

# A TAXONOMIC REVISION OF THE SOCIALLY PARASITIC *MYRMICA* ANTS (HYMENOPTERA: FORMICIDAE) OF THE PALAEARCTIC REGION

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**Abstract.**— A taxonomic review is made of the 15 described species of socially parasitic *Myrmica*, found in the Palaearctic, and 3 apparently free-living *Myrmica* species that have characteristics of the “parasitic syndrome”. Notes on the current taxonomic status and biological knowledge of each species are given. Earlier synonymies are discussed and one new synonymy is made: *M. sammitica* Mei = *M. laurae* Emery. Also, the synonymy of *M. myrmecophila* Wasmann with *M. sulcinodis* Nylander is confirmed and it is suggested that the type specimen is neither an ergatoid queen nor a social parasite, but a worker parasitized by *Mermis*. The status of *M. symbiotica* Menozzi remains unclear: it is not an ergatoid queen but could be a pseudogyne worker of a parasitic species with as yet undescribed queens. Keys are given for the identification of all castes of the 10 recognised species of social parasite (including *M. symbiotica*) and the 3 associated free-living species.



**Key words.**— Taxonomy, *Sifolinia*, *Sommimyrmica*, *Symbiomyrmica*, new synonyms, key.

## INTRODUCTION

Myrmecologists first recognised that some ant species can parasitize other ant species during the late 19<sup>th</sup> century and by the early 20<sup>th</sup> century, and a number of socially parasitic ants had been described (see Wheeler 1910). Wheeler recognised four broad groups of parasitic ants: temporary social parasites, slave-makers, degenerate slave-makers and permanent (or true, workerless) social parasites; with some modification of terminology, these groups are still broadly recognised (see Wilson 1971; Hölldobler and Wilson 1990). Biologists have described various morphological and behavioural characteristics associated with the parasitic life-style and these were summarised as the “inquiline syndrome” by Wilson (1971, 1984). With a few exceptions, most social parasites are believed to be closely related to their host species, with host and parasite having a common ancestor. This generalisation known as “Emery’s rule” envisages a long period of geographic isolation leading to the establishment of a pair of free-living sibling species, which eventually, compete with each other when isolation ends. Usually one of such sibling pairs of species is out-competed and goes extinct, but theoretically, the

“weaker” one could persist by parasitizing the more successful species (see Wilson 1971; Hölldobler and Wilson 1990). Several authors (including Elmes, based on observations of genus *Myrmica*) hypothesised a more rapid evolution of social parasites by a process of “sympatric speciation” within populations; a careful review of this somewhat contentious hypothesis was provided by Bourke and Franks (1995).

The first true social parasite of *Myrmica* ants was found living in a nest of *Myrmica lobicornis* Nylander, in 1869 at the foot of the Swiss Diablerets, by Edouard Bugnion (Forel’s brother-in-law); much later, Forel (1895) described this species as *Myrmica myrmicoxena*. During the first half of the 20<sup>th</sup> century four more social parasites of *Myrmica* were found: *Myrmica myrmecophila* Wasmann (1910) from a nest of *Myrmica sulcinodis* Nylander, and three species representing monotypic genera: *Sifolinia* (*S. laurae*) Emery, 1907 based on single alate queen, *Sommimyrmica* (*S. symbiotica*) Menozzi, 1925, found in the nest of *Myrmica rubra* (L.), and *Symbiomyrmica* (*S. karavajevi*) Arnoldi, 1930, living with *M. scabrinodis* Nylander. A further 13 species (10 Palaearctic and 3 Nearctic) have been described since then. Three of the Palaearctic species were placed in the

genus *Sifolinia* (*S. pechi* Samšiňák, 1957; *S. winterae* Kutter, 1973; *S. kabylica* Cagniant, 1970) and 7 in the genus *Myrmica* (*M. bibikoffi* Kutter, 1963; *M. lemasnei* Bernard, 1968; *M. faniensis* van Boven, 1970; *M. hirsuta* Elmes, 1978; *M. samnitica* Mei, 1987; *M. ereptrix* Bolton, 1988; *M. microrubra* Seifert, 1993a). Two Nearctic species were placed in *Myrmica* (*M. lampra* Francoeur, 1968 and *M. quebecensis* Francoeur, 1981) and one in the monotypic genus *Paramyrmica* (*P. colax*) Cole, 1957; these North American species are not considered in this paper. There were several synonymies of the Palaearctic species, most importantly Bolton (1988) synonymised all at the generic level in genus *Myrmica* while Seifert (1993b, 1996) revived from synonymy genus *Symbiomyrma*. In the Palaearctic, prior to this paper, 12 species of social parasites were recognised: 9 in genus *Myrmica* and 3 in its satellite genus *Symbiomyrma*.

All the above mentioned species of social parasites show some combination of the characteristics of the inquiline syndrome (Wilson 1971; see also Arnoldi 1930, 1933; Kutter 1973; Wilson 1984; Bolton 1988; Doves 1990; Hölldobler and Wilson 1990), principally the absence of workers, reduced size of queens, widening of the waist (especially the postpetiole) and the development of a plate-like tooth (Kutter's "Parasitendorn") on the ventral surface of the postpetiole. In addition, *Myrmica* social parasites tend to be much more hairy than free-living species, and to show a much greater reduction of the spurs on the tibiae of the mid and hind legs. When myrmecologists find, living in a *Myrmica* colony, an individual, possessing some combination of these characteristics, they usually suspect that it is a social parasite. However, several apparently free-living species of *Myrmica* have characteristics of the inquiline syndrome and could be mistaken for social parasites; most notable from the Palaearctic are *Myrmica vandeli* Bondroit, 1919, *Myrmica arnoldii* Dlussky, 1963 and *Myrmica luteola* Kupyanskaya, 1990. In this paper therefore, we review these three species in addition to the 15 described forms of Palaearctic *Myrmica* social parasites; we make redescriptions and drawings where necessary, make new synonymies and provide an identification Key for all castes.

## MATERIAL AND METHODS

### Source of material

This revision is based both on material collected by the authors in different parts of Europe and Asia (totalling several hundred specimens), and examination of the type specimens from various Museums and private collections. Here we break with the tradition of abbreviating museum names to initials, used by some other authors and in our previous publications on *Myrmica*, instead we use the names of the museum's home city

because we feel that this is intuitively clearer for non-specialist taxonomists. Institution and abbreviation: The Natural History Museum, London, UK (LONDON), Naturhistorisches Museum, Basle, Switzerland (BASLE), Museum d'Histoire Naturelle, Geneva, Switzerland (GENEVA), Museum of Bologna University, Italy (BOLOGNA), Institute royal des Sciences Naturelles de Belgique, Brussels, Belgium (BRUSSELS), Museo Civico di Storia Naturale "Giacomo Doria" di Genova, Italy (GENOVA), Institute of Zoology of the Ukrainian National Academy of Sciences, Kiev, Ukraine (KIEV), Zoological Museums of Moscow State University, Russia (MOSCOW), Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia (PETERSBURG), Biological and soil Institute of Russian Academy of Sciences, Vladivostok, Russia (VLADIV), Museum and Institute of Zoology Polish Academy of Sciences (WARSAW), Natuurhistorisch Museum Maastricht (MAASTRICHT) and from the collections of Graham Elmes, Institute of Terrestrial Ecology, UK (ELMES), Maurizio Mei, Istituto di Zoologia, Roma, Italy (MEI), Henri Cagniant, Toulouse, France (CAGNIANT).

### Measurements and indices

A large number of morphometrics and indices can be used in studies of *Myrmica* species (for details see Radchenko and Elmes 1998, 1999); here we use the following measurements (socially parasitic species only, not the 3 free-living ones): HL – length of head in dorsal view, measured in a straight line from the anterior point of median clypeal margin to mid-point of the occipital margin; HW – maximum width of head in dorsal view behind the eyes; FW – minimum width of frons between the frontal lobes; FLW – maximum width between external borders of the frontal lobes; SL – maximum straight-line length of antennal scape seen in profile; AL – diagonal length of the alitrunk seen in profile from the neck shield to the posterior margin of propodeal lobes (workers) and from the antero-dorsal point of alitrunk to posterior margin of metapleural lobes (queens and males); PPW – maximum width of postpetiole from above; ESL – maximum length of propodeal spine in profile. The **indices** used are: Frontal – FI = FW/HW; Frontal-lobe – FLI = FLW/FW; Scape<sub>1</sub> – SI<sub>1</sub> = SL/HL; Scape<sub>2</sub> – SI<sub>2</sub> = SL/HW; Post-petiole – PPI = PPW/HW; Spine-length – ESLI = ESL/HW.

## TAXONOMY

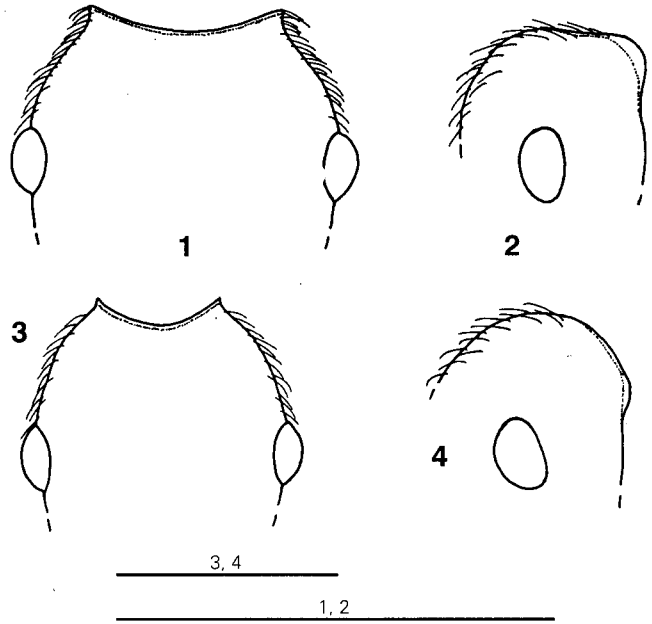
### The generic position of the social parasites of *Myrmica* species

Despite the attempts of several authors to distinguish and clarify the relationship between genus *Myrmica* and its various parasitic "satellite genera"

(e.g. Kutter 1973), there always remained a fundamental problem in discriminating them from "true" *Myrmica* species. For example, *M. hirsuta* clearly differs from *S. karavajevi*, but is not a "typical" *Myrmica* species, having many attributes of the inquiline syndrome. This led Elmes (1978) to suggest that species like *M. hirsuta* are directly derived from highly polygynous microgyne-like ancestors, and that the parasitic species, together with *Myrmica* microgynes, represent stages in a hypothetical evolutionary sequence. He concluded that *Sitolinia* should be synonymised with *Myrmica* but stopped short of formally doing this "until more convincing morphological proof ... is available". Bolton (1988) provided the convincing arguments; he could find no diagnostic characters for any of the satellite genera that were not also present in *Myrmica*, and he formally synonymised *Sitolinia* Emery, *Sommimyрма* Menozzi, *Symbiomyrma* Arnoldi and *Paramyrmica* Cole with genus *Myrmica*. However, Seifert (1993b) did not entirely agree with Bolton's treatment and revived from synonymy genus *Symbiomyrma* to include *S. karavajevi* (and its synonyms *S. pechi*, *S. winterae* and *M. faniensis*), *S. lemasnei* and *S. kabylica*.

Seifert (1993b) separated *Symbiomyrma* from *Myrmica* on their smaller sized (AL) queens and a different shape of their head margins: the posterior margin of the head in *Symbiomyrma* queens have a narrow collar-like ridge with slightly prominent postero-ventral angles (Figs 1, 2) that Seifert could not find present in other species of *Myrmica*. However, although the unusual shape the head of *Symbiomyrma* well separates it from all European species of *Myrmica*, the separation is not generally so obvious and distinct outside of Europe. For example, workers and queens from the *ritae*-group of *Myrmica* species also have prominent and slightly pointed postero-ventral angles of the head, and a narrow collar-like ridge, which is only slightly less developed than in *Symbiomyrma* queens (compare Figs 1, 2 and 3, 4). Furthermore, the shape the head of *M. erepatrix* is intermediate between that of "normal" *Myrmica* and *Symbiomyrma*. This leaves only body size as the main discriminating morphological feature (Seifert 1993b).

However, the reduced size of *Symbiomyrma* queens, compared to "normal" *Myrmica*, is not a very clear feature: the maximum size we recorded for *Symbiomyrma* species (HW < 0.85 and AL < 1.44 mm) was almost the same as the minimum recorded for *Myrmica* species (HW > 0.87 and AL > 1.50 mm in *M. laurae* and *M. myrmicoxena*). Furthermore, the smallest ergatoid queens (morphologically distinct from workers) of *M. microrubra* that we have found in the Elmes Collection, are less (HW = 0.84 and AL = 1.38 mm) than the maximum for *Symbiomyrma*. Males cannot be separated by size. For example, maximum sizes recorded for *Symbiomyrma* (HW = 0.74 and AL = 1.36 mm)



Figures 1-4. Details of structure of *Myrmica* species (queens). 1, 2. *M. karavajevi*, paratype. 3, 4. *M. serica* Wheeler. (1, 3) Occipital margin of head, postero-dorsal view; (2, 4) posterior part of head, lateral view.

are much larger than the smallest measured male of *M. arnoldii* (HW = 0.62 and AL = 1.18 mm).

