

A new socially parasitic *Myrmica*, with a reassessment of the genus (Hymenoptera: Formicidae)

BARRY BOLTON Department of Entomology, British Museum (Natural History),
London

ABSTRACT. *Myrmica ereptrix*, a new species socially parasitic on *Myrmica rugosa*, is described from a single female discovered in Kashmir, India. A synoptic table of the known social parasites in genus *Myrmica* is given and the genus-level names *Paramyrmica*, *Sommimyrmica* and *Sifolinia* are discussed and newly synonymized with *Myrmica*. The genus *Myrmica* is redefined for all castes. An outline is given of the evolution of the characteristic venation of *Myrmica* alates. The structure of the metasternal process in genera of the *Myrmica*-group is discussed and used in the generic diagnosis for the first time.

Introduction

During the first half of this century it was standard practice, whenever a new socially parasitic myrmicine ant was discovered, to describe it in a genus separate from its host. The reasoning and logic behind this procedure was never explained in any detail. Merely being a social parasite, or even an assumed social parasite, seemed all that was needed for the setting up of a separate genus. Considering that true socially parasitic species are generally closely related to their hosts (Wilson, 1971, and included references) it is difficult to understand the old fashion which automatically made separate genera of them. Nevertheless, the activities of earlier ant students along these lines has resulted in a large number of small, usually monotypic, genera. Characteristically these tended to differ from their hosts by showing a reduction in expression or a partial masking of some of the host's genus-level characters, and the superimposition of features attributable to the acquisition of a socially

parasitic lifeway, and hence paralleled in many diverse groups (Wilson, 1984). Such weakly defined taxa have been termed 'satellite genera' by Kutter (1973).

In the past few years it has become increasingly clear that the satellite genera clustered around the major holarctic genus *Myrmica* are congeneric with it. The majority of these satellites were founded on species assumed to be, or known to be, socially parasitic. As such they exhibited some to many of those morphological and behavioural changes associated with the lifeway, which Wilson (1971) listed and termed the inquiline (or parasitic) syndrome.

The recent discovery of a new socially parasitic *Myrmica* from Kashmir has prompted this present survey of the small genera which are taxonomically very close to *Myrmica*, to estimate if any of them could validly be retained as separate genera. Analysis of those characters which had been proposed initially or invoked later to isolate the satellite genera has shown them all to be either gradient with one another and with *Myrmica*, universal or widely represented elsewhere in parasitic and non-parasitic *Myrmica*, attributable to the inquiline syn-

Correspondence: Mr B. Bolton, Department of Entomology, British Museum (Natural History), Cromwell Road, London SW7 5BD.

drome, or in a few cases to be the results of probable misinterpretation of the material examined. All this, plus the fact that new characters investigated show a marked uniformity across *Myrmica* and the former satellite genera, has resulted in the genus-level names *Paramyrmica*, *Sommimyrmica* and *Sifolinia* (= *Symbiomyrmica*) falling into the synonymy of *Myrmica*, and has allowed a redefinition of the genus.

During the survey it was seen that the new parasitic species, described here as *Myrmica ereptrix*, showed an interesting intermediate stage in the evolution of the characteristic venation pattern of *Myrmica* (Figs. 6, 7). Other *Myrmica* alates were then found in the collections of the British Museum (Natural History) which showed an entire sequence of vein reduction. The sequence ran from that pattern considered plesiomorphic in the Myrmicinae, through the pattern usually seen in *Myrmica* and its close relatives, to that very derived condition supposedly characteristic of the type-species of *Sifolinia* (Figs. 3–9). This sequence of vein reduction is very different from that outlined earlier for the pheidoline myrmicines (Bolton, 1982) and may constitute an apomorphy of the entire *Myrmica*-group of genera.

In the following sections the new species is described and a tabular synopsis of the thirteen certain and one dubious socially parasitic species of *Myrmica* is given. This is followed by a new diagnosis of *Myrmica* and discussion of the new

genus-level synonyms. The paper concludes with sections discussing the venation of *Myrmica* and its evolution, and the morphology of the metasternal process. This last structure presents some features useful in the revised generic diagnosis and is of potentially great value in assessing the phylogeny of myrmicine genera and genus-groups.

***Myrmica ereptrix* sp.n.** (Figs. 1, 5)

HOLOTYPE FEMALE (alate). TL 6.1, HL 1.24, HW 1.10, CI 89, SL 0.86, SI 78, AL 1.96, maximum width of alitrunk 1.16 (measurements in millimetres, as defined in Bolton, 1982).

With characters diagnostic of *Myrmica* as listed below. Mandibles finely longitudinally costulate-rugulose and armed with about 8 teeth (basalmost teeth not clearly visible in holotype, concealed by projection of clypeus). Median portion of clypeus narrowly prominent anteriorly as in all species of the *Myrmica rugosa*-group, the clypeus longitudinally rugulose. Frontal triangle weakly shagreenate and subopaque. Frontal lobes short and evenly shallowly convex, widely separated. Width across margins of frontal lobes at maximum separation 0.57 (0.52×HW) in full-face view. Maximum diameter of eye 0.30 (0.27×HW). Entire dorsum of head finely and densely intricately rugulose to reticulate-rugulose. Direction of sculpture divergent-longitudinal on

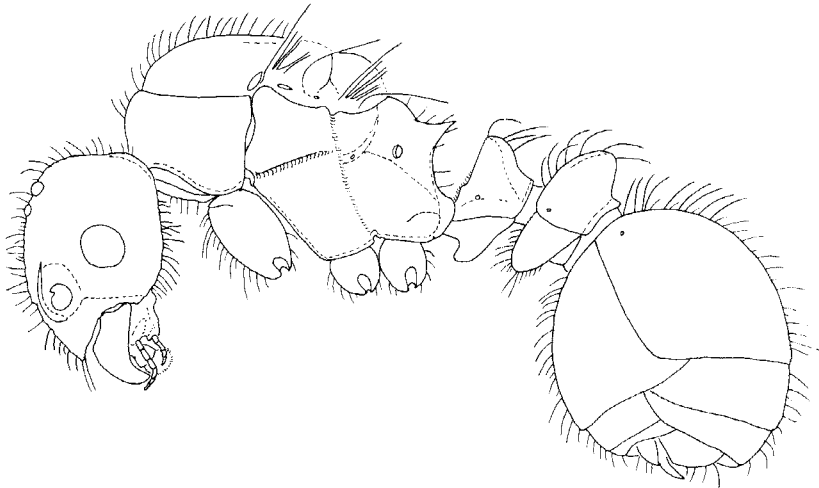


FIG. 1. Profile of head and body of *Myrmica ereptrix*, holotype female.

the cephalic dorsum to level of posterior ocelli, transverse behind this level. Antennal scapes evenly and shallowly curved basally, not sharply angulate nor possessing cuticular lobes, flanges or other outgrowths basally. Hind tibiae with narrow but conspicuous spurs which are feebly and finely pectinate; middle tibiae lacking spurs. Forewing length 5.12. Main venation of right forewing as Fig. 5, that of left forewing corresponding to that shown in Fig. 6 but portion of *r-m* close to *Rs* very feeble and almost effaced. Structure of alitrunk as shown in Fig. 1. Sides of pronotum narrowly longitudinally rugulose with a few faint reticular cross-meshes. Remainder of alitrunk longitudinally to obliquely costulate except for a small patch on the anepisternum, immediately below the level of the spiracle, which is smooth. Pronotal dorsum transversely rugulose. Mesoscutum longitudinally rugulose except for a small smooth anteromedian U-shaped patch. Scutellum irregularly rugulose dorsally, transversely rugulose posteriorly. Propodeal dorsum weakly transversely arched-rugulose, the declivity smooth and highly polished. Metapleural glands only moderately large but with a conspicuous orifice dorsally on the bulla, best seen in posterodorsal view. Shape of petiole and postpetiole as in Fig. 1. Petiole high and narrow in profile, with a short anterior peduncle and a large keel-like subpetiolar process. Postpetiole short and very deep; maximum length 0.34, maximum height 0.92, the shapes of the two segments reflecting changes evolved in many socially parasitic myrmicines. In dorsal view both segments very much broader than long, the dorsal surface of the petiole very shallowly concave in posterior view, the postpetiole dorsal outline evenly convex. All dorsal and lateral surfaces of head and body equipped with numerous short standing hairs which are erect to subdecumbent. Similar hairs present on gastral sternites and sternite of postpetiole. Antennal scapes and legs with dense short suberect to subdecumbent pilosity. Dorsal surfaces of petiole, postpetiole and first gastral tergite with longer stouter hairs which are curved or directed posteriorly. These longer hairs minutely barbate apically, as are some of the longer hairs elsewhere on the body. Gaster dorsally also with sparse short decumbent pubescence between the longer standing hairs. Colour dark brown to blackish brown everywhere.

Holotype female, INDIA: Kashmir,

Gulmarg, 20.vii.1986, 2800 m, *Picea* forest (P. H. Williams) (BMNH).

The holotype female was found in a nest of *Myrmica rugosa*. It is mounted on a pin above two workers from the host colony, and a red label on the pin states '*erepatrix* female holotype (top) + 2 *rugosa* host workers'. Further workers from the host series are present in BMNH under *M. rugosa*, also with a red label stating '*rugosa* host of *erepatrix*'.

Comments

As in all true socially parasitic forms *M. erepatrix* is closely related to its host and is obviously a member of the same species-group. It is immediately separated from the host female by the bizarre inquiline syndrome modifications to the petiole and postpetiole and the absence of spurs on the middle tibiae. The venation, different on the two forewings, gives an indication of the way in which the characteristic *Myrmica* pattern has arisen, as discussed under venation, below.

In the broadened sense of genus *Myrmica* envisaged in this paper, thirteen true socially parasitic species and one dubious form are now known, out of a world fauna approaching 100 species for the entire genus. The socially parasitic species have been summarized in Table 1.

Definition of genus *Myrmica*

MYRMICA Latreille

Myrmica Latreille, 1804: 179. Type-species:

Formica rubra L., 1758: 580, by subsequent designation of Latreille, 1810: 437.

Sifolinia Emery, 1907: 49. Type-species:

Sifolinia laurae Emery, 1907: 49, by monotypy. Syn.n.

Sommimyrmica Menozzi, 1925: 25. Type-species:

Sommimyrmica symbiotica Menozzi, 1925: 25, by original designation. Syn.n.

Symbiomyrmica Arnoldi, 1930: 267. Type-species:

Symbiomyrmica karavajevi Arnoldi, 1930: 267, by monotypy. [Synonymized with *Sifolinia* by Samšiňák, 1964: 156.]

Paramyrmica Cole, 1957: 37. Type-species:

Paramyrmica colax Cole, 1957: 37, by original designation. Syn.n.

TABLE 1. The socially parasitic species of *Myrmica*.

Species	Notes	Original generic combination	<i>Myrmica</i> host-species	Distribution	References
<i>bibikoffi</i>	1	<i>Myrmica</i>	<i>sabuleti</i> , or free-living	Switzerland	Kutter, 1963, 1973, 1977
<i>colax</i>	1	<i>Paramyrmica</i>	<i>striolagaster</i>	U.S.A.	Cole, 1957
<i>erepatrix</i>	2	<i>Myrmica</i>	<i>rugosa</i>	India	This paper
<i>fantiensis</i>	2	<i>Myrmica</i>	<i>scabrinodis</i>	Belgium	Van Boven, 1970; Kutter, 1973
<i>hirsuta</i>		<i>Myrmica</i>	<i>sabuleti</i>	U.K.	Elmes, 1978, 1983
<i>kabylica</i>		<i>Sifolinia</i>	<i>aloba</i>	Algeria	Cagniant, 1970; Kutter, 1973
<i>karavajevi</i> (= <i>pechi</i>)	3	<i>Symbiomyrma</i>	<i>scabrinodis</i> , <i>sabuleti</i> , <i>rubra</i> , <i>rugulosa</i>	Czechoslovakia, U.K., Poland, U.S.S.R.	Arnoldi, 1930; Samsiňák, 1957, 1964; Pisarski, 1962; Yarrow, 1968; Bernard, 1968; Kutter, 1969, 1973
<i>lanpra</i>		<i>Myrmica</i>	<i>alaskensis</i>	Canada	Francœur, 1968, 1981; Kutter, 1973
<i>laurae</i>	2, 4	<i>Sifolinia</i>	Unknown	Italy	Emery, 1907; Kutter, 1973
<i>lemasnei</i>	5	<i>Myrmica</i>	<i>sabuleti</i>	France	Bernard, 1968; Kutter, 1973
<i>myrmicoxena</i>		<i>Myrmica</i>	<i>lobicornis</i>	Switzerland	Forel, 1894; Bernard, 1968; Kutter, 1969, 1973, 1977; Van Boven, 1970
<i>quebecensis</i>		<i>Myrmica</i>	<i>alaskensis</i>	Canada	Francœur, 1981; Francœur & Loisel, 1984
<i>symbiotica</i>	6	<i>Sommimyrmica</i>	<i>rubra</i>	Italy	Menozzi, 1925; Kutter, 1973
<i>winterae</i>		<i>Sifolinia</i>	<i>uginodis</i>	Switzerland	Kutter, 1973, 1977
<i>myrmecophila</i>	7	<i>Myrmica</i>	—	—	Wasmann, 1910; Bernard, 1968; Van Boven, 1970; Kutter, 1973

Notes. 1. Worker caste retained, lost in all others listed except *symbiotica* where the sole specimen known may be a pathological or a gynecoid worker, and not a female as originally assumed.

2. Males undiscovered in these species, known for all others listed except *symbiotica*, see notes 1 and 6.

3. The wide host range apparently exhibited by *karavajevi* raises the suspicion that the species-level taxonomy may be faulty, or that some misidentification of the hosts has occurred.

4. *M. laurae*, *sensu* Yarrow, 1968, was a misidentification of British specimens now referred to *karavajevi*; see Kutter, 1973; Bolton & Collingwood, 1975.

5. Transferred from *Myrmica* to *Sifolinia* by Kutter, 1973; reverting here to *Myrmica*.

6. Possibly an ergatoid female or more likely a pathological worker, almost certainly not a true social parasite; see discussion under *Sommimyrmica*.

7. Van Boven (1970) stated that *myrmecophila* was an ergatoid worker [*recie*: gynecoid worker] of *M. sulcinodis* and hence its junior synonym. Kutter (1973) was of opinion that *myrmecophila* represented a *Mermis*-infested worker of *sulcinodis*. Whichever, it seems that the correct placement of *myrmecophila* is in the synonymy of *sulcinodis*, as Van Boven said.

Dodecamyrmica Arnoldi, 1968: 1803 [as subgenus of *Myrmica*]. Type-species: *Myrmica arnoldii* Dlussky, 1963: 194, by original designation. [Synonymy by Francoeur, 1981: 759.]

DIAGNOSIS OF WORKER. Monomorphic terrestrial to subarctic myrmicine ants with the following combination of characters.

- 1 Palp formula 6, 4.
- 2 Mandibles broad and strongly dentate, with 6–10 teeth which decrease in size from apex to base.
- 3 Strongly differentiated median clypeal seta absent.
- 4 Median portion of clypeus broad and shallowly biconvex, with a somewhat swollen appearance.
- 5 Clypeus broad posteriorly, broadly inserted between anterior portions of the frontal lobes.
- 6 Well defined frontal triangle present immediately behind posteromedian clypeal margin.
- 7 Frontal carinae and antennal scrobes absent.
- 8 Eyes situated at or usually slightly in front of the midlength of the sides.
- 9 Anterior tentorial pit situated closer to the outer margin of the antennal socket than to the lateral margin of the head.
- 10 Antennae with 12 segments, with a variably developed apical club of 3–4 segments.
- 11 Alitrunk elongate and low, promesonotum not domed-convex in profile.
- 12 Propodeal spiracle low on side (just above or abutting junction with metapleuron), at or usually slightly behind the propodeal midlength.
- 13 Propodeal spines and metapleural lobes present, the latter usually broadly angular.
- 14 Metasternal process and ancillary structures present, as discussed below.
- 15 Tibial spurs of middle and hind legs usually pectinate but showing all stages of reduction to absent.
- 16 Petiole nodiform, with a short anterior peduncle and an anteroventral process present.
- 17 Petiolar spiracle approximately at midlength of peduncle or behind this level, never located close to the petiole–alitrunk articulation.
- 18 Sting strong and simple, never spatulate and always lacking appendages.
- 19 Cuticle thick and with an armoured appearance; usually the cuticle strongly sculptured.

DIAGNOSIS OF FEMALE. Characters 1–10 and 12–19 as worker. Additional characters of female include:

- 20 Radial (=marginal) cell of forewing open (at arrow in Fig. 3); otherwise venation as discussed below.
- 21 Parapsidal grooves or impressions present.

- 22 Axillae fused into a transverse band which runs across the width of the dorsal alitrunk.
- 23 Ocelli present.

DIAGNOSIS OF MALE. Characters 1, 3, 4, 7, 8, 14–17, 20–23 as worker and female, but sting (18) absent sculpture (19) usually much weaker. Varying from the above in the following:

- 2 Mandibles proportionately smaller, with 5–9 teeth.
- 5 Frontal lobes vestigial to absent, the broad posterior curve of the clypeus inserted between the anterior portions of the antennal sockets.
- 6 Frontal triangle frequently as in worker and female, but may be obliterated in some.
- 9 Anterior tentorial pit as worker or slightly farther from outer margin of antennal socket.
- 10 Antennae with 12–13 segments, lacking elongate or fusion-segments. Flagellum apically varying from weakly to distinctly clavate; club when present of 3–5 segments.
- 12 Propodeal spiracle varying in position from just in front of to just behind the midlength.
- 13 Propodeum rounded to armed; metapleural lobes conspicuous.

Additional character of male:

- 24 Notauli present and complete on mesoscutum.

The new genus-level synonyms

Paramyrmica

This genus was originally raised by Cole (1957) to contain only the species *P. colax*. Every character which he put forward to isolate the genus is duplicated elsewhere in *Myrmica*. Of the supposed genus-level characters which he gave, most are widely exhibited or are universal in *Myrmica* species. Two of Cole's characters appear to be mis-stated. He says that in *P. colax* the anterior clypeal margin is straight and that the mandibles have a total of 6 teeth. Paratype workers of *colax* in BMNH show a convex anterior clypeal margin and have a dental count of 7–8, a much more usual number in *Myrmica* workers although a few species with only 6 teeth are known.

Two other characters exhibited by *colax* require discussion. First, the promesonotal suture of the worker was stated to be distinctly impressed. There is no suture, only an arcuate shallow impression marking the original track of the suture. The pronotum and mesonotum are as immovably fused in *colax* as elsewhere in

workers of the *Myrmica* genus-group. Most *Myrmica* species do not have an impression between pronotum and mesonotum but some impression is visible in oriental region species such as *smythiesi*, *everesti* and *specularis*. In the genus as a whole a change in intensity, form, density or direction of sculpture, or some other superficial indication of the former promesonotal suture track, is widely exhibited. The character is therefore gradient and variable, and of no value as a genus-level diagnostic feature.

Second, Cole (1957) indicated that in *colax* the spurs of the middle and hind tibiae are small and relatively weakly developed; the spurs being pectinate in most workers but simple in some. Variation in size of tibial spurs and development of pectination show remarkable differences even in a relatively limited fauna (Kutter, 1978, Fig. 24), and Francoeur (1981) has pointed out that reduced spurs are not restricted to parasitic forms. In fact the genus *Myrmica* shows a finely stepped and complete sequence of reduction of the middle and hind tibial spurs, from large and strongly pectinate to absent. Most species in the genus have strongly to moderately developed spurs which are distinctly to partially pectinate, including the parasitic species *hirsuta*, *lampra* and *myrmicoxena*. The new species described here, *ereptrix*, has feebly pectinate but quite distinct spurs on the hind tibiae, but lacks spurs on the middle tibiae. As mentioned above, *colax* shows individuals in which spurs are pectinate, and others in which they are simple. Species such as *alaskensis*, *alpestris* and *jessensis* have spurs which are of normal size but have their pectination reduced to a few barbs. In *rugiventris*, *aloba* and *vandeli* the spurs are reduced in size and the pectination is reduced or is represented only by minute serrations or tiny barbules. Finally, in species such as *quebecensis*, *bibikoffi* and *arnoldii* the spurs are minutely barbulate to smooth, or even absent. Thus the size and degree of development of pectination of the tibial spurs shows no consistency whatever in the genus *Myrmica*, and the character does not deserve the reliance placed upon it in the past as a diagnostic feature of the genus.

In summary, *colax*, although an evolutionarily somewhat isolated species, is definitely a member of genus *Myrmica*, as first suggested by Francoeur (1968), and the genus-level name *Paramyrmica* is here formally synonymized under *Myrmica*.

Sommimyрма

Menozzi (1925) stated that the holotype, and still the only known specimen, of *S. symbiotica* is probably an ergatoid female. This was because though worker-like the specimen possesses small ocelli and has a rather voluminous gaster. He characterized *Sommimyрма* as being close to *Sifolinia* as it lacked tibial spurs on the middle and hind legs. All other characters cited, both by Menozzi (1925) and later by Kutter (1973), are duplicated in or are diagnostic of *Myrmica*, except for the following.

The antennal club of *symbiotica* is thickened and moniliform.

The clypeus of *symbiotica* has a small posteromedian circular impression.

As is now obvious, the tibial spurs in *Myrmica* show a finely graded sequence of development from long and pectinate to absent, with all intermediate stages demonstrated, as discussed under *Paramyrmica*. Genera cannot be delimited by drawing lines through some stage of the sequence as such lines are necessarily arbitrary and the taxa thus produced without significance. The slight thickening of the antennal club, which I am not sure is outside the normal range of variation in *Myrmica*, and the presence of a small clypeal impression, are interesting at species-level but are hardly genus-level characters sufficient to separate *symbiotica* from all other *Myrmica*. Many *Myrmica* species exhibit autapomorphic characters of this magnitude and some seem decidedly more bizarre in appearance than *symbiotica* (for example *colax*, *ravasinii*, *rugiventris*, and several species of the Oriental region). All of these, like *symbiotica*, are decidedly *Myrmica* as far as their universal diagnostic characters are concerned.

Having established that *symbiotica* belongs in *Myrmica*, the only problem remaining is the fact that the holotype was discovered in a nest of *Myrmica rubra*. Menozzi (1925) described it as an ergatoid female and Kutter (1973) regarded it as a permanent social parasite. The latter opinion is difficult to accept as permanently socially parasitic females appear never to be ergatoids. The few ergatoids previously described as being permanent social parasites are now known to be autoparasitic females (Bolton, 1986), bizarre in appearance and reproductive strategy but forming perfectly normal colonies.

It is difficult to imagine how an ergatoid

female could possibly function as a permanent social parasite. The disadvantages of such a combination appear to preclude the possibility of its arising, and selection against it would be strong. An ergatoid social parasite would be faced with enormous problems. For instance, how could her offspring disperse to infest new host colonies? The search area for uninfested host colonies would necessarily be very small as the ergatoid is confined to walking. Predation pressure on such females would be intense, and their general failure rate would be high as the time available to be spent on searching would be short. This last arises from the fact that her energy reserves would be minimal as she relies entirely upon a host to provide all food. Permanent social parasites appear mostly, perhaps entirely, incapable of feeding themselves, and freshly mated females do not carry the large bodily-stored energy reserves of their claustral colony-founding counterparts.

There seem to be five possibilities to account for the strange appearance of *symbiotica*, as follows:

- 1 It is an ergatoid female of *M. rubra*, the species in whose nest it was found. This seems unlikely as ergatoids are otherwise unknown in *rubra*.
- 2 It is an ergatoid female of some other *Myrmica* species, brought into the *rubra* nest by the workers, as prey. The same objection applies as in 1; ergatoids appear otherwise unknown in *Myrmica*.
- 3 It is permanent social parasite. Unlikely for the reasons discussed above and because it would be utterly unlike any other permanent social parasitic myrmicine ant both in morphology and behaviour.
- 4 It is not a true female at all but a pathological worker which is displaying some female-like or bizarre characters. Circumstantial evidence such as the facts that only one specimen was found in the nest and nothing like it has ever been found again, leads to the suspicion that this is a reasonable interpretation of *symbiotica*.
- 5 It is gynecoid worker of *rubra*, perhaps with some genetically induced or pathologically induced bizarre features. This also seems a reasonable possibility, but this, like option 4, remains really in the realm of speculation.

Sifolinia

The genus-level name *Sifolinia* was based upon a single female specimen from Italy, described by Emery (1907) as *S. laurae*. Characters which he gave to isolate the genus were the following: Mandibles with a long apical tooth

and several smaller teeth. Clypeus posteriorly broadly rounded. Frontal triangle present but short. Frontal lobes widely separated. Eyes at midlength of sides. Antennae 12-segmented with an indistinct club of 4 segments. Propodeum armed. Petiole short, with a dentiform ventral process. Postpetiole broad, with a large obtuse process ventrally. Tibial spurs absent from middle and hind legs. Forewing venation the same as illustrated in Fig. 9 of this paper.

He suggested that *S. laurae* was a parasitic species but strangely supposed that it was allied to *Harpagoxenus*, a leptothoracine; Kutter (1973) affirmed its relationship with *Myrmica*. Of the characters noted only the lack of tibial spurs, the venation, and the inquiline syndrome form of the petiole and postpetiole, separated *Sifolinia* from *Myrmica* as it was understood at that time.

Later, with the discovery and description of males attributable to *Sifolinia* (Arnoldi, 1930; Pisarski, 1962; Cagniant, 1970; Kutter, 1973), it became obvious that this sex duplicated the characters noted for the female except that the male antennae were also 12-segmented, not 13-segmented as was to be expected. It was also found that the palp formula was 6, 4 throughout *Sifolinia*, as in *Myrmica*. By the time of the latest review of *Sifolinia* (Kutter, 1973), five species had been placed in the genus: *kabylica*, *karavajevi* (= *pechi*), *laurae*, *lemasnei* and *winterae*.

Unfortunately the descriptions of *Sifolinia* species after the original description of *laurae*, and the discovery of additional parasitic forms in *Myrmica*, has nullified the apparent morphological differences invoked to separate the two as discrete genera.

Reductions, modifications in form, and loss of tibial spurs from the middle and hind legs, are now known to occur widely in *Myrmica* and form a finely stepped sequence, as discussed under *Paramyrmica*, above. At least one species described in *Sifolinia*, *S. kabylica*, retains spurs in a reduced form (Cagniant, 1970). Venation in *Sifolinia* also falls into the sequence of reduction illustrated for *Myrmica* (Figs. 6–9) and discussed below. The advanced appearance of the venation shown by *S. laurae* (Emery, 1907) and *karavajevi* (Arnoldi, 1930; Yarrow, 1968) also occurs in *M. kurokii* (Fig. 9). Conversely *S. kabylica* and *winterae* have venations which approximate Fig. 8, or a condition between

those indicated in Figs. 7 and 8 (Cagniant, 1970; Kutter, 1973).

The form of the petiole and postpetiole, inquiline syndrome characteristics, are at least as well developed in *Myrmica erepatrix* (Fig. 1) as in any of the former *Sifolinia* species.

As for the reduction of antennal segment count from 13 to 12 in the males of species described in *Sifolinia*, Francoeur (1981) has already pointed out in his synonymy of *Dodecamyrmica* that such an event is not significant at generic level. He showed that in *Myrmica* at least two species, *M. lampra* (a workerless social parasite) and *M. arnoldii* (a normal species with a worker caste), have males with 12-segmented antennae. Further, the reduction in antennal segment count in males of parasitic species is not restricted to *Myrmica*; it is also shown in *Monomorium* (DuBois, 1986; Bolton, 1987).

Francoeur & Loiselle (1984) note that the male genitalia of species described in *Sifolinia* show some interesting differences from those in *Myrmica*. It is certainly to be expected in socially parasitic forms that reproductive isolating mechanisms separating social parasites from host will rapidly evolve, and that these isolaters will be expressed in the morphology of the male genitalia. Such modifications may validly be regarded as part of the inquiline syndrome and, while taxonomically useful at species or even species group level, should not be considered as critical at genus-level without the support of other, stronger criteria which do not depend upon the inquiline syndrome for their development.

In summary I fully concur with Wilson's (1984) suggestion that *Sifolinia laurae*, and all other species added to *Sifolinia* later, are congeneric with *Myrmica*, and hereby formally synonymize the two genus-level names.

Venation in *Myrmica*

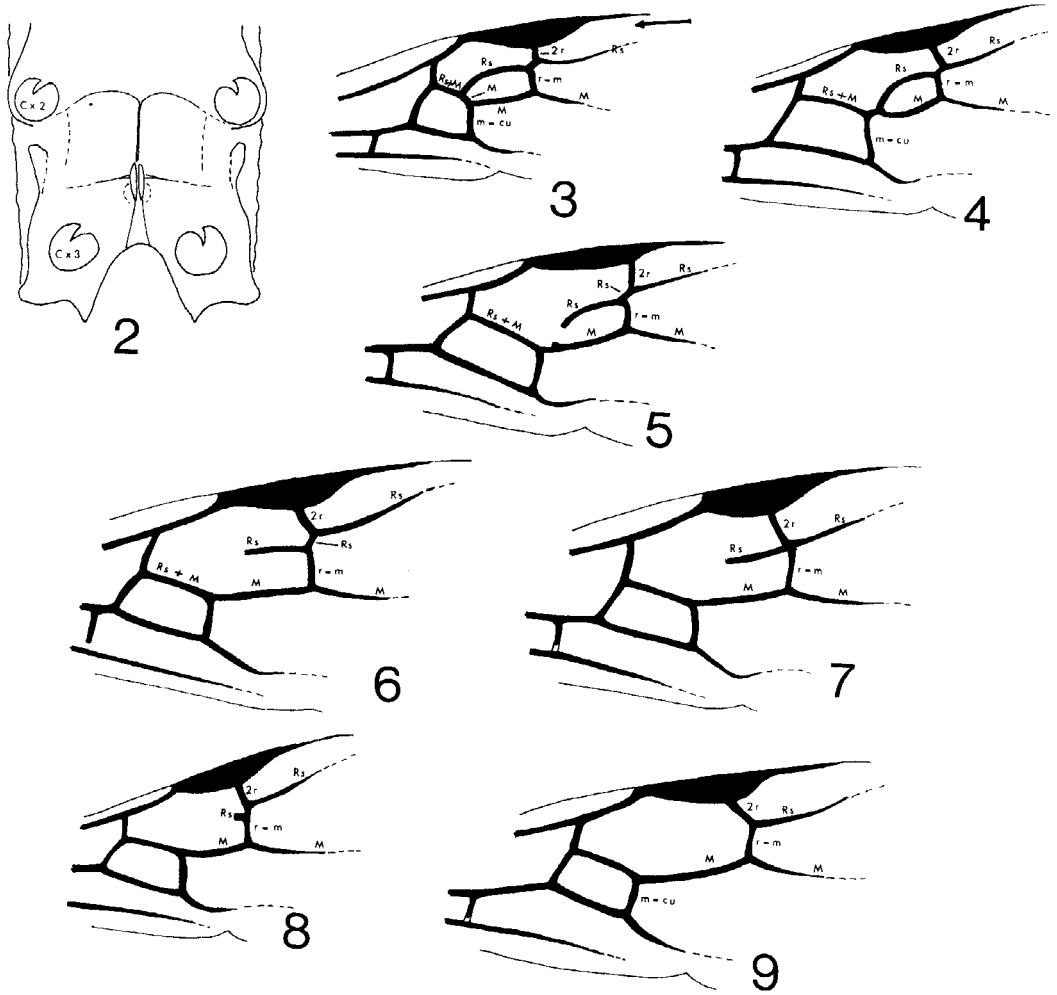
The most usual forewing venation seen in *Myrmica* is as illustrated in Figs. 6 and 7, both of which may be found in a single nest-series. The two appear to be freely interchangeable and sometimes both may occur on opposite wings of the same individual. The venation pattern indicated in Figs. 6 and 7 accounts for over 90% of specimens encountered during this study.

The presence of a free proximal abscissa of *Rs* implies that the basal portion of *Rs*, to its junction with *Rs+M*, has been lost. This usual venation pattern has been used in keys to males and alate females to separate *Myrmica*, and its immediate ally *Manica*, from other Palaearctic myrmicine ants (Bolton & Collingwood, 1975; Kutter, 1977). However, as is indicated by Figs. 3–5, forewings can sometimes be found which illustrate how this characteristic venation has arisen. Some also show (Figs. 8, 9) developments beyond this usual state.

Figs. 3 and 4 show venations in *Myrmica* which duplicate the initial stages in the evolution of the typically pheidoline venation discussed by Bolton (1982: 339, and Figs. 35–43). Fig. 3 indicates the relative positions of *Rs+M*, *Rs*, and *M* which is plesiomorphic for the subfamily Myrmicinae. Fig. 4 shows the continuing fusion of *Rs* and *M* distally on the wing, to a point beyond the junction with cross-vein *m-cu*. In both specimens figured (Fig. 3, male of *M. emeryana*; Fig. 4, male of *M. incompleta*) the opposite wing has the normal venation shown in Figs. 6 and 7.

The difference in method of vein reduction from the sequence seen in the pheidolines is illustrated in Fig. 5 (female of *M. erepatrix*; opposite wing shows normal *Myrmica* venation). Instead of the fusion of *Rs* with *M* gradually moving distally on the wing until cross-vein *r-m* vanishes, as in the pheidolines (Bolton, 1982), *Rs* in *Myrmica* and its allies breaks away from *M*. The free floating proximal abscissa of *Rs* thus produced then shortens (Figs. 5, 6, 8) until the abscissa has entirely vanished (Fig. 9). In this terminal position the distal portion of *Rs* which remains appears to arise abruptly from the point of junction of cross-veins *2r* and *r-m*. (Figs. 6, 7, two females of *M. sulcinodis* from a nest-series; Fig. 8, male of *M. schencki* in which the opposite wing is normal; Fig. 9, female of *M. kurokii*, other female in same series with venation as in Figs. 6, 7.)

The venation seen in Fig. 9 is also the stage reached by some species which formerly constituted *Sifolinia*. Yarrow (1968) has pointed out that in any given series some *M. karavajevi* may lose cross-vein *m-cu* whilst others retain it. Kutter's (1977: 55, Fig. 61) illustration of the forewing of *M. myrmicoxena*, and Francoeur & Loiselle's (1984) photograph of the wing of *M. quebecensis* indicate a further possible reduction; a break between *r-m* and *M*, possibly



FIGS. 2-9. *Myrmica* species. 2, posterior portion of ventral alitrunk in *ruginodis* worker (Cx=coxal cavity). 3-9, right forewings of: 3, *emeryana* male; 4, *incompleta* male; 5, *erepatrix* holotype female; 6 and 7, *sulcinodis* females to show normal variation in venation; 8, *schencki* male; 9, *kurokii* female.

caused by a secondary shortening of the main vein *M*. This feature is foreshadowed on the left forewing of the *M. erepatrix* holotype, where *r-m* is reduced and very faint where it approaches *Rs*.

Metasternal process in *Myrmica*

With the alitrunk in ventral view and the middle and hind legs removed, the metasternal process in *Myrmica* workers and females is as follows.

On each side of the midline between the middle and hind coxal cavities (Cx2 and Cx3 in Fig. 2) is a sharply raised longitudinal flange or plate,

the two very closely approximated and together forming the metasternal process proper (Fig. 2), which in profile is strongly prominent. Only an extremely narrow longitudinal slit separates the two flanges. In most species the flanges are thin but in a few they are somewhat thickened and more robust.

Anteriorly on the metasternal process a narrow laterally directed carina of variable length arises from each flange and runs towards the ventrolateral margin of the alitrunk. In some species (*margaritae*, *kotokui*, *rubra*, *ruginodis*, *karavajevi*, *pinetorum*, *punctiventris*) this is the only laterally directed carina arising from the

metasternal process. In many others, however, a similar laterally or anterolaterally directed carina also arises from the posterior end of each flange (*kurokii*, *sulcinodis*, *gallieni*, *rugulosa*, *specularis*, *scabrinodis*, *specioides*, *bibikoffi*, *fortior*, *sabuleti*, *aloba*, *rugiventris*, *colax*, *rugosa*, *jessensis*). This posteriorly situated carina may sometimes be more strongly developed than its anterior counterpart (*schencki*, *deplanata*).

In all species, close to the posterior end of the metasternal process, the flanges partially or entirely conceal the small open metasternal pit. Behind the level of the pit the flanges are reduced to a pair of post-processional carinae which diverge posteriorly and run back between the hind coxae. This divergent pair of carinae meet the inverted U-shaped cuticular edge of the alitrunk–petiole articulatory surface where it is inserted between the hind coxae.

Males show essentially the same structure of metasternal process as do the workers and females, but in a somewhat finer, less strongly developed form.

Among other genera of the *Myrmica*-group *Manica* has the metasternal process basically very similar to *Myrmica*. However, where this latter genus has closely approximated and usually narrow flanges constituting the main part of the process, *Manica* has them reduced so that the ventral midline is visible between them. In *Manica hunteri* the flanges are very low and less well developed medially than either the anterior or posterior lateral carinae. In *M. rubida*, *bradleyi* and *mutica* the median flanges have been replaced by a pair of longitudinal crudely arched-convex thickened lobes; the lateral carinae in these species are also reduced. Post-processional carinae may be conspicuous (*rubida*), or reduced and very faint (*mutica*, *hunteri*, *bradleyi*).

In *Pogonomyrmex*, *Epebomyrmex* and *Hylomyrma* the metasternal process consists of a pair of a pair of high, tooth-like or triangular points, one on each side of the ventral midline. Post-processional carinae are absent as the floor of the alitrunk has been eroded away behind the process, along the tracks occupied by the carinae in *Myrmica*, to form a very deep, narrow, open articulation for the petiole. This articulatory excavation extends forwards beyond the anterior margins of the hind coxae and usually terminates just behind the metasternal pit. A similar

organization of the posteroventral alitrunk is seen extensively in the *Tetramorium*-group of genera, whilst a few species-groups retain a structure similar to that seen in *Myrmica*.

Huberia striata, type-species of its genus, duplicates the metasternal structure seen in *Myrmica*. The only other species in *Huberia*, *H. bruni*, has the metasternal process and ancillary structures very reduced but derived from the condition shown by *striata*. Similarly, in an undescribed small species of *Eutetramorium* (in BMNH) the metasternal process is reduced to a vestige and its lateral carinae lost. The post-processional carinae are, however, enhanced and relatively very strong.

References

- Arnoldi, K.V. (1930) Studien über die Systematik der Ameisen 6. Eine neue parasitische Ameise, mit Bezugnahme auf die Frage nach der Entstehung der Gattungsmerkmale bei den parasitären Ameisen. *Zoologischer Anzeiger*, **91**, 267–283.
- Arnoldi, K.V. (1968) Important contributions to the myrmecofauna of the U.S.S.R., with descriptions of new forms. *Zoologicheskii Zhurnal*, **47**, 1800–1822 [in Russian].
- Bernard, F. (1968) Les fourmis d'Europe occidentale et septentrionale. *Faune de l'Europe et du bassin méditerranéen*, **3**, 411 pp. Masson & Cie, Paris.
- Bolton, B. (1982) Afrotropical species of the myrmicine ant genera *Cardiocondyla*, *Leptothorax*, *Melissotarsus*, *Messor* and *Cataulacus*. *Bulletin of the British Museum (Natural History) (Entomology)*, **45**, 307–370.
- Bolton, B. (1986) Apterous females and shift in dispersal strategy in the *Monomorium salomonis*-group. *Journal of Natural History*, **20**, 267–272.
- Bolton, B. (1987) A world review of the *Solenopsis* genus-group and revision of Afrotropical *Monomorium* Mayr. *Bulletin of the British Museum (Natural History) (Entomology)*, **54**, (in press).
- Bolton, B. & Collingwood, C.A. (1975) Royal Entomological Society of London, *Handbooks for the Identification of British Insects*, **6**, part 3(c), Hymenoptera, Formicidae, 34pp.
- Cagniant, H. (1970) Une nouvelle fourmi parasite d'Algérie: *Sifolinia kabylica* (nov.sp.) *Insectes Sociaux*, **17**, 39–48.
- Cole, A.C. (1957) *Paramyrmica*, a new North American genus of ants allied to *Myrmica* Latreille. *Journal of the Tennessee Academy of Science*, **32**, 37–42.
- Dlussky, G.M. (1963) Two new species of ants from eastern Transbaikalie. *Entomologicheskoe Obozrenie*, **42**, 190–194 [in Russian].
- DuBois, M.B. (1986) A revision of the native New World species of the ant genus *Monomorium* (*minimum*-group). *University of Kansas Science Bulletin*, **53**, 65–119.

- Elmes, G.W. (1978) A morphometric comparison of three closely related species of *Myrmica*, including a new species from England. *Systematic Entomology*, **3**, 131–145.
- Elmes, G.W. (1983) Some experimental observations on the parasitic *Myrmica hirsuta* Elmes. *Insectes Sociaux*, **30**, 221–234.
- Emery, C. (1907) Una formica nuova italiana spettante ad un nuovo genere. *Rendiconto delle sessioni della R. Accademia delle Scienze dell' Instituto di Bologna*, (N.S.) **11**, 49–51.
- Forel, A. (1894) Ueber den Polymorphismus und Ergatomorphismus der Ameisen. *Verhandlungen der Gesellschaft Deutscher Naturforscher und Ärzte*, **66** Versamml. 2. Abtheilung für Entomologie, 142–147.
- Francoeur, A. (1968) Une nouvelle espèce du genre *Myrmica* au Québec. *Naturaliste Canadian*, **95**, 727–730.
- Francoeur, A. (1981) Le groupe néarctique *Myrmica lampra*. *Canadian Entomologist*, **113**, 755–759.
- Francoeur, A. & Loiseleur, R. (1984) Description du mâle et notice sur la biologie de *Myrmica quebecensis* Francoeur. *Revue d'Entomologie du Québec*, **29**, 3–11.
- Kutter, H. (1963) Miscellanea myrmecologica 1. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **36**, 129–137.
- Kutter, H. (1969) Die sozialparasitischen Ameisen der Schweiz. *Neujahrsblatt Herausgegeben von der Naturforschenden Gesellschaft in Zürich*, **1969**, 62pp.
- Kutter, H. (1973) Über die Morphologischen beziehungen der Gattung *Myrmica* zu ihren Satellitengenera *Sifolinia* Em., *Symbiomyrma* Arnoldi, und *Sommimyrmica* Menozzi. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **46**, 253–268.
- Kutter, H. (1978) *Insecta Helvetica Fauna*, **6a**, Hymenoptera, Formicidae, Figs. 1–404. Zürich.
- Latreille, P.A. (1804) *Nouveau Dictionnaire d'Histoire Naturelle*, **24**, Tableau méthodique des Insectes, 129–200.
- Latreille, P.A. (1810) *Considérations générales sur l'ordre naturel des Animaux composant les classes des Crustacés, des Arachnides, et des Insectes*; avec un tableau méthodique de leurs genres, disposés en familles, 444pp. Paris.
- Linnaeus, C. (1758) *Systema naturae*. Regnum animale, edn. 10, 824pp. Lipsiae.
- Menozi, C. (1925) *Res mutinenses*. Formicidae. *Atti della Società dei Naturalisti e Matematici di Modena*, (6) **8** [1924]. 22–47.
- Pisarski, B. (1962) Sur *Sifolinia pechi* Samš. trouvée en Pologne. *Bulletin de l'Académie Polonaise des Sciences*, (2), **10**, 367–369.
- Samšičák, K. (1957) *Sifolinia pechi* n.sp. *Ročenka Československé Společnosti Entomologické*, **53**, [1956]. 167–170.
- Samšičák, K. (1964) Zur Kenntnis der Ameisenfauna der Tschechoslowakei. *Časopis Československé Společnosti Entomologické*, **61**, 156–158.
- Van Boven, J.K.A. (1970) *Myrmica faniensis*, une nouvelle espèce parasite. *Bulletin et Annales de la Société Royale Entomologique de Belgique*, **106**, 127–132.
- Wasmann, E. (1910) Nachträge zum sozialen Parasitismus und der Sklaverei bei den Ameisen. *Biologischen Centralblatt*, **30**, 453–524.
- Wilson, E.O. (1971) *The Insect Societies*, 548pp. Cambridge, Mass.
- Wilson, E.O. (1984) Tropical social parasites in the ant genus *Pheidole*, with an analysis of the anatomical parasitic syndrome. *Insectes Sociaux*, **31**, 316–334.
- Yarrow, I.H.H. (1968) *Sifolinia laurae* Emery, 1907, a workerless parasitic ant new to Britain. *The Entomologist*, Oct. 1968, 236–240.

Accepted 21 February 1987