and a second *Baccharis* species, probably *B.angulata*, in pastured riparian grassland next to the Río Santa María. The *Baccharis* species are dominant in this community; other plants include *Salix humboldtiana*, *Prosopis*, *Juncus*, and various grasses. The town of Santa María has an average annual rainfall of 182 mm and is located in the Argentinian desert biome known as *monte* (Morello, 1958).

Pseudomyrmex inquilinus queens were recovered from two out of six nests of the host species. The contents of the two parasitized nests are summarized in Table 2. Both nests contained a dealate host queen and sexual pupae of the host species. Thus *P.inquilinus* was not inhibiting sexual reproduction in its host.

Brief observations on behaviour were made in the field during the collection of nest no. 12844. Most of the *P.inquilinus* queens were close to the host queen. One was riding on the back of the host queen gaster, holding on with her mandibles around the anterior peduncle of the petiole. (The concave masticatory margins of the *P.inquilinus* mandibles make them well-suited for this task.) As the nest was broken open *Pseudomyrmex* host workers were seen encountering *P.inquilinus* queens and no antagonistic behaviour ensued. The single parasite male was in the upper part of the twig nest, where most of the host males were concentrated, while the nine parasite queens and the host queen occurred in the lower portions of the nest. The entire host nest occupied a hollow section of the dead twig about 0.5 m in length (out of a total length of about 1 m).

At the type locality (Santa María) and at neighbouring sites

near Amaichá del Valle (Tucumán Province) two species of *Pseudomyrmex* were found to be common inhabitants of dead *Baccharis* stems, both members of the *P.pallidus* group: *P. sp.* PSW-64 (six nests collected, two parasitized by *P.inquilinus*) and *P.rufiventris* (Forel) (five nests sampled, none parasitized). The sample sizes are too small to draw any firm conclusions about host specificity. During a 9-day period of collecting *Pseudomyrmex* in northern Argentina (in Córdoba, Catamarca and Tucumán provinces) a total of 24 nests of *P.rufiventris* was sampled and none was parasitized. Both the parasite and its only known host (*P. sp.* PSW-64) were found only in the vicinity of Santa María.

Phylogenetic affinities of *Pseudomyrmex inquilinus*

Pseudomyrmex inquilinus bears a superficial resemblance to its host species: the queen is the same bright orange-brown colour, standing pilosity is scarce on the head and mesosoma, the integument has a similar lustrous sheen, head shape is similar, and the male is dark brown with light appendages, as in the host species. Hence, the first impression in the field was that this was a member of the *P.pallidus* group, modified for life as a social parasite on another member of the same group, as in the case of *Pseudomyrmex leptosus*, a workerless inquiline from Florida (Ward, 1985; Klein, 1987) and the only other example known in the genus and subfamily.

More careful scrutiny of *P. inquilinus* soon forced the abandonment of this idea. It proved to possess none of the apomorphic characteristics of the *P.pallidus* group. In fact it is not placeable in any of the nine major species groups which have been recognized in the genus (Ward, 1989a). The nine species groups are reasonably well defined and most or all of them are likely to be monophyletic. Collectively they encompass about 85% of the 180-odd species in the genus. There is a remaining heterogeneous assemblage of about twenty-five unplaced (*incertae sedis*) species, and *P. inquilinus* is phenetically most similar to a small subset of these, centred around *P.subater* (Wheeler & Mann) and *P.duckei* (Forel).

Thus it would seem to be a foregone conclusion that Emery's Rule is contradicted here. None the less it could be salvaged – albeit with special pleading – if *P.inquilinus* could be shown to be a sister group of the *P.pallidus* group. While an investigation of the phylogenetic relationships of all 180 or more *Pseudomyrmex* species was beyond the scope of this study, a subset of taxa was chosen, appropriate for probing the cladistic relationships of parasite and host. These taxa included the *P.pallidus* group, two species (*P.gebelli*, *P.oki*) allied to that group, *P.inquilinus*, and three taxonomically isolated species (*P.duckei*, *P.filiformis*, *P.subater*), with suggestive similarities to *P.inquilinus*. Also included was the *P.viduus* group, which appeared in a basal position in an earlier cladistic analysis of the genus (Ward, 1991), and the genus *Tetraponera* which served as an outgroup. *Tetraponera* is the probable sister genus of *Pseudomyrmex* (Ward, 1990). Note that because some species and species groups of *Pseudomyrmex* are being excluded this test is biased in favour of support of Emery's Rule.

A data set of nineteen morphological characters was

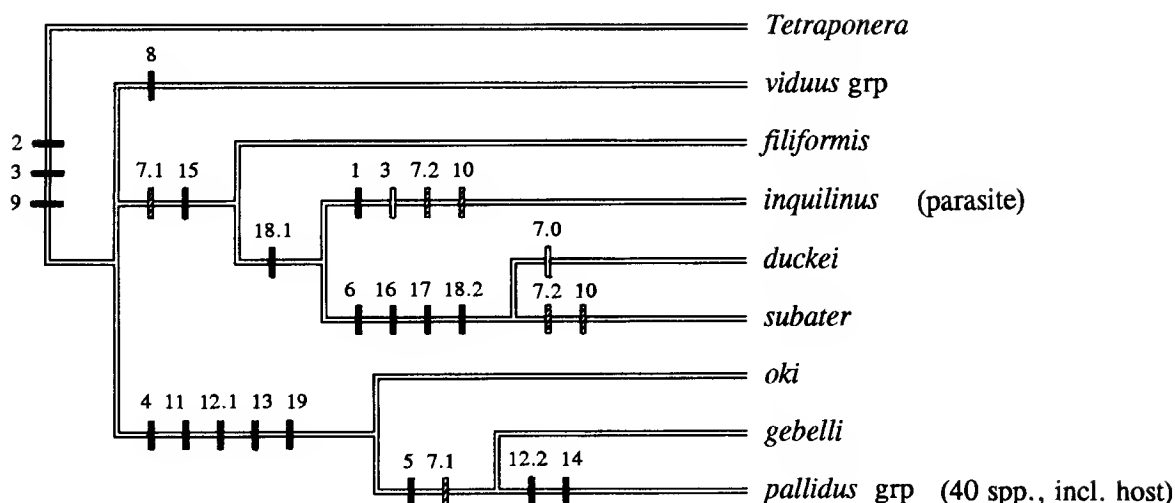


Fig. 25. Phylogenetic relationships among *Pseudomyrmex inquilinus*, its host's species group (*P.pallidus* group), and other *Pseudomyrmex* taxa. This is one of three most parsimonious trees, and also the strict consensus of those three trees. Character state changes are marked, with solid bars indicating unique forward changes, cross-hatched bars convergences, and open bars reversals. Numbers refer to the characters (see text under 'Materials and methods'). This tree has a length of 27, consistency index 0.81.

developed, of which ten were worker- or queen-based, and nine were male-based (primarily male genital characters) (Table 1). Cladistic analysis of the data set using the *ie* (implicit enumeration) option of HENNIG86 yielded three most parsimonious trees of length 27 and consistency index (CI) 0.81. The consistency index drops to 0.77 if one excludes autapomorphies of the terminal taxa (three characters) and non-reversing synapomorphies of the ingroup (two characters). Figure 25 illustrates the strict consensus tree; it is also one of the three most parsimonious trees, the other two involving resolutions of the basal trichotomy.

The results confirm that *P.inquilinus* does not have close phylogenetic affinities to its host species or its host species group. It appears to be more closely related to *P.subater* and *P.duckei*, two of the taxonomically isolated species not belonging to any of the larger *Pseudomyrmex* species groups. The most parsimonious trees place *P.inquilinus* in a clade with *P.subater* and *P.duckei*. *P.filiformis* is a sister species to these three, and together they can be said to form a rather weakly defined '*P.filiformis* complex'. The two species, *P.gebelli* and *P.oki*, placed in the *incertae sedis* group of *Pseudomyrmex* (Ward, 1989a), appear as successive outgroups of the *pallidus* group. Finally, relationships among the *viduus* group, the *filiformis* complex, and [*oki* + (*gebelli* + *pallidus* group)] are not well resolved, leaving a basal trichotomy.

Discussion

The preceding analysis, although based on an incomplete set of taxa and a relatively small number of characters, nevertheless indicates rather clearly that, in the case of *P.inquilinus*, there is not a recent sister-group relationship between the parasite and host lineages. As such, one can exclude the possibility that *P.inquilinus* arose by sympatric speciation from its current host or an immediate ancestor of that host. The results leave

open the question of the origin of parasitic habits in *P.inquilinus*. It may be possible to gain some insight into this problem by examining the natural histories of three species that are apparently related to *P.inquilinus*, namely *P.filiformis*, *P.subater* and *P.duckei*.

P.duckei is a rarely encountered rainforest species ranging from Guatemala to Bolivia. Only one queenright colony has been collected by the author: it was monogynous and unremarkable in composition. The queens of *P.duckei* are 'normal' in morphology, i.e. similar to workers but larger in size, and they give no obvious indication of being parasitic at any stage of their life cycle. *P.subater* is widely but patchily distributed from Mexico and the West Indies south to Bolivia and Brazil. The queens of this species are unusually small, being about the same size as the workers but differing in the scarcity of their pilosity. Little is known about the biology of *P.subater*, but field observations in the dry forests of western Mexico (Jalisco) and the Dominican Republic suggest that it is a rather aggressive species that is both polygynous and polydomous (P. S. Ward, unpublished data). Collections of this species from the Bahamas, sent to the author by Blaine Cole, included a heterospecific nest sample, containing workers of both *P.subater* and *P.cubaensis* (Forel), the latter being an unrelated species in the *P.oculatus* group (Ward, 1985, 1989a). This suggests the possibility of parasitic behaviour on the part of *P.subater*. Moreover, old references to mixed-nest associations of Bahamian *P.'flavidula'* and *P.'elongata'* (Wheeler, 1905; Mann, 1920) can be reinterpreted in the light of the preceding observations. Examination of museum material shows that Wheeler's and Mann's records of *P.'elongata'* refer to a mixture of *P.subater* and *P.cubaensis* (Ward, 1985; present study). *P.flavidulus* does not occur in the West Indies and the records of '*flavidula*' are mostly misidentifications of *P.pallidus* (Ward, 1985). It is also true, however, that queens of Bahamian *P.subater* are a bright-orange colour (in contrast to the dark brown of the workers) that makes them look superficially like

Table 3. Social parasites in the ant genus *Pseudomyrmex*.

| Parasite | Host | Type of parasitism | Reference |
|---------------------|-----------------------------------------------------------------|-----------------------------------------------------|---------------------------|
| <i>P.seminole</i> | <i>P.pallidus</i> | Temporary social parasitism | Ward, 1985 |
| <i>P.filiformis</i> | <i>P.elongatus</i> , <i>P.holmgreni</i> <i>P. sp.</i> PSW-14 | Temporary social parasitism | Present study |
| <i>P.subater</i> | <i>P.cubaensis</i> , ? <i>P.pallidus</i> | Temporary social parasitism (?) | Ward, 1985; present study |
| <i>P.leptosus</i> | <i>P.ejectus</i> | Workerless inquilinism, intolerant of host queen | Ward, 1985; Klein, 1987 |
| <i>P.inquilinus</i> | <i>P. sp.</i> PSW-64 | Workerless inquilinism, tolerant of host queen | Present study |

those of *P.pallidus*. So there is circumstantial evidence to indicate that, at least in the Bahamas, *P.subater* parasitizes the nests of *P.cubaensis* (and perhaps also those of *P.pallidus*). Because monospecific nests of *P.subater* are also encountered, in the West Indies and elsewhere, the behaviour apparently represents temporary social parasitism or facultative dulosis. The situation begs for a detailed study.

For *P.filiformis* there is more definitive evidence of temporary social parasitism. This species ranges from Mexico to Peru, Bolivia and Brazil. The queens are peculiar in appearance, with strikingly elongate heads and sturdy mandibles (Wheeler, 1919; Fig. 2). Over the last 10 years the author has collected about twenty-four nest series of *P.filiformis*. Most of these were large and mature colonies, monospecific in composition, and containing no more than a single functional queen (one colony had two physogastric queens). The author has encountered only three incipient colonies of *P.filiformis*, and all involved dealate queens cohabiting with several (4–8) workers of a different species, in small dead twigs. The host species were *P. sp.* PSW-14 (an undescribed species near *P.ejectus*), *P.holmgreni* (a member of the *P.pallidus* group, like the first species), and *P.elongatus* (Mayr) (in the *P.oculatus* group), and they were accompanied by one, two and one dealate queens, respectively, of *P.filiformis*. Most of the brood could not be identified to species, but in all three instances it included some worker pupae of the host species. No host queens were present. The host species are common and widespread in Central and/or South America.

Thus, two of the three species to which *P.inquilinus* appears to be related exhibit evidence of being temporary social parasites on common but distantly related congeners. This suggests a comparable intermediate stage preceding the evolution of the workerless condition in *P.inquilinus*. It would be useful to have more detailed phylogenetic and behavioural data on the species allied to *P.filiformis*, of which there are several undescribed species in addition to *P.duckei* and *P.subater* (P. S. Ward, unpublished data). If *P.duckei* is both non-parasitic and a sister species of *P.subater* (as in Fig. 25) then, in view of the likely irreversibility of the parasitic habit, one would have to postulate multiple origins of temporary social parasitism in this group of ants.

The only other workerless social parasite known in the genus *Pseudomyrmex*, *P.leptosus* Ward from Florida, is a member of the *P.pallidus* group (Ward, 1985) and hence represents an origination of the workerless condition separate from that of

P.inquilinus. The host species of *P.leptosus* is *P.ejectus* (F. Smith), a member of the same species group. A cladistic analysis indicated that *P.leptosus* is not a sister species of its host; rather it is more closely related to two non-host species, *P.pallidus* and *P.seminole* (Ward, 1989b). Interestingly, *P.seminole* is a facultative temporary social parasite of *P.pallidus* (Ward, 1985). One important difference between *P.leptosus* and *P.inquilinus* is that the former species apparently does not tolerate the presence of the host queen (Klein, 1987).

To summarize, there are now two known independent originations of workerless inquilinism in the ant genus *Pseudomyrmex*, and in both cases phylogenetic analysis indicates that (i) the parasite is more closely related to other free-living taxa than to its host, and (ii) among the parasite's close relatives are some species exhibiting habits of temporary social parasitism. Although the comparative data are still sparse, the most plausible route to permanent social parasitism in *Pseudomyrmex* involves interspecific exploitation of congeners. Looking at the known social parasites in this genus we observe a suggestive ethocline from temporary social parasitism (*P.seminole*, *P.filiformis*, and probably *P.subater*) to workerless, queen-intolerant parasitism (*P.leptosus*) to queen-tolerant inquilinism (*P.inquilinus*) (Table 3). The known hosts of these parasites are common, facultatively polygynous species drawn from two different species groups (*P.oculatus* group, *P.pallidus* group). Most unparasitized colonies of the host species contain a single functional queen, but multiple-queen colonies are encountered at least occasionally. Insofar as this polygyny is due to readoption of recently mated daughter queens into the nest – the pattern observed in most polygynous ants (Buschinger, 1990; Hölldobler & Wilson, 1977, 1990) – these species may be more vulnerable than strictly monogynous species to interspecific (congeneric) parasitism.

Concluding remarks

In all three instances where cladistic methods have been used to test the validity of Emery's Rule in ants, it has been found wanting (Table 4). A fourth study, involving socially parasitic polistine wasps, also concluded that the rule did not hold (Carpenter *et al.*, 1993; see also Choudhary *et al.*, 1994). To the extent that other studies fail to support Emery's Rule, the theory that social parasites evolve sympatrically from their hosts is seriously undermined. Because social parasitism has

Table 4. Cladistic tests of Emery's Rule in ants.

| Parasite | Host | Emery's Rule supported? | Reference |
|--------------------------------|----------------------|-------------------------|---------------|
| <i>Pseudomyrmex leptosus</i> | <i>P.pallidus</i> | No | Ward, 1989b |
| <i>Pseudomyrmex inquilinus</i> | <i>P. sp. PSW-64</i> | No | Present study |
| <i>Cataglyphis hanna</i> | <i>C.bicolor</i> | No | Agosti, 1994 |

arisen numerous times in ants (and in other social Hymenoptera) it is certainly too early to issue a blanket rejection of Emery's Rule. There is no reason to believe that the ant taxa that have been tested (*Pseudomyrmex*, subfamily Pseudomyrmecinae; *Cataglyphis*, subfamily Formicinae) are representative of the diverse array of social parasites seen among the ants. At the very least, however, the rule should be treated with greater circumspection. More detailed taxonomic, phylogenetic and genetic investigations are needed of other groups of social parasites, particularly in the species-rich genera *Myrmica* and *Leptothorax* (*sensu lato*). A recent promising study by Baur *et al.* (1996), using sequences from the ITS-1 region near the 5.8S rRNA gene, demonstrated a relationship at the level of tribes and species groups between several myrmicine social parasites and their respective hosts, but the low level of sequence variation among closely related species and the incomplete sampling of relevant taxa (admittedly a complete survey would be a daunting task) precluded effective phylogenetic inference at the species level.

A final point of discussion concerns the plausibility of the sympatric speciation model. Even if Emery's Rule is found to be valid for some ant parasites, simple alternative explanations involving allopatric differentiation are available (Wilson, 1971; Hölldobler & Wilson, 1990; see also Pearson, 1981). The sympatric models, favoured by Buschinger (1970, 1990) and Bourke & Franks (1991) (see also West-Eberhard, 1986), face the obstacle of producing prezygotic isolation by disruptive selection in the presence of continuing gene flow. The antagonism between selection and recombination that jeopardizes this process (Felsenstein, 1981) would be manifested in the case of an incipient microgyne parasite by the difficulty in building up linkage disequilibrium among genes affecting three different traits: selfish (parasitic) behaviour, body size, and mating habits. This could be ameliorated if positive assortative mating were linked by pleiotropy to the disruptively selected trait(s) (Rice & Hostert, 1994), but it is difficult to imagine that choice of mating venue (e.g. near the nest rather than in a mating swarm) and therefore mate would be ineluctably tied to parasitic behaviour and small body size (cf. Bourke & Franks, 1991). In a species that remains facultatively polygynous one would expect that some non-parasitic queens would continue to mate near, and return to, the nest. Moreover, dispersal and colonization of new nests would have to persist (or develop?) as a behaviour in the proto-parasite. Finally, the parasitic reproductive behaviour is unexpressed as a male phenotype, further diluting the strength of disruptive selection. In the light of these considerations, the intraspecific route to interspecific social parasitism remains problematic.

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