It might be that *Symbiomyrma* species differ from the *Myrmica* social parasites by using more than one host species. This certainly is the case for *S. karavajevi* that has been recorded with several different species of *Myrmica* hosts, whereas parasites such as *M. hirsuta* and *M. microrubra* appear to host-specific. This could indicate that *S. karavajevi* is less closely related to its hosts than is normal for *Myrmica* social parasites. However, very little is known about the biology of the other two species of *Symbiomyrma*. Queens of *M. hirsuta* and *M. microrubra* have fairly similar behaviours to the queens of their hosts (Elmes 1976, 1983) whereas the behaviour of *S. karavajevi* queens in host nests is different (Elmes, unpublished observations). However, even if queens of all *Symbiomyrma* species have quite different behaviours from that the other *Myrmica* social parasites, it is not normally regarded as sufficient to separate genera; for example, the biology of socially parasitic species within the genus *Myrmoxenus* Ruzsky or within *Chalepoxenus* Menozzi is very different (Buschinger 1990).

We consider that erecting a separate genus for three species that are clearly very similar to *Myrmica*, is not warranted, especially when the only discriminating feature is the size of one of the castes; one could make equally valid separations based for example, on petiolar lobes or number of joints of the male antennae (see below). Therefore we formally synonymise genus *Symbiomyrma* once more with genus *Myrmica*.

### Species groups of *Myrmica* social parasites

Although, we consider that *M. karavajevi*, *M. lemasnei* and *M. kabylica* are not sufficiently different from *Myrmica* to be considered as a separate genus, we agree with Seifert (1993b) that they differ from all other *Myrmica* on a subtle combination of size and body sculpture (see below) and we suspect they have different life-history strategies compared to the other socially parasitic *Myrmica*. Therefore we consider them as a new and distinct species-group (sensu Radchenko 1994a; Radchenko and Elmes 2001a) within *Myrmica* - the *karavajevi*-group. The features of the *karavajevi*-group are apparent in Table 1, which indicates how the Palaearctic species (10 social parasites, excluding clear synonyms, and 4 presumed free-living, species) vary in respect of eight features of the inquiline syndrome (see Wilson 1971 and Introduction). Several features do not appear to be useful in defining species groups. For example, the number of joints of the male antenna would place *M. laurae* in the *karavajevi*-group along with the free-living *M. arnoldii*, which shows many features of the inquiline syndrome, and *M. tschekanovskii* which shares no other parasitic characters. Similarly, we consider that wing venation is not useful in this context: some species have cubital cells that are not partially separated and even open distally rather than being partly separated by a short vein as in "normal" *Myrmica*, but this feature is not reliable, often varying within species.

	Worker caste found	Small sized queen	Subpetiolar flanges	Wide postpetiole	Generally hairy	Reduced tibial spurs	Usually an undivided cubital cell	Male with 12-jointed antennae
Parasites								
<i>karavajevi</i>	-	++	++	+	+	+	+	+
<i>lemasnei</i>	-	++	++	+	+	+	+	+
<i>kabylica</i>	-	++	++	+	+	+	+	+
<i>myrmicoxena</i>	-	+	+	+	-	+	+	-
<i>symbiotica</i>	+	?	-	+	-	+	?	?
<i>laurae</i>	-	+	+	+	++	+	+	+
<i>bibikoffi</i>	+	-	-	+	+	+	-	-
<i>hirsuta</i>	+	+	-	+	++	-	-	-
<i>erepatrix</i>	-	+	++	++	-	+	-	?
<i>microrubra</i>	?	+	-	-	-	-	-	-
Free-living								
<i>vandeli</i>	++	-	-	-	+	+	-	-
<i>arnoldii</i>	++	++	+	+	-	+	-	+
<i>luteola</i>	++	++	+	-	+	+	-	-
<i>tschekanovskii</i>	+	?	-	-	-	+	-	+

Table 1. Comparison of the main characteristics of the inquiline syndrome, present in 10 socially parasitic and 4 presumed free-living species of *Myrmica*.

++ = strongly present, + = present, - = absent and ? = unknown

*M. laurae* has the same combination of characteristics as the *karavajevi*-group except that its queens are significantly larger. However, we do not place it in this group because by the shape of its scape the queens clearly belong to the *scabrinodis*-group together with *M. symbiotica*, *M. bibikoffi*, *M. hirsuta* and *M. vandeli*. Recently, moderately strong evidence has been produced to show that *M. vandeli* may be a temporary social parasite of *M. scabrinodis* colonies (Elmes, Radchenko and Thomas, in press), in which case, all these five social parasites belong to the same species-group as their host species.

*M. microrubra* might occasionally produce workers but to date small worker-like ergatoid queens have been observed.

We propose to place *M. myrmicoxena* and *M. arnoldii* provisionally, together as the *myrmicoxena*-group, despite their wide geographic separation, because they are very similar morphologically and clearly differ from other *Myrmica* species. The host of *M. myrmicoxena* is *M. lobicornis*. The life history of *M. arnoldii* is unknown, but it often coexists with other species of the *lobicornis*-group, which contains the most abundant and dominant *Myrmica* species of South Siberia and Mongolia. Extrapolating from the observations of *M. vandeli* (Elmes, Radchenko and Thomas, in press) we predict that *M. arnoldii* might be shown to be a temporary social parasite of a Siberian *lobicornis*-group species.

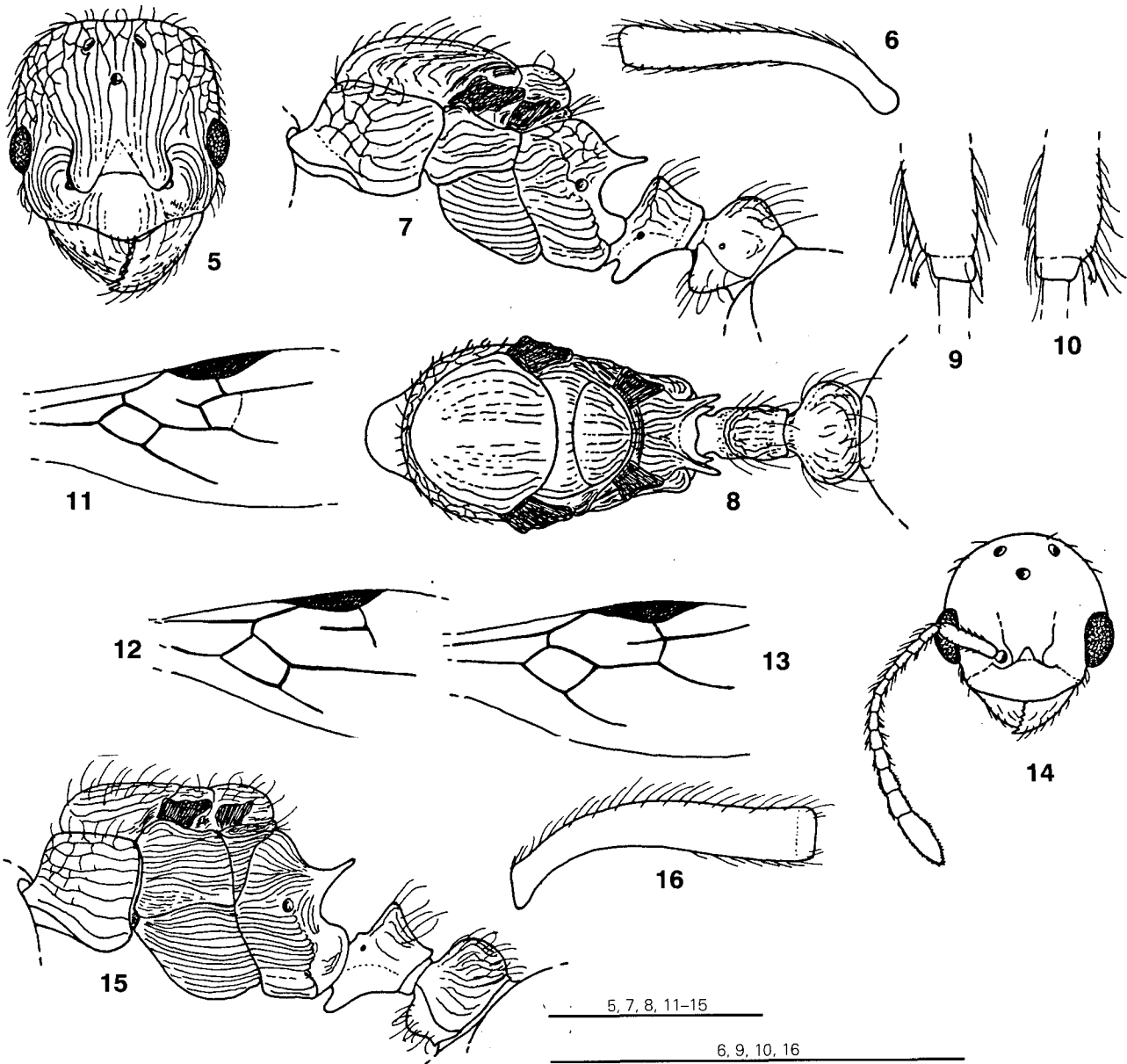
Of the remaining species considered in Table 1, *M. erepatrix* clearly belongs to the *rugosa*-group, as does its host *M. aimonissabaudiae* Menozzi, despite the peculiar, gross development of its postpetiole (see Radchenko and Elmes 2001a). *M. microrubra* belongs to the *rubra*-group, and there are good reasons to suppose that it is a "form", maybe a genetic polymorphism of *M. rubra*, as suggested by Elmes (1976) rather than a separate species (this might only be resolved by genetic studies). Nothing is known of the biology of *M. luteola*, purely on the grounds of its unusual combination of characters we placed it with *Myrmica mirabile* Elmes and Radchenko in the *luteola*-group (Elmes and Radchenko 1998), speculating that *M. luteola* might have a temporary socially parasitic life-style.

### REVIEW OF SPECIES

#### *Myrmica myrmicoxena* Forel, 1895 (Figs 5–14)

*Myrmica myrmicoxena* Forel, 1895: 143, q; Emery 1908a: 181, q, m, Fig. 12; Forel 1910: q, m; 1915: 28, 30, 31, q, m (in Key); Arnoldi 1930: 270; van Boven 1970: 129, Fig. 3; Kutter 1973: 257; 1977: 67, q, m, Figs 58–65; Seifert 1988: 41; 1993b: 17; Bolton 1995: 281.

**Material examined.** Lectotype queen (upper specimen on the pin, our designation), [Switzerland] "Anzeindaz,



Figures 5–14. Details of structure of *Myrmica* species. 5–11. *M. myrmicoxena*, lectotype queen. 12, 13. Paralectotypes queens. 14. male (after Kutter 1977). 15, 16. *M. arnoldii*, queen. (5, 16) antennal scape, lateral view; (7, 15) alitrunk and waist in profile; (8) alitrunk and waist from above; (9) distal part of tibia of hind leg; (10) distal part of tibia of middle leg; (11–13) part of forewing with cubital and discoidal cells; (14) head and antenna, dorsal view.

*M. myrmicoxena*, Type bei *M. lobicornis*" (GENEVA); paralectotypes (our designation): 2 queens (middle and bottom) on the same pin as lectotype (both without postpetiole and gaster); 2 queens (one specimen without head), "Anzeindaz, 20 août [18]69, *Myrmica! mixtissima*" (Sic!), "*M. myrmicoxena* For., Type, Anzeindaz" (GENEVA); 1 queen (with 1 worker of *M. lobicornis* on the same pin), "*lobicornis* q anormale variété, parmi des w normales. Anzeindaz, Alp. Vaudoisses, 1900 mètres, 20 août", "*Myrmica myrmicoxena* For." (GENEVA).

**Measurements and indices** (queens, n=6) (data of lectotype are in brackets). HL 1.02–1.05 (1.03), HW 0.94–0.97 (0.94), SL 0.67–0.70 (0.67), AL 1.52–1.58 (1.54) mm; FI 0.45–0.46 (0.46), FLI 1.16–1.21 (1.21), SI<sub>1</sub> 0.65–0.66 (0.65), SI<sub>2</sub> 0.71–0.72 (0.71), PPI 0.56–0.57 (0.56), ESLI 0.18–0.23 (0.23).

Forel (1874, pp. 78–79) described from the Swiss Alps unusual queens and males of *Myrmica*, found in a nest of *M. lobicornis*, but did not give them a name for another 20 years. Then he made an extremely brief

description of the queens, calling them *M. myrmicoxena* (Forel 1895), but he did not include the males to the type series. Emery (1908a) made a formal description of the males, based on Forel's (1874) original description, and Forel (1910, 1915) made further short additions to the description of queens and males. Kutter (1977) made some new notes on *M. myrmicoxena* and published the first drawings of the queen and male; Seifert (1988) followed Kutter's description. Despite these publications, we remained uncertain about some features of the morphology of *M. myrmicoxena* and felt that it should be redescribed in a more modern style. We do this for the queens but unfortunately, we have not located the males and can only provide notes of their main features based on the published data.

**Queens** (redescription). Head longer than broad, with subparallel sides, narrowly rounded occipital corners and straight or at most very weakly concave occipital margin; anterior clypeal margin broadly convex, without medial notch. Frons wide, but frontal carinae distinctly curved and frontal lobes somewhat extended. Antennal scape relatively short, does not reach occipital margin, weakly curved at the base, with no angle or carina.

Alitrunk quite short and high, propodeal spines rather thin, finger-like, slightly extended at the base. Petiolar node in profile subtriangular, without dorsal plate; ventral surface of petiole with small, not extended, narrowly rounded process. Postpetiole wide and high, with relatively small, broadly rounded ventral process.

Spur on middle and hind tibiae reduced, always distinctly shorter than width of tibiae, but varying from relatively long and with short "brush" of bristles to non-pectinate, extremely short and setae-like. The venation of forewing varies from the typical for genus *Myrmica* with the cubital cell partly separated by short vein and closed distally (Fig. 13), to the cubital cell being partly separated by a short vein, but open distally (Fig. 12), to the cubital cell being partly separated by a short vein, open distally, but with an additional cross-vein (Fig. 11).

Sculpture of whole body quite coarse. Frons with longitudinal, slightly sinuous rugae, occiput and sides of head with reticulation; antennal sockets surrounded by concentric rugae; clypeus with longitudinal rugae. Sides and dorsum of alitrunk with longitudinal rugae. Petiolar node with irregular short sinuous rugae and reticulation, postpetiole dorsally with sparse fine rugosity, more or less smooth. Surfaces between rugae on whole body smooth and shiny.

Head and alitrunk with fairly sparse, straight, standing hairs; petiolar node with less than 10 standing hairs. Appendages with numerous semidecumbent hairs. Head and alitrunk reddish-brown, appendages lighter, reddish-yellow.

**Males** (based on Forel 1874, 1910, 1915; Kutter 1977; see also Key). Antennae 13-jointed, antennal scape short,  $SI_1 = SI_2 = 0.35$  (based only on Kutter's 1977 drawing).

Head margins with short hairs. Cubital cell of forewing partly separated by short vein, but open distally (after Kutter 1977; but Forel 1910: 29 wrote that "wing venation is absolutely the same as in other *Myrmica*"). Spur on tibiae of middle legs well developed and pectinate.

**Taxonomic notes.** The queens of *M. myrmicoxena* are most similar to those of *M. arnoldii*, a South Siberian and Mongolian species, differing mainly by a somewhat narrower frons and smaller size (see Key below). Their host species (or possible host species in the case of *M. arnoldii*) belong to the *lobicornis*-group of *Myrmica* species, but they are unlikely to belong to that group because their males have relatively short antennal scape, compared to males of *lobicornis*-group, which is a feature of the *scabrinodis*-group. Therefore we place them together in the *myrmicoxena*-group (see above). However, a close relationship between the European *M. myrmicoxena* and Central Asian *M. arnoldii* seems unlikely. One important difference is that the antennae of *M. myrmicoxena* males (as drawn by Kutter 1977) have the normal 13-joints whereas those of *M. arnoldii* are 12-jointed. Kutter was normally a careful and accurate draftsman but it is just possible that he drew what he expected to see (13 segments rather than 12), therefore it is important to try and locate the males of *M. myrmicoxena* to check this feature.

**Distribution.** *M. myrmicoxena* is known only from the type locality in the Swiss Alps.

**Biology.** The type specimens taken in 1869 are the only record for this species. It was found in a nest *M. lobicornis*, at altitude 1900 m (probably under a stone). It is probably workerless and almost certainly a social parasite of *M. lobicornis*. It would pay myrmecologists to search again for this interesting species in the type locality, during August or September, in order to compare and contrast its biology with that of *M. arnoldii*.

### *Myrmica arnoldii* Dlussky, 1963 (Figs 15, 16, 121–126)

*Myrmica arnoldii* Dlussky, 1963: 191, w, Figs 1, 4, 5, Russia; Pisarski 1969: 227; Dmitrienko, Petrenko 1976: 20; Pisarski, Krzysztofiak 1981: 155; Francoeur 1981: 758; Radchenko 1994a: 44; 1994b: 134, Figs 1a, 3a; 1994c: 76; Bolton 1995: 277.

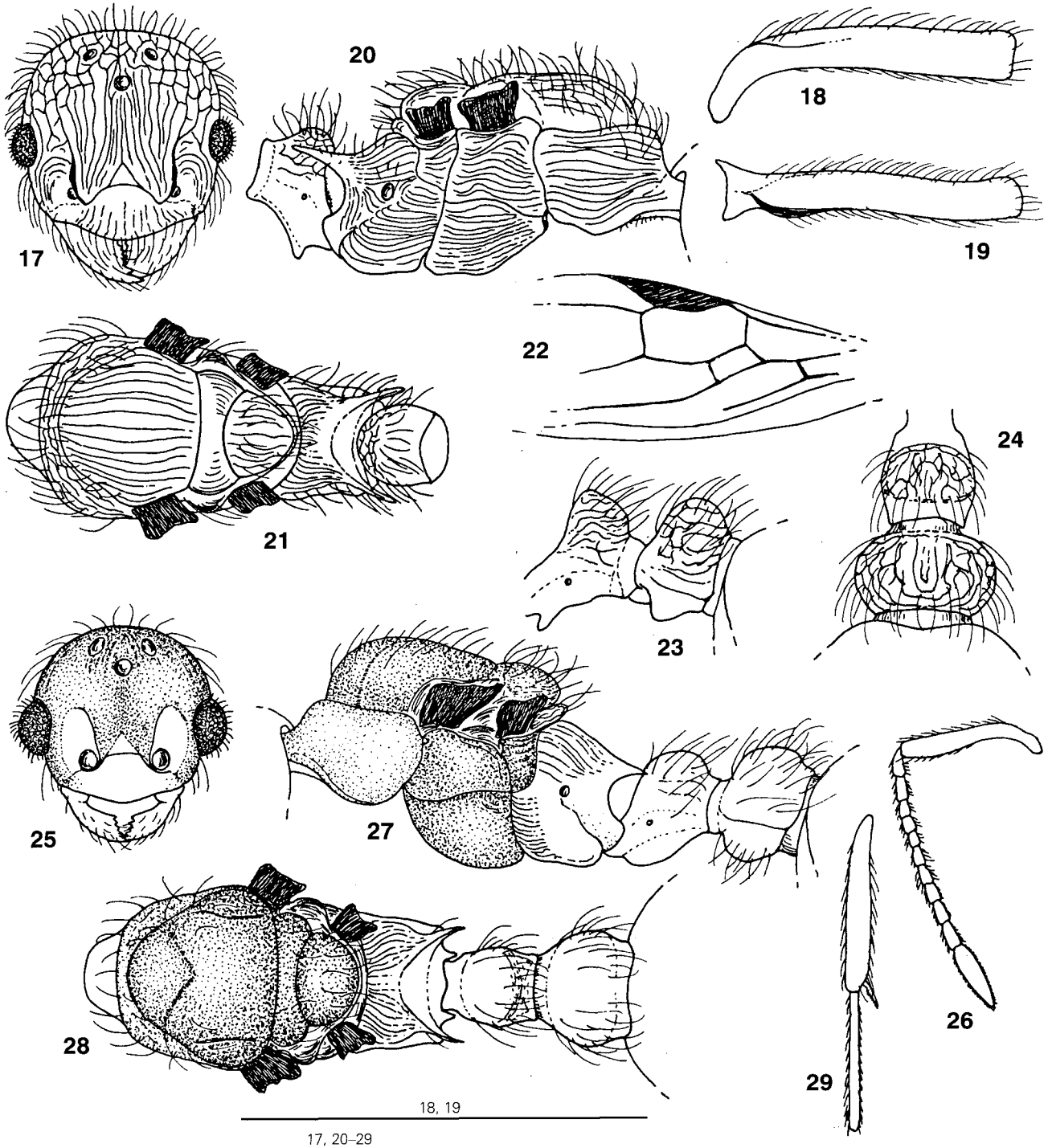
*Myrmica* (subgen. *Dodecamyrmyca*) *arnoldii*: Arnoldi, 1968: 1803, q, m.

**Material examined** Holotype worker, [Russia], Chita province, Sretensk distr., Ust'-Dunaevskoe, 12.ix.1957, leg. Dlussky (PETERSBURG); paratypes: 8 workers from the nest of holotype; 6 workers, same locality, 7.ix.1957 (MOSCOW). Non-type material: more than hundred workers, about 50 queens and males from different regions of South Siberia and Mongolia (MOSCOW, ELMES, WARSAW, KIEV).

**Taxonomic notes.** This unusual species has a rather uncertain taxonomic position. It well differs from almost all

other free-living Palearctic *Myrmica* species by several features, many of which are considered as socially-parasitic: males have 12-jointed antennae (this feature led Arnoldi 1968 describe subgenus *Dodecamyrmica*); the petiole and postpetiole of all castes have ventral lobes,

which are most developed in queens; the spurs on tibiae of mid- and hind legs are often reduced (more frequently in female castes); they are small, queens are little larger than workers (AL workers, queens and males < 1.5, 1.8 and 1.6 mm, respectively). The body sculpture, colour and shape of



Figures 16-29. Details of structure of *Myrmica laurae*. 17-22. *M. laurae*, holotype queen. 23-28. *M. samnitica* [jun. syn. of *M. laurae*]. 23, 24. Paratype queen. 25-29. Paratype male. (17, 25) Head, dorsal view; (18) antennal scape, lateral view; (19) antennal scape, dorsal view; (20, 27) alitrunk and waist in profile; (21, 28) alitrunk and waist from above; (22) part of forewing with cubital and discoidal cells; (23) petiole and postpetiole, lateral view; (24) petiole and postpetiole from above; (26) antenna; (29) tibia and first tarsal joint of hind leg.

petiole (subtriangular when viewed in profile, Figs 7, 15) of queens are similar to that of *M. myrmicoxena*, and they differ, as noted above, by their slightly larger size and wider frons (see Key). Males differ by the number of antennal segments, 12 rather than 13, as discussed above.

**Distribution.** South Siberia from Tuva to eastern Transbaikalia, and Mongolia.

**Biology.** Despite its typically "socially-parasitic" features, *M. arnoldii* has only been found living in independent colonies. Dlussky reported that in Siberia colonies lived mainly in larch forests, but also in steppe-like habitats, with nests usually being built in decaying wood and rarely in the soil. This accords with the more recent samples from Mongolia taken by M. Woyciechowski (Kraków): colonies were living on northern and western slopes in mountain *Larix-Betula* forest at about 1000 m altitude, nests were usually in rotten tree stumps but sometimes in the soil or moss, they were quite populous and usually polygynous. We suggest that *M. arnoldii* might be a temporary social parasite, or represents a hypothetical step in the evolution of social parasites, or even is a social parasite that has reverted to a free-living lifestyle. In any case, this interesting species would make an ideal subject for further study.

#### *Myrmica laurae* (Emery, 1907)

(Figs 17–29)

*Sifolinia laurae* Emery, 1907: 49, q, 3 Figs, Italy; Emery 1908b: 550; 1916: 151, Fig. 33; Bondroit 1918: 167; Arnoldi 1930: 270; Bernard 1968: 156; Baroni Urbani 1971: 75; Kutter 1973: 257, Figs 1a, 3, 4, not Yarrov 1968: 239.

*Myrmica laurae*: Bolton 1988: 4; Seifert 1993b: 17; Bolton 1995: 280.

*Myrmica samnitica* Mei 1987: 457, q, m, Figs 1–15, Italy; Seifert 1993b: 17; Bolton 1995: 283, *syn. nov.*

**Material examined.** *Sifolinia laurae*: Holotype queen (alate, without postpetiole and gaster), "Siena, Coggi" (GENOA). Non-type material: 8 queens, 1 male, [Italy] Lazio, Rieti Tarano, Vocabole Campana, 13.ix.1987, leg. M. Mei (with workers, queens and males of host species, *M. scabrinodis*); 2 queens, 4 males, [Italy], Abruzzo, Collelongo, Prati di S. Elio, 13.x.1990, leg. M. Mei (with workers of *M. scabrinodis*) (MEI, ELMES).

*Myrmica samnitica*: Paratypes, 3 queens, 1 male, [Italy], Abruzzo, Ovindoli, M. Mangola, 15.viii.1983, 1400 m., leg. M. Mei (MEI, ELMES).

**Measurements and indices.** Queens (n=14, data of holotype are in brackets): HL 0.95–1.09 (1.03); HW 0.87–1.05 (0.98); SL 0.68–0.79 (0.75); AL 1.50–1.85 (1.76) mm; FI 0.41–0.49 (0.49); FLI 1.05–1.17 (1.10); SI<sub>1</sub> 0.70–0.75 (0.73); SI<sub>2</sub> 0.74–0.80 (0.77); PPI 0.62–0.69 (postpetiole lost); ESLI 0.35–0.41 (0.41); males (n=6): HL 0.76–0.82; HW 0.77–0.84; SL 0.60–0.67; AL 1.50–1.96 mm; SI<sub>1</sub> 0.76–0.79; SI<sub>2</sub> 0.78–0.80; PPI 0.70–0.75; ESLI 0.23–0.35.

**Taxonomic notes.** Mei (1987) noted that *M. samnitica* was very similar to *Sifolinia laurae* by long standing

hairs, venation of forewings etc., but *S. laurae* well differed because spurs on middle and hind tibiae were completely absent. However, Mei was probably basing this assertion on earlier descriptions of *M. laurae* (perhaps made under low magnification). Our examination of the holotype of *M. laurae* showed the middle and hind tibiae had distinct, but greatly reduced, short spurs with no pectination. Examination of paratype queens of *M. samnitica* and other specimens collected by Mei from Lazio and Abruzzo (see above), showed that individuals varied greatly in tibial spur development, ranging from almost fully developed and pectinate to short and non pectinate. Thus we could find no consistent morphological feature to separate *M. samnitica* queens from *M. laurae*, and considered these names as synonyms. Superficially, *M. laurae* queens most resemble those of *M. hirsuta*.

*M. laurae* well differs from most other socially parasitic *Myrmica* species by combination of the following features (see also Key and Figs 17–29): eyes in both sexes with conspicuous hairs, length of the longest hairs 0.035 (queens) – 0.040 mm (males); generally a very hairy species; cubital cell on forewings closed and not partly separated by short vein; males with 12-jointed antennae, antennal scape long and slender, feebly curved at the base; antennal scape of queen not angulate, gradually curved at the base, but with distinct narrow longitudinal ridge.

**Distribution.** Central Italy.

**Biology.** When Emery (1907) described *S. laurae* it was presumed to be a social parasite though its host was unknown. Mei (1987) identified the host of *M. samnitica* as *M. sabuleti* Meinert. However, in the non-type series Mei collected from Abruzzo and Lazio, the specimens mounted with them as hosts were *M. scabrinodis* (see above). The worker specimens of these *M. scabrinodis* have relatively large scape lobes and could easily be mistaken for *M. sabuleti*, alternatively it is quite possible that *M. laurae* could use several different host species as does *M. karavajevi* (see below). No workers have been found. The type series of *M. samnitica* was found with its host colony at altitude 1400m, living under a stone, in a shaded clearing in a *Pinus nigra* wood.

#### *Myrmica symbiotica* (Menozzi, 1925)

(Figs 30–36)

*Sommimyrmica symbiotica* Menozzi, 1925: 25, ergatoid queen (?), Fig. 1, Italy; Arnoldi 1930: 270; Baroni Urbani 1971: 74; Kutter 1973: 263.

*Myrmica symbiotica*: Bolton 1988: 3; 1995: 284.

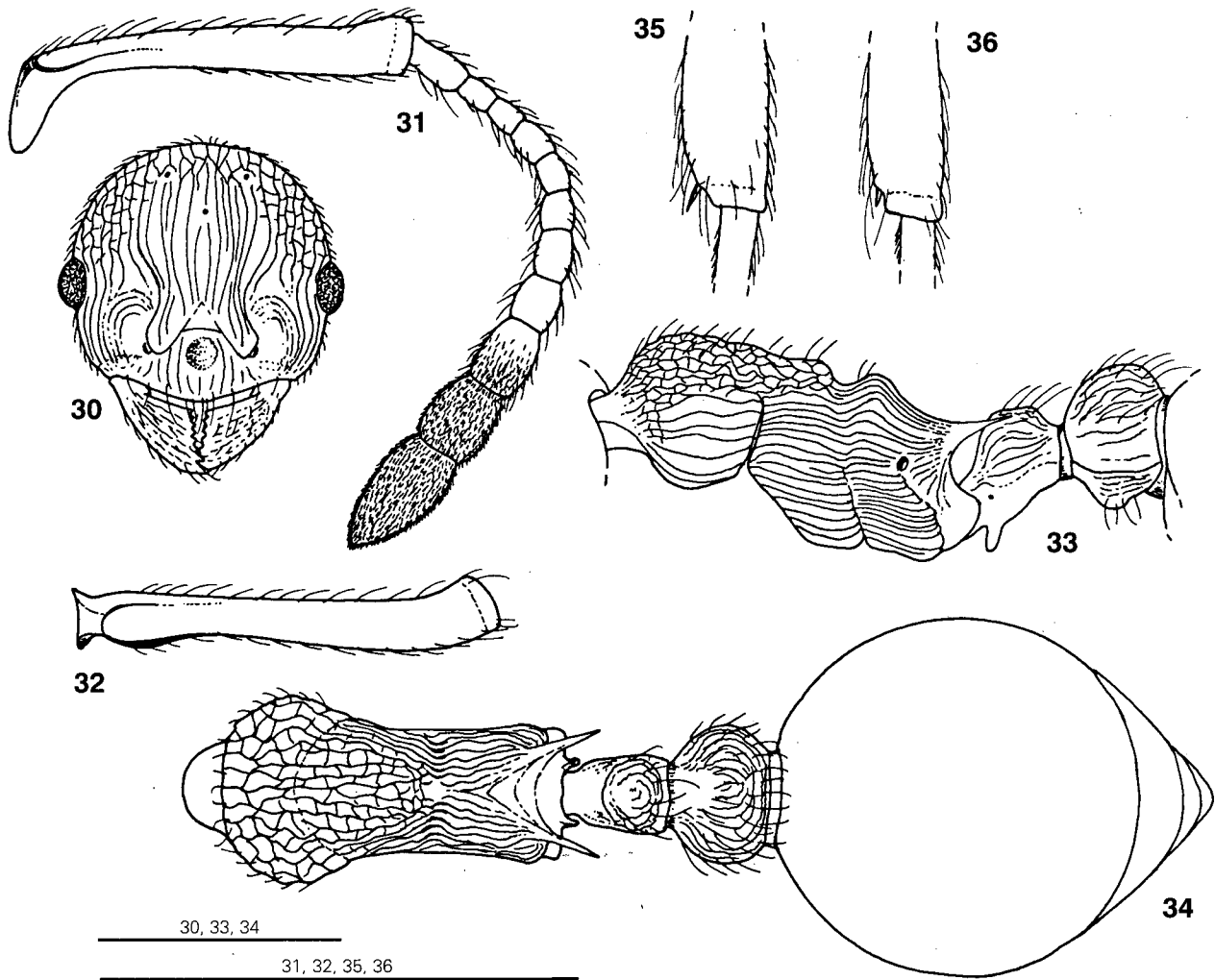
**Material examined.** Holotype "gynomorph worker", "Sestola (Emilia)", "*Sommimyrmica symbiotica* Menoz., Typus" (BOLOGNA).

**Measurements and indices** (holotype worker). HL 1.03, HW 0.96, SL 0.88, AL 1.56 mm; FI 0.38, FLI 1.31, SI<sub>1</sub> 0.84, SI<sub>2</sub> 0.91, PPI 0.60, ESLI 0.39.



**Taxonomic notes.** Menozzi (1925) described this monotypic genus based on a single specimen, collected in the nest of *M. rubra* (*M. laevinodis* Nylander sensu Menozzi) in Central Italy, and suggested that it is an ergatoid queen because it has three minute ocelli and an enlarged gaster. Menozzi considered genus *Sommimyрма* to be closely related to *Sifolinia* based on the lack of spurs on the tibiae of mid- and hind legs. He distinguished *Sommimyрма* from *Sifolinia* by the type specimen's thick and nodiform antennal club; presence of deep and big foveolate impression on the clypeus; deep metanotal groove; tibia of forelegs with longitudinal groove on the inner surface. Kutter (1973) merely repeated Menozzi's opinion, and pointed out that postpetiole of *S. symbiotica* is quite wide. When Bolton (1988) synonymised the genus, he quite logically expressed doubts that an ergatoid queen could be a social parasite.

Menozzi's original description of *S. symbiotica* is quite full and complete. Therefore here we only contribute drawings of the holotype (Figs 30–36) and list the main combination of features which distinguish it from other *Myrmica* species. These are: head with 3 minute ocelli; clypeus with big foveolate impression basally; antennal scape angulate at its base, with a narrow but distinct longitudinal lobe (similar to those of some *M. scabrinodis* or *M. specioides* Bondroit); curved frontal carinae with relatively narrow frons, but somewhat wider than in *M. scabrinodis* (FI 0.38, FLI 1.31); promesonotal dorsum saddle-shape (seen in profile), with the trace of scutum; metanotal groove very deep and abrupt; petiole and postpetiole without ventral lobes; petiole with distinct dorsal plate (similar to that of *M. scabrinodis*); postpetiole wide (PPI 0.60); gaster somewhat enlarged; mid- and hind tibial spurs strongly reduced, very short, thick, not pectinate; not a hairy species, petiole with only 6 long standing hairs.



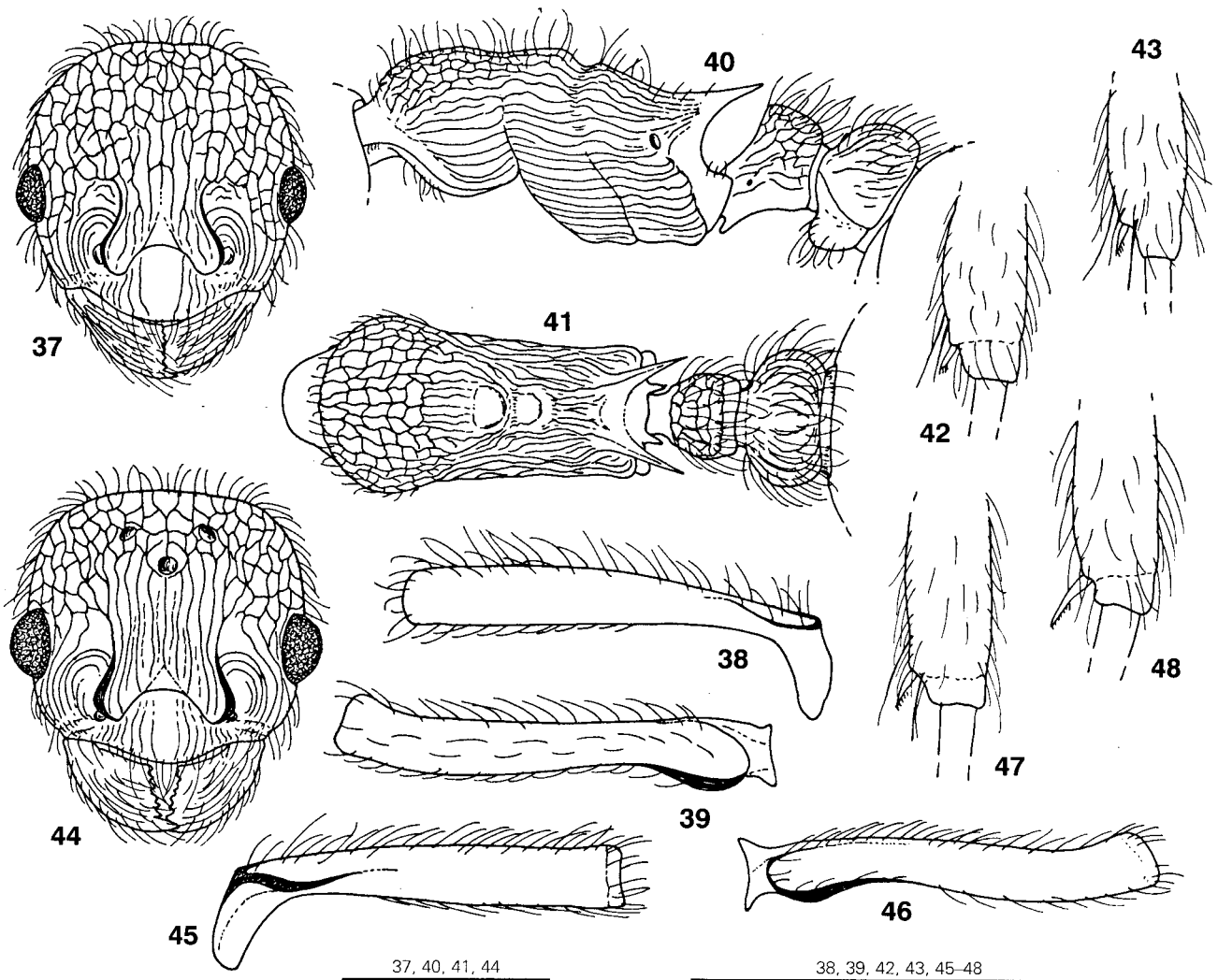
Figures 30–36. Details of structure of *Myrmica symbiotica* (holotype worker). (30) Head, dorsal view; (31) antenna, lateral view; (32) antennal scape, dorsal view; (33) alitrunk and waist in profile; (34) alitrunk, waist and gaster from above; (35) distal part of tibia of hind leg; (36) distal part of tibia of middle leg.

Bolton (1988) made several suggestions to account for this unusual specimen: e.g. it is ergatoid queen or gynecoid worker; perhaps simply an aberrant specimen of *M. rubra*; or possibly it is an ergatoid female of another *Myrmica* species that was caught by workers of *M. rubra* and taken to their nest as prey. Having had the benefit of seeing the specimen, we suggest that the holotype of *M. symbiotica* is a pseudogyne worker rather than ergatoid queen (hence we placed it in our Key for workers). The shape of its alitrunk and the presence of minute ocelli make it most similar that of the gynomorphic workers of *M. hirsuta* (see below), so that it could be the worker form of a social parasite with unknown queens.

The holotype undoubtedly belongs to the genus *Myrmica* and can be placed in the *scabrinodis*-group. The characters given by Menozzi are not sufficient to separate it from *Myrmica*: the antennal club not so thick and nodiform, as stressed by Menozzi (see Fig 31),

neither is the longitudinal groove on the inner surface of the tibia of forelegs as conspicuous as described, being merely a very shallow longitudinal impression. The most peculiar feature, never seen in any other *Myrmica* so far, is the big foveolate impression on the clypeus, but with only a single specimen this feature could simply be some type of aberration. One possibility is that it is an aberrant specimen from the *scabrinodis*-group (most probably *M. scabrinodis*) created by *Mermis* parasite infestation, it shares superficial features with such parasitized workers and pseudogynes recorded in many species of *Myrmica*. If so, how did it get into a *M. rubra* colony, one of the most aggressive *Myrmica* species in the Palaearctic? Bolton's (1988) suggestion, that it could be specimen taken as prey is an attractive possibility.

Thus the taxonomic and "biological" position of *M. symbiotica* remains unclear. On the one hand it could be a pseudogyne of a good species from *scabrinodis*-group,



Figures 37–48. Details of structure of *Myrmica bibikoffi*. 37–43. Paratype worker. 44–48. Paratype queen. (37, 44) Head, dorsal view; (38, 45) antennal scape, lateral view; (39, 46) antennal scape, dorsal view; (40) alitrunk and waist in profile; (41) alitrunk and waist from above; (42, 47) distal part of tibia of hind leg; (43, 48) distal part of tibia of middle leg.

and on the other hand it might simply be some sort of aberrant specimen. Little further can be done with this species unless "real" queens and males are discovered.

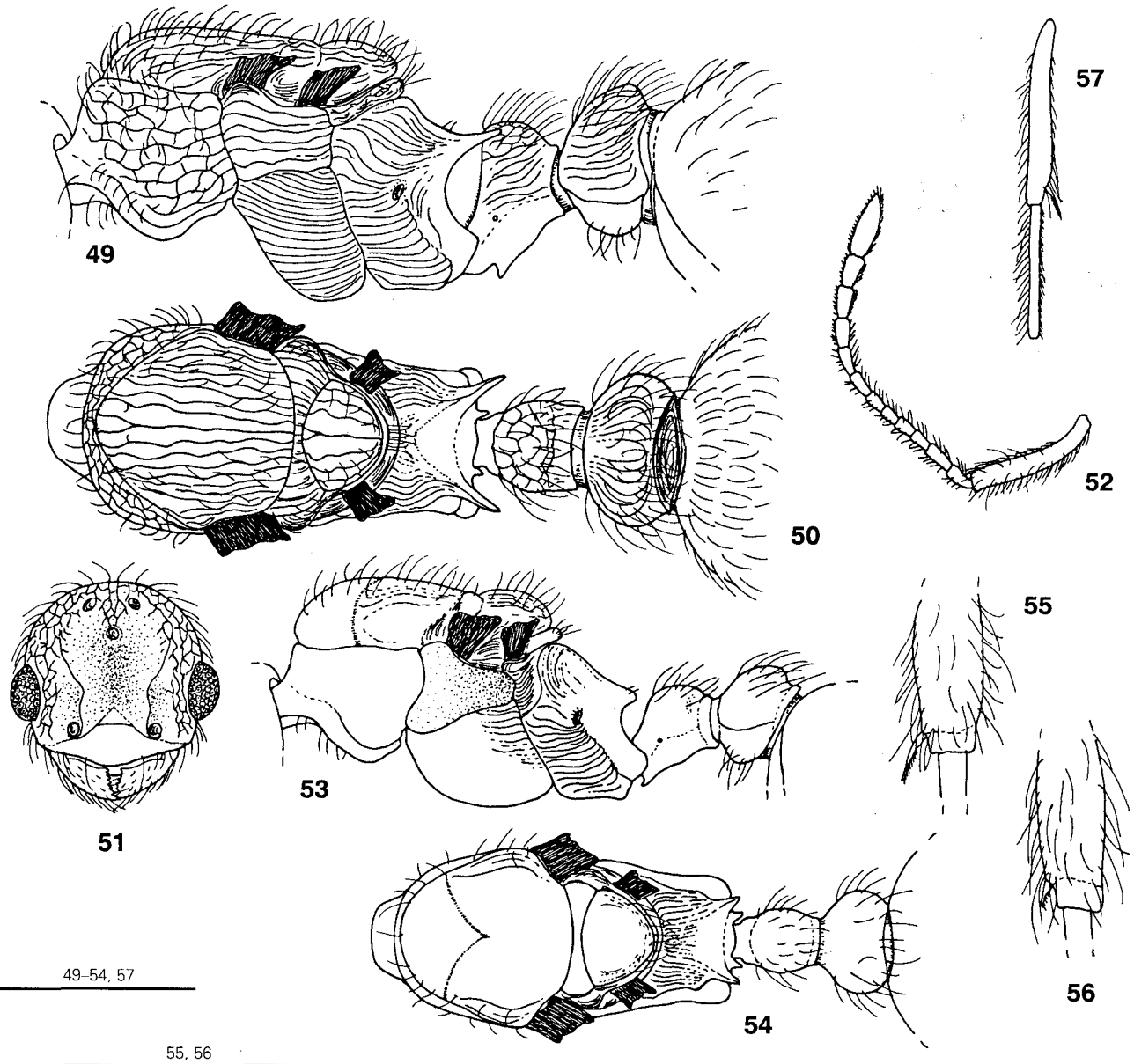
**Distribution.** Known only from the holotype from Central Italy. In his original description Menozzi gave the type locality as Mt. Calvanella, near road Fanano-Pievepleago, the holotype is labelled "Sestola (Emilia)", which is generally corresponds with more precise data in the original paper.

**Biology.** Unknown, except the holotype was found in a nest of *M. rubra*.

*Myrmica bibikoffi* Kutter, 1963  
(Figs 37–57)

*Myrmica bibikoffi* Kutter, 1963: 130, w, q, m, Figs 1–11, Switzerland; 1973: 255; 1977: 65, Figs 36–38; Bolton 1988: 4; 1995: 277.

**Material examined.** Syntypes: 4 workers, 1 queen, 3 males, [Switzerland], Vaulion, Canton Vaud, 5.viii. 1949, leg. M. Bibikoff (LONDON). Non-type material: 1 worker, 1 queen, 2 males, Germany, Schwarbische Alb, Erpfingen, limestone grassland, sunny hill slope, beneath stone, EU 489, 02.viii.1998, leg. K. Rościszewski (ELMES).



Figures 49–57. Details of structure of *Myrmica bibikoffi*. 49, 50. Paratype queen. 51–57. Paratype male. (49, 53) Alitrunk and waist in profile; (50, 54) alitrunk and waist from above; (51) head, dorsal view; (52) antenna; (55) distal part of tibia of hind leg; (56) distal part of tibia of middle leg; (57) tibia and first tarsal joint of hind leg.

**Measurements and indices.** Workers (n=5): HL 1.10–1.28; HW 0.94–1.16; SL 0.82–1.04; AL 1.50–1.78 mm; FI 0.34–0.35; FLI 1.40–1.47; SI<sub>1</sub> 0.75–0.86; SI<sub>2</sub> 0.85–0.91; PPI 0.51–0.59; ESLI 0.36–0.43; queens (n=2): HL 1.24–1.40; HW 1.22–1.34; SL 0.96–1.00; AL 2.14 mm; FI 0.35–0.39; FLI 1.26–1.37; SI<sub>1</sub> 0.71–0.77; SI<sub>2</sub> 0.79–0.80; PPI 0.60–0.61; ESLI 0.30–0.35; males (n=5): HL 0.84–0.94; HW 0.80–0.87; SL 0.56–0.69; AL 1.78–1.86 mm; SI<sub>1</sub> 0.64–0.74; SI<sub>2</sub> 0.68–0.78; PPI 0.55–0.57; ESLI 0.07–0.20.

**Taxonomic notes.** This quite conspicuous species clearly belongs to the *scabrinodis*-group. *M. bibikoffi* is characterized by strongly reduced spurs on the hind and mid tibiae, a coarse reticulated sculpture on head and alitrunk, wide postpetiole of workers and queens, and hairy body. It is similar to *M. hirsuta* and shares the same host, *M. sabuleti*. Queens are larger than those of *M. hirsuta* and also differ by their body sculpture and narrower frons (see Key).

**Distribution.** Till now this rare species has been found 3 times in the Alps and south Germany: at the type locality, at Tessin (probably Germany) (Kutter 1973) and near Erpfingen, Baden-Wurtemberg, Germany (see above).

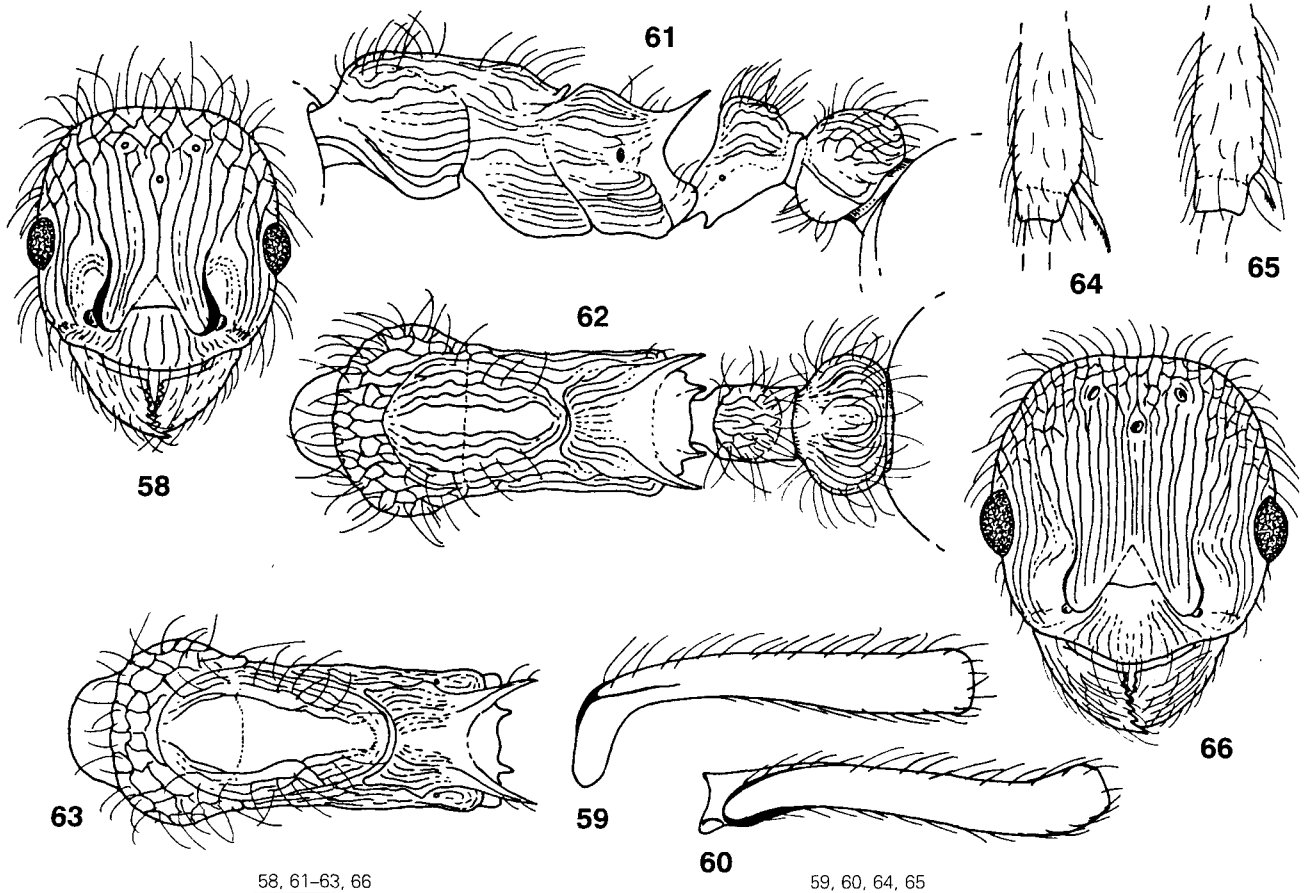
**Biology.** Bibikoff found all castes of this species living independently, but the two other colony samples

were collected in the nests of *M. sabuleti* where only workers of the host species were found. This suggests that *M. bibikoffi* might be a temporary social parasite, which in some ecological situations can only survive as a permanent social parasite.

*Myrmica hirsuta* Elmes, 1978  
(Figs 58–66)

*Myrmica hirsuta* Elmes, 1978: 131, q, m, Fig. 2, England; Collingwood 1979: 51, Fig. 68; Assing 1987: 78; Bolton 1988: 4; Seifert 1988: 42, Figs 97–99, 121, 154, 155; Vepsäläinen and Pisarski 1982: 328; Elmes 1994: 439, w; Bolton 1995: 278; Saaristo 1995: 155; Seifert 1993b: 15; 1996: 234; Czechowska and Radchenko 1997: 53, Figs 1–5, 11–13; Radchenko et al. 1997: 491, Figs 68, 69; Czechowski et al. 2002: 31, Plate X, Figs 5, 17, 18.

**Material examined.** Paratypes, 34 queens and 19 males, Durlleston Country Park, Purbeck, Dorset, UK, under stone, limestone grassland, leg. G. W. Elmes, 1973 (in 9 different infested colonies of *M. sabuleti*). Non-type material: 113 queens, 12 males from 4 sites in southern England; 1 queen, 1 male, Zeilerberg, Leitha Mts., Austria; 2 queens, 2 males, Unstrut, Germany; 110 queens, 45 males, 3 workers,



Figures 58–66. Details of structure of *Myrmica hirsuta*. 58–65. “Pseudogyne” workers. 66. Paratype queen. (58, 66) Head, dorsal view; (59) antennal scape, lateral view; (60) antennal scape, dorsal view; (61) alitrunk and waist in profile; (62) alitrunk and waist from above; (63) alitrunk from above; (64) distal part of tibia of hind leg; (65) distal part of tibia of middle leg.

1 gynandromorph, Langbjerg, Mosbjerg, Denmark; 1 queen, 5 males, Bukksetkeresat, Hungary; 25 queens, 5 males, Koverhar, Hanko, Finland; 5 queens, 5 males, Pieniny Mts, southern Poland, 49°25'N, 20°23'W (ELMES, WARSAW).

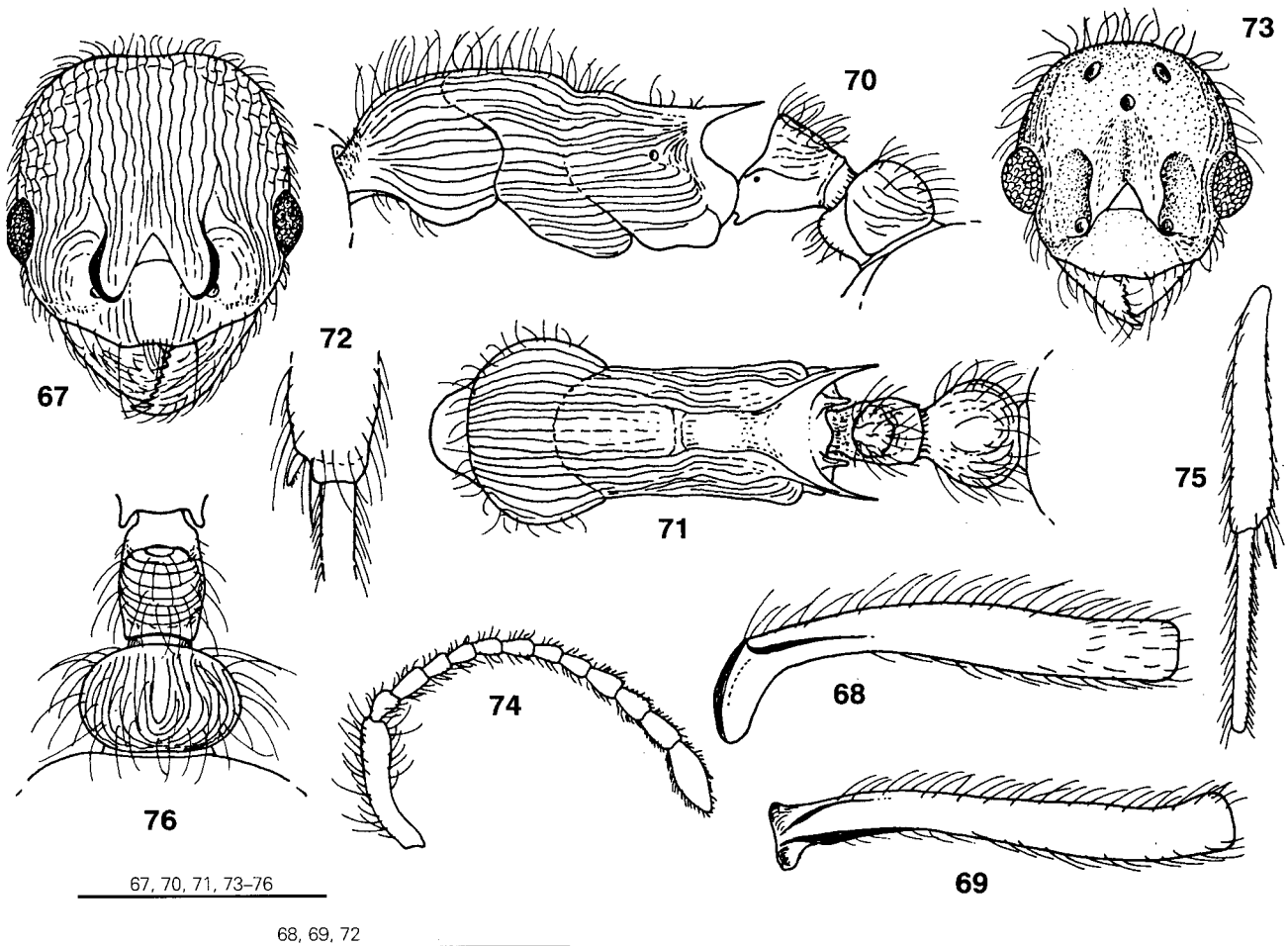
**Measurements and indices.** Workers (n=3): HL 1.02–1.06; HW 0.88–0.95; SL 0.78–0.80; AL 1.46–1.56 mm; FI 0.40–0.42; FLI 1.17–1.23; SI<sub>1</sub> 0.75–0.78; SI<sub>2</sub> 0.84–0.91; PPI 0.55–0.58; ESLI 0.34–0.37; queens (n=36, paratypes): HL 1.00–1.18; HW 0.88–1.10; SL 0.72–0.88; AL 1.62–2.00 mm; FI 0.39–0.46; FLI 1.10–1.30; SI<sub>1</sub> 0.68–0.81; SI<sub>2</sub> 0.73–0.84; PPI 0.57–0.72; ESLI 0.24–0.36; males (n=21, paratypes): HL 0.82–0.94; HW 0.80–0.88; SL 0.43–0.50; AL 1.66–1.92 mm; SI<sub>1</sub> 0.50–0.58; SI<sub>2</sub> 0.52–0.63; PPI 0.63–0.73; ESLI 0.06–0.12.

**Taxonomic notes.** The holotype is in the Natural History Museum (London) and was not examined for this study because paratypes from the same host-nest series were available. When Elmes (1978) described *M. hirsuta* from southern England, he considered it to be a workerless social parasite of *M. sabuleti*. Later, in infested nests

from Denmark he found two workers (Elmes 1994), both are pseudogyne, having minute ocelli and at least a trace of scutum (see Figs 58, 61–63). *M. hirsuta* is generally most similar to *M. bibikoffi* (see notes above and Key) while the queens are superficially similar to *M. laurae*.

**Distribution.** The species has now been found from many sites in southern England. It appears to be very widely distributed throughout Western Europe with records from Germany, Hungary, Austria, Denmark, Sweden, southern Finland, southern Poland, Czech Republic and Yugoslavia.

**Biology.** In Central Europe *M. hirsuta* is clearly and obligatory social parasite of *M. sabuleti*. It produces workers only very rarely: three entire host colonies of *M. sabuleti* from Denmark were collected and examined yielding only 3 *M. hirsuta* workers. It is probable that if host colonies for other related social parasites, such as *M. laurae*, were exhaustively searched in the same way, a few workers of these species might be located. Its nearest relative, *M. bibikoffi* (see above), has been recorded as free living. So, these species might illustrate



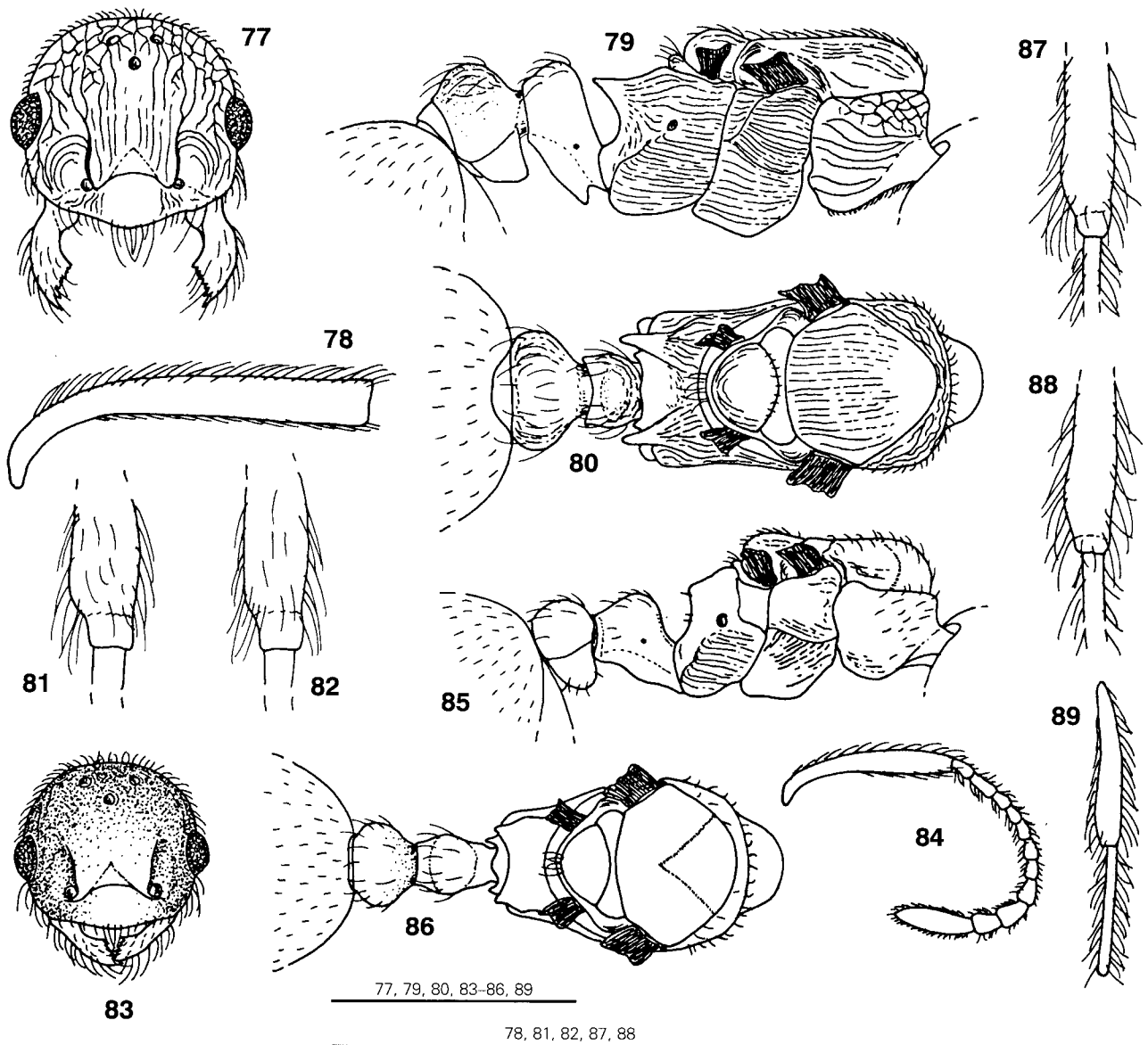
Figures 67–76. Details of structure of *Myrmica vandeli*. 67–72. Worker. 73–75. Paralectotype male. 76. Lectotype queen. (67, 73) Head, dorsal view; (68) antennal scape, lateral view; (69) antennal scape, dorsal view; (70) alitrunk and waist in profile; (72) alitrunk and waist from above; (72) distal part of tibia of hind leg; (74) antenna; (75) tibia and first tarsal joint of hind leg; (76) petiole and postpetiole from above.

trend from temporary social parasitism and facultative social parasitism (with some workers) in certain ecological conditions, to obligatory social parasitism with just a few workers being produced in some conditions. In northern Europe, *M. hirsuta* has been found living in *M. lonae* colonies. This could indicate a degree of host transference but equally might indicate that *M. lonae* is only an "ecological race" of *M. sabuleti*. In our experience *M. hirsuta* occurs wherever a strong population of *M. sabuleti* exists, but on average only about 1 in 50–100 host colonies are infested (Elmes 1983). Thus one has to examine a large number of host colonies before finding *M. hirsuta*; generally this is easier when the host lives under stones.

*Myrmica vandeli* Bondroit, 1919  
(Figs 67–76)

*Myrmica vandeli* Bondroit, 1919: 148, q, m, Figs 1, 2, France; Bernard 1968: 122; Kutter 1977: 71, w, Figs 107–117; Agosti, Collingwood 1987: 53; Seifert 1988: 33, Figs 114, 132, 147, 156–158, 164, 166; 1993b: 12; Bolton 1995: 284; Seifert 1996: 226; Elmes and Thomas 1985: 97; Elmes, Radchenko and Thomas (in press).

**Material examined.** Lectotype queen (our designation), "Les Ganges, Jura", "*Myrmica vandeli* Bondr. Type" (upper specimen on the pin with 2 queens and 2 males) (BRUSSELS); paralectotypes: 1 queen, 2 males from the pin of lectotype; 2 queens, 6 males with same labels as lectotype; 1 queen, 2 males, "Les Ganges pres Pontarlier"; 1 male (without waist and gaster), "Pontarlier, A. Vandel",



Figures 77–89. Details of structure of *Myrmica karavajevi*. 77–82. Paratype queen. 83–89. Paratype male. (77, 83) Head, dorsal view; (78) antennal scape, lateral view; (79, 85) alitrunk and waist in profile; (80, 86) alitrunk and waist from above; (81, 87) distal part of tibia of hind leg; (82, 88) distal part of tibia of middle leg; (84) antenna; (89) tibia and first tarsal joint of hind leg.

“Les Ganges, fin Août 1918”; 2 males, “St. Colombe, Doubs, 2.ix.1919”, 1 male, “Ganges-Marboz, Doubs, 3.ix.1919” (BRUSSELS). Non-type material: several tens workers, queens and males from Great Britain, Switzerland, France, Poland and Czechia (ELMES, WARSAW, KIEV).

**Taxonomic notes.** *M. vandeli* has several “socially parasitic” features, such as reduced spurs and hairy body and is similar to *M. bibikoffi* and *M. hirsuta*, differing from the latter by the size of its queens, details of sculpture, shape of postpetiole, etc. (see also Key). Several records have been made of it living in mixed colonies with *M. scabrinodis* workers, which suggests that it might in some circumstances be a facultative, temporary, social parasite of *M. scabrinodis* (Elmes, Radchenko and Thomas, in press).

**Distribution.** France, Germany, Great Britain, Switzerland, Austria, Poland, Czechia, Slovakia, and Yugoslavia.

**Biology.** This species lives in warm, humid places and is particularly abundant in marshes and bogs in the southern foothills of the Alps. Almost always it lives in association with *M. scabrinodis*, perhaps preferring slightly moister nest sites. We have never located mixed colonies among strong populations of *M. vandeli*, only from more northern marginal populations where *M. vandeli* is much rarer. This led us to suggest that at the centre of its range it might be a free-living competitor of *M. scabrinodis* while at the margins it is out competed and resorts to temporary social parasitism to establish colonies (Elmes, Radchenko and Thomas, in press). This species might be an example of Emery’s rule “in action” (see Introduction).

***Myrmica karavajevi* (Arnoldi, 1930)**  
(Figs 77–89)

*Symbiomyrma karavajevi* Arnoldi, 1930: 269, q, m, Figs 1–5, Ukraine (Sic!) (also described as new by Arnoldi, 1933: 41); Seifert 1993b: 15; 1996: 236; Saaristo 1995: 158.  
*Sifolinia karavajevi*: Samšiňák 1964: 156; Kutter 1973: 258 (misspelled as *S. karawajewi*), Figs 1d, 2b, 6, 7; Pisarski 1975: 16;

Bolton and Collingwood, 1975: 18; Doves 1977: 147, Fig. 1; Arnoldi, Dlussky 1978: 535, Fig. 187, 8; Collingwood 1979: 58; Maavara 1981: 6; Blinov 1985: 7; Saaristo 1986: 97, Fig. 2; Agosti and Collingwood 1987: 53.

*Myrmica karavajevi*: Bolton 1988: 4; 1995: 280; Czechowski et al. 2002: 33.  
= *Sifolinia pechi* Samšiňák 1957: 167, q, Figs 1, 2, Czechia; Pisarski 1962: 367, m, syn. of Samšiňák 1964: 156; Kutter 1973: 262; Bolton 1995: 281 (misspelled as *S. pechei*).  
= *Sifolinia laurae*: Yarrow 1968: 239, q, m, Figs 1–6, England, not Emery 1907 et al., misidentification.  
= *Myrmica faniensis* van Boven, 1970: 127, q, Figs 1, 2, Belgium; Kutter 1973: 257, Fig. 10, syn. of Seifert 1993b: 15.  
= *Sifolinia winterae* Kutter, 1973: 263, q, m, Figs 1c, 2a, 8, 9b, 13g–k, 14, 15, Switzerland; 1977: 73, Figs 114–116; Bolton 1988: 7; 1995: 284, syn. of Seifert 1993b: 15.

**Material examined.** *Myrmica karavajevi*: paratypes queen and male, [Ukraine] “Zmiev, prov. Kharkov, 29.ix.1929, K. Arnoldi”, “*Symbiomyrma karawajewi* (Sic!) K. Arn., paratypus” (LONDON). Non-type material: several tens of queens and males from England, France, Germany, Poland, Czechia, Finland, Sweden, Ukraine, Belarus, Moldova and Russia (LONDON, BASLE, WARSAW, KIEV, MOSCOW, PETERSBURG, ELMES).

*Sifolinia winterae*: paratype male, “Nax, V5, 19.vii.1971, leg. A. Buschinger”, “Typus”; 1 queen, “Pont de la Morge, Wallis bei Nax, 21.vii.1971, leg. A. Buschinger”, “*Sifolinia winterae* q, *M. ruginodis* w” (GENEVA) (see also notes below).

*Myrmica faniensis*: holotype queen, “Hautes Fagnes, Baraque Michel, 31-5-195, v. B.-R.”, “*Myrmica faniensis* nov. spec., holotype, det. Van Boven, 1969” (MAASTRICHT).

**Measurements and indices.** Queens (n=31): HL 0.78–0.89; HW 0.73–0.84; SL 0.71–0.80; AL 1.16–1.44 mm; FI 0.42–0.49; FLI 1.03–1.07; SI<sub>1</sub> 0.83–0.92; SI<sub>2</sub> 0.89–1.00; PPI 0.55–0.62; ESLI 0.26–0.33; males (n=12): HL 0.66–0.79; HW 0.65–0.73; SL 0.63–0.79; AL 1.14–1.28 mm; SI<sub>1</sub> 0.91–1.01; SI<sub>2</sub> 0.97–1.10; PPI 0.54–0.63; ESLI 0.09–0.16.

**Taxonomic notes.** *M. karavajevi* has clear affinities with *M. lemasnei* and *M. cagnianti* (see above and Key). We summarise the main features that we find useful for separating these three species in Table 2.

<i>M. karavajevi</i> (Figs 77–89)	<i>M. lemasnei</i> (Figs 90–101)	<i>M. kabylica</i> (Figs 102–114)
<b>Queens</b>		
<ul style="list-style-type: none"> <li>■ first gastral tergite with only sparse short decumbent pubescence;</li> <li>■ postpetiolar dorsum without reticulation;</li> <li>■ surface of head, alitrunk and waist smooth or at most superficially punctured, appears shiny;</li> </ul>	<ul style="list-style-type: none"> <li>■ first gastral tergite in its basal half with conspicuous, quite long suberect hairs;</li> <li>■ postpetiolar dorsum with distinct reticulation;</li> <li>■ surface of head, alitrunk and waist smooth or at most superficially punctured, appears shiny;</li> </ul>	<ul style="list-style-type: none"> <li>■ first gastral tergite with only sparse short decumbent pubescence;</li> <li>■ postpetiolar dorsum without reticulation;</li> <li>■ surface of head, alitrunk and waist finely but densely punctured, appears dull;</li> </ul>
<b>Males</b>		
<ul style="list-style-type: none"> <li>■ first gastral tergite with only sparse short decumbent pubescence</li> <li>■ surface of scutum and scutellum not punctured, smooth and shiny</li> </ul>	<ul style="list-style-type: none"> <li>■ first gastral tergite in its basal half with conspicuous, quite long suberect hairs</li> <li>■ surface of scutum and scutellum not punctured, smooth and shiny</li> </ul>	<ul style="list-style-type: none"> <li>■ first gastral tergite with only sparse short decumbent pubescence</li> <li>■ surface of scutum and scutellum finely but densely punctured, appears dull</li> </ul>

Table 2. The main features for comparison of three closely related *Myrmica* social parasites (*Symbiomyrma* sensu Seifert 1993b).

Arnoldi (1930) writing in German, first described the species (and new genus) *Symbiomyrma karavajevi* from eastern Ukraine (Kharkov region) and repeated his description in the Russian language in 1933. Perhaps because of a mind set created by the "Iron Curtain" all Western authors (including Bolton 1995) have given the type locality erroneously as "Russia". *S. karavajevi* was considered to be workerless socially parasitic species with its primary host being *M. scabrinodis*.

Samšičák (1957) described a new species (*Sifolinia pechi*), which he presumed to be a social parasite from Czechia (Bohemia), and placed in the hitherto monotypic genus *Sifolinia*; his description was based on a single queen found on the ground while observing a nuptial flight of *M. rubra*. Pisarski (1962) found this species in southern Poland and described the males. However, Samšičák (1964) considered *S. pechi* as a junior synonym of *Symbiomyrma karavajevi*, and at the same time synonymised *Symbiomyrma* with genus *Sifolinia*. We have not study the holotype of *S. pechi*, only Pisarski's material from Poland. Without any doubt, the males and queens from Poland are the same species as *S. karavajevi*. Given that Pisarski, an excellent taxonomist, saw the holotype of *Sifolinia pechi* and identified his material as this species, we are confident in accepting the Samšičák's (1964) synonymy. On the other hand we have seen specimens of "*Sifolinia laurae*" sensu Yarrow (1968) (queens and males from Southern England, Dorset) in the "LONDON" collection and entirely agree with Kutter (1973) and Bolton and Collingwood (1975), that these specimens are *M. karavajevi*.

When van Boven (1970) described *Myrmica faniensis* (from Belgium, based on single dealate queen) he compared it with all other known socially parasitic *Myrmica* species, from which it well differs, but he did not compare it with known species of *Sifolinia*. Kutter (1973) supposed that *Myrmica faniensis* should be junior synonym of *S. karavajevi*, but it was Seifert (1993b) who formally synonymised these species (without making any comments). Our examination of the holotype of *M. faniensis* showed that it lies within the range of variation seen for *S. karavajevi*, thus we entirely agree with Seifert's synonymy.

Finally, Kutter (1973) described *S. winterae* based on holotype queen, found in Switzerland by Mrs. Winter 17.ix.1970 near Schwyz road. He also described, as a paratype, the male collected by A. Buschinger 19.vi.1971 in Valais, near Nax, but for some reason Kutter failed to include in the type series several queens, collected by Buschinger at the same time. We have studied the paratype male and one of the non-type queen, collected by Buschinger (GENEVA). The holotype queen is missing: We obtained a queen (BASLE) with labels fully corresponding to Kutter's (1973) data for holotype of *S. winterae* (i.e. "leg. Winter, 17.ix.1970, 1400m, Schwyz, CH", "*Sifolinia winterae*", "Typus"), but this specimen is

the queen of *M. hecate* Weber (a distinctive Himalayan species, queens and males of which were described by Radchenko and Elmes 2002), probably remounted in error after several specimens had fallen from their pins. Obviously Kutter's original description and drawings were based on another specimen very similar to the queen, collected by Buschinger (GENEVA).

The main features distinguishing *S. winterae* from *S. karavajevi*, according to Kutter, are a slightly different shape of propodeal spines and the pilosity of the body. However, both of these features are very variable in the studied nest series of *M. karavajevi* from France, Russia and Ukraine; using Kutter's characters we would identify some specimens (from the same series) as *M. karavajevi* and others as *S. winterae*. Therefore we agree with Seifert's (1993b) opinion that *S. winterae* is junior synonym of *M. karavajevi*.

**Distribution.** Ukraine, European part of Russia, Belarus, Moldova, Estonia, Finland, Sweden, Norway, Poland, Czechia, Germany, Belgium, Austria, Switzerland, Italy, France, England.

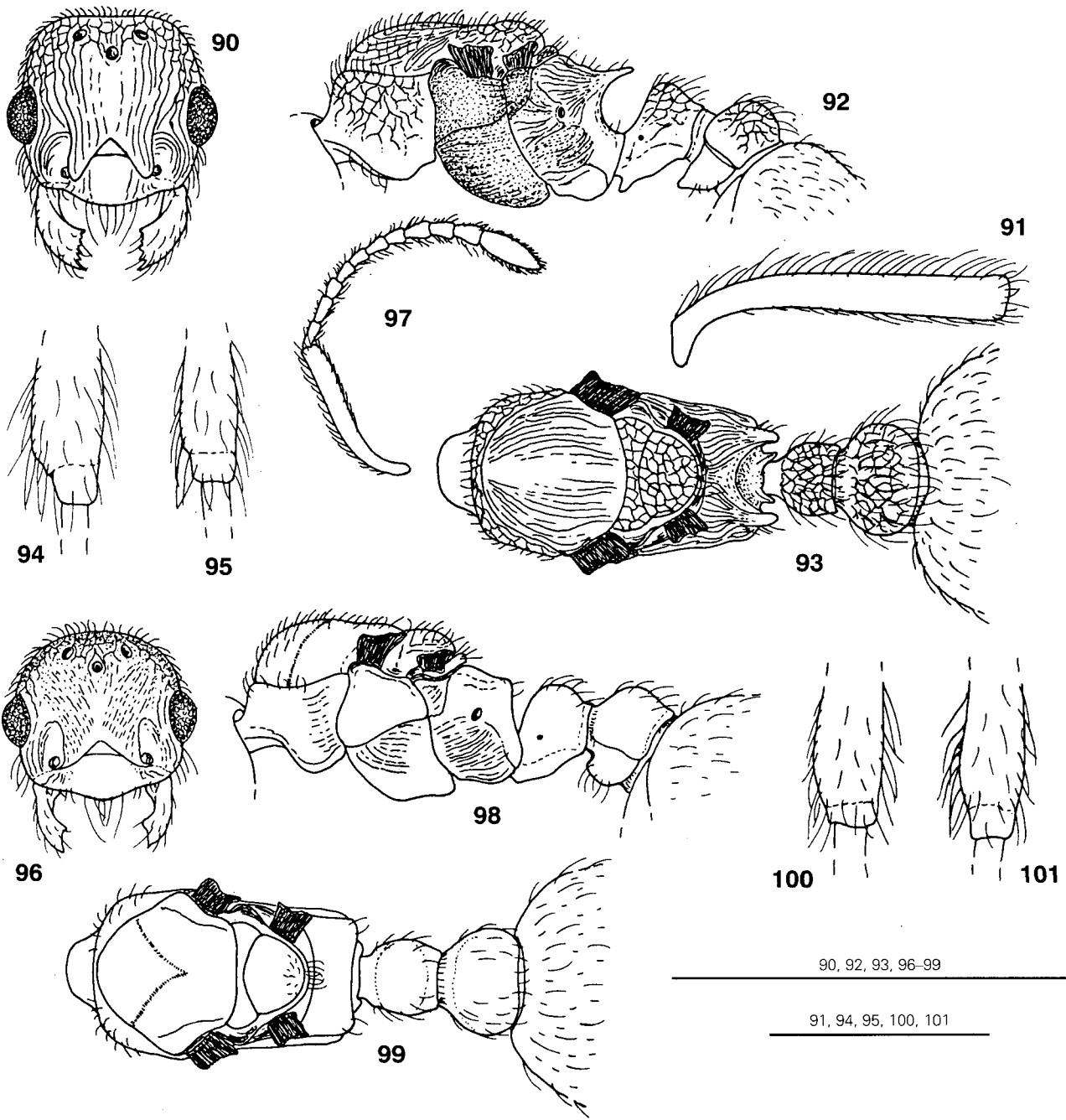
**Biology.** *M. karavajevi* is probably the most widespread of the workerless *Myrmica* social parasites. It is nowhere common, and usually myrmecologists can find one or two infested colonies and no more, despite repeated searching. On a few sites it has been found in the same population of host ants in different years (e.g. in Finland by Savolainen and in France by Elmes).

It is catholic in its choice of host species and is perhaps a generalist social parasite specialising on species from the *scabrinodis*-group of *Myrmica*. Arnoldi (1930, 1933) found it with *M. scabrinodis*; in England its host was *M. sabuleti*; Elmes found it with *M. scabrinodis* in France; in Poland host species was *M. gallienii* (Pisarski 1962 noted as host species *M. rugulosa*, misidentification, material examined); in Finland it hosts appear to be *M. scabrinodis* and *M. lonae* while we found *M. karavajevi* near St. Petersburg in a nest of *M. lonae*. Similarly, the host worker on the same pin as a *S. winterae* queen (GENEVA) was *M. gallienii* (although determined as *M. ruginodis* by Kutter). One common feature is that all its hosts live in warm but relatively wet places in marshes, meadows and forest glades. The host colony of *M. sabuleti* from England lived in rather cool damp conditions, which begs the question whether a cryptic ecomorph of *M. sabuleti*, with biology similar to *M. lonae*, exists in England (Elmes, unpublished).

*Myrmica lemasnei* Bernard, 1968  
(Figs 90–101)

*Myrmica lemasnei* Bernard, 1968: 123, q, Figs 120, 127, France; Bolton 1988: 4; 1995: 280.  
*Sifolinia lemasnei*: Kutter 1973: 258, m; Espadaler 1981: 121, q, m.  
*Symbiomyrma lemasnei*: Seifert 1993b: 17.





Figures 90-101. Details of structure of *Myrmica lemasnei*. 90-95. Queen. 96-101. Male. (90, 96) Head, dorsal view; (91) antennal scape, lateral view; (92, 98) alitrunk and waist in profile; (93, 99) alitrunk and waist from above; (94, 100) distal part of tibia of hind leg; (95, 101) distal part of tibia of middle leg; (97) antenna.

**Material examined.** 1 male, "Col. de l'Ouillat, leg. Le Masne, Nr. 2", "*Sifolinia lemasnei*, male Nr. 2", "Cotypus"; 1 queen, "Col. de l'Ouillat, leg. Le Masne", "*Sifolinia lemasnei*, queen Nr. 2" (BASLE); 2 queens, N. Spain, Jaca, Huesca, 28.x.1978, leg. Espadaler (KIEV, ELMES).

**Measurements and indices.** Queens (n=3): HL 0.88-0.90; HW 0.82-0.85; SL 0.77-0.79; AL 1.40-1.44 mm; FI 0.45-0.49; FLI 1.03-1.05; SI<sub>1</sub> 0.86-0.90; SI<sub>2</sub> 0.91-0.95;

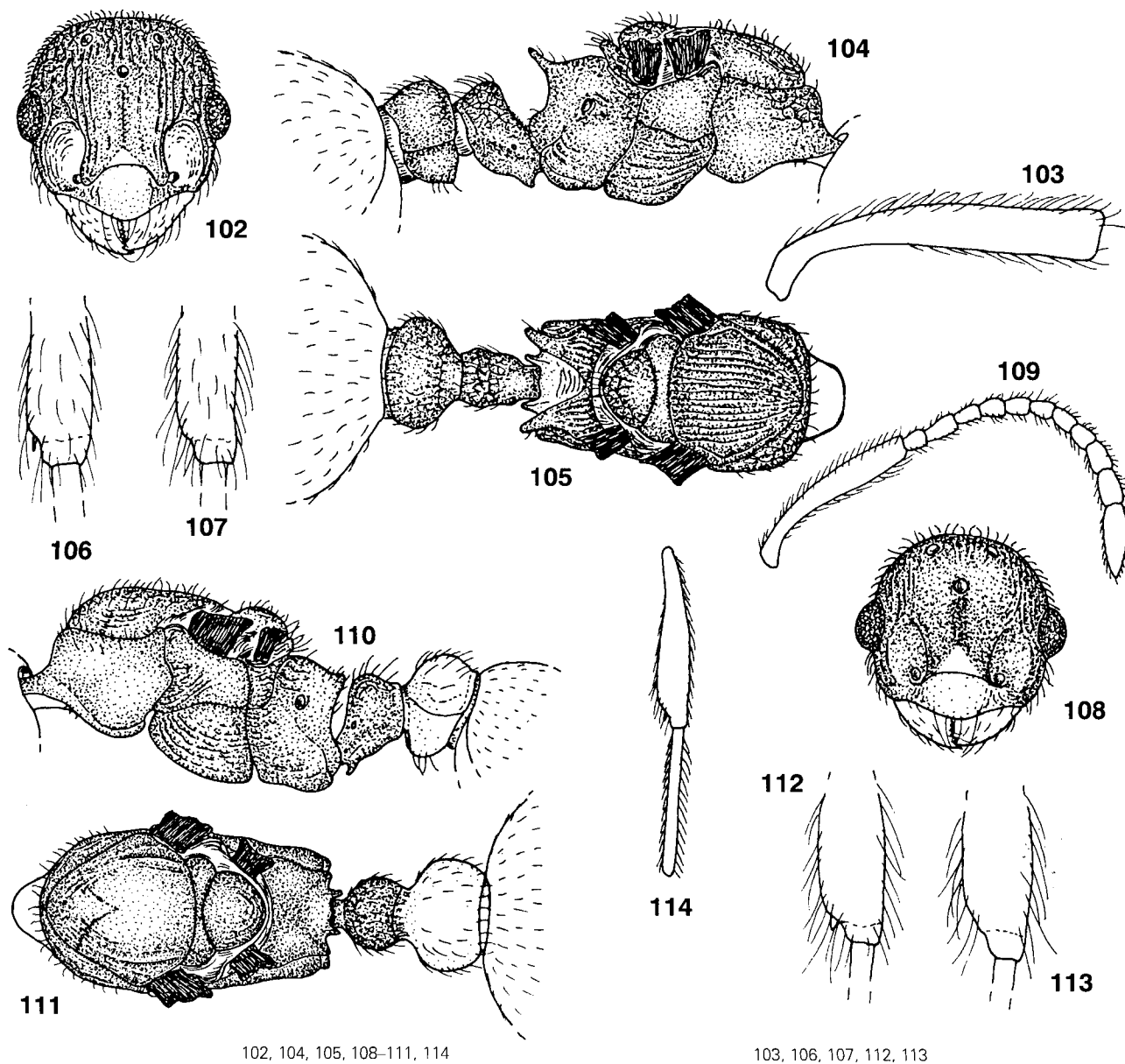
PPI 0.56-0.60; ESLI 0.31-0.332; male: HL 0.77; HW 0.74; SL 0.75; AL 1.32 mm; SI<sub>1</sub> 0.97; SI<sub>2</sub> 1.01; PPI 0.65; ESLI about 0.00 (propodeal practically unarmed).

**Taxonomic notes.** This is clearly a good species, but its nomenclature is somewhat uncertain. The problem is that the holotype appears to be lost and the original description of Bernard (1968) does not fully conform to the later specimens and description given by Kutter (1973).

Bernard's collection is stored in the Museum National d'Histoire Naturelles, Paris and specialists from that museum kindly checked his collection but could not locate the type specimen. It is possible that Le Masne had a collection but if he did, we have no idea where it might be.

Bernard described *M. lemasnei* from a single dealate queen, collected by Le Masne in a nest of *M. sabuleti* in the forest in French Pyrenees near the Spanish border (coll de l'Ouillat, 900 m, April 1939). In contrast, Kutter (1973: 258) stated that the holotype was collected in 1950 and "now seems to be lost", but gave no further reasons for his statements. However, Kutter made a very clear redescription of

queens of *S. lemasnei* and gave a first description of males, based on 8 queens and 3 male "cotypes", collected by Le Masne in July 1956 from Col de l'Ouillet, the type locality for *M. lemasnei* (note: according to the Code of Zoological Nomenclature these males can not considered as types). Kutter (1973) transferred *M. lemasnei* to the genus *Sifolinia* based on his (later collected) specimens and characters in Bernard's original description, such as petiole and postpetiole having ventral lobes, a relatively small body size, a rounded head and socially parasitic life-style. We investigated 1 male "cotype" sensu Kutter and one of the queens from same series and found them to

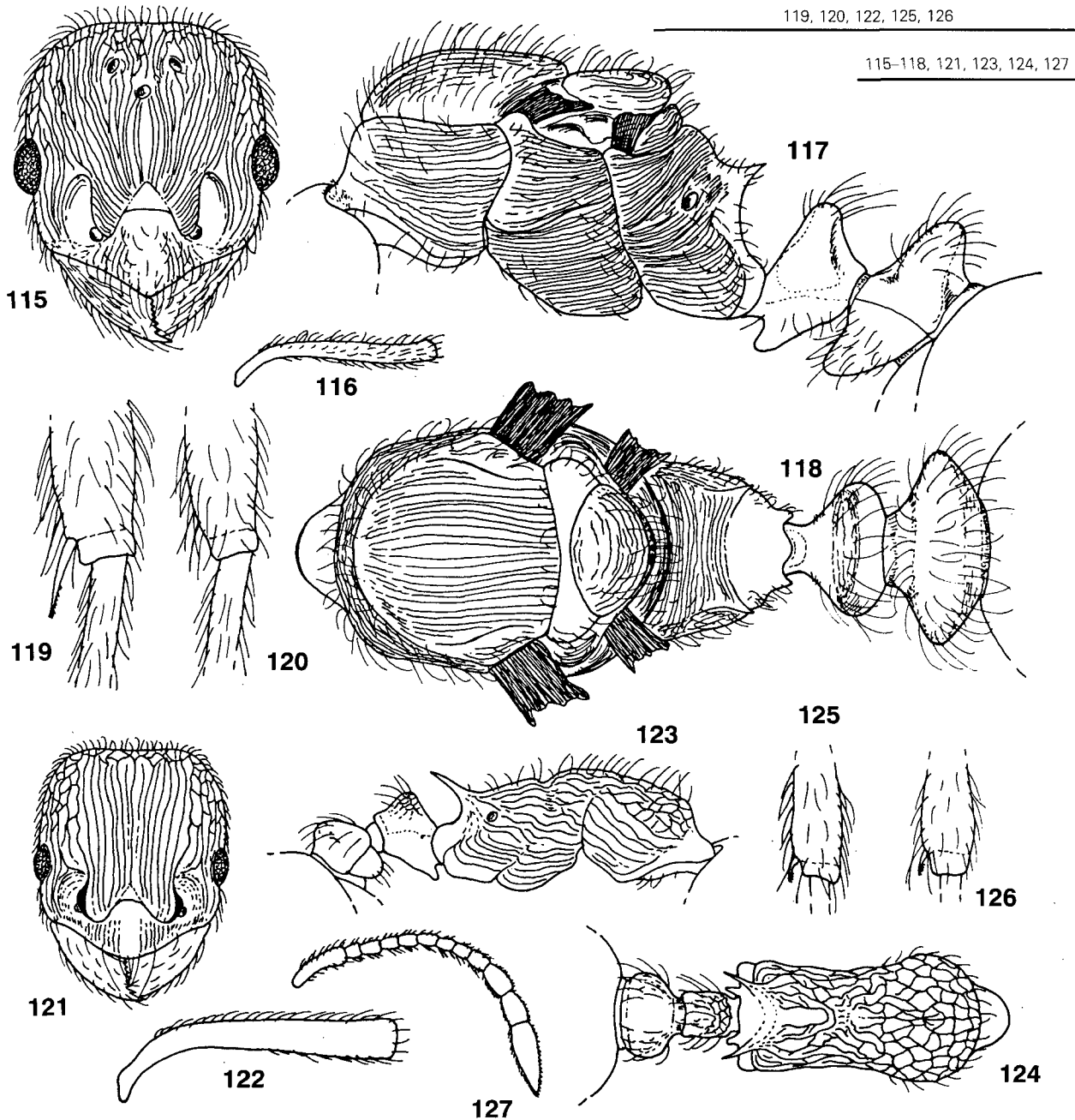


Figures 102–114. Details of structure of *Myrmica kabylica*. 102–107. Syntype queen. 108–114. Syntype male. (102, 108) Head, dorsal view; (103) antennal scape, lateral view; (104, 110) alitrunk and waist in profile; (105, 111) alitrunk and waist from above; (106, 112) distal part of tibia of hind leg; (107, 113) distal part of tibia of middle leg; (109) antenna; (114) tibia and first tarsal joint of hind leg

totally agree with Kutter's description, as did 2 queens collected by Espadaler, from northern Spain, and identified by him as *S. lemasnei* (Espadaler 1981).

While Kutter's specimens are a good species, now placed once more in *Myrmica*, the question remains whether it is the same species that Bernard described? It is quite possible that Le Masne by chance collected one species of social parasite in 1939 and a second in 1956. Alternatively we could simply dismiss Bernard's original

description as being poor and inadequate and accept Kutter's later description, except for one significant statement. Bernard (1968: 124) wrote: "... base du scape en angle presque droit, légèrement rebordé mais bien moins que celui de *sabuleti*..." ("...antennal scape curved at about right angle, with fine ridge, but it is much smaller than that in *M. sabuleti*..."). This would make it quite different from *S. lemasnei* sensu Kutter, which, like *M. karavajevi* and *M. kabylica*, has antennal scape



Figures 115-127. Details of structure of *Myrmica* species. 115-120. *M. ereptrix*, holotype queen. 121-127. *M. arnoldii* (121-126. Paratype worker. 127. Male). (115, 121) Head, dorsal view; (116, 122) antennal scape, lateral view; (117, 123) alitrunk and waist in profile; (118, 124) alitrunk and waist from above; (119, 125) distal part of tibia of hind leg; (120, 126) distal part of tibia of middle leg; (127) antenna.

that is gradually curved at the base and without any trace of a longitudinal ridge or lobe. Unfortunately, the photograph of the holotype (Bernard 1968, Fig. 127) is of poor quality and does not help to resolve this. On the other hand, there are clear inconsistencies in Bernard's description which might support the contention that the description of the scape is simply a further error: for example, (i) in the text the size said to be 3 mm, but in the corresponding figure shows it to be 3.9 mm (the latter is more probable), (ii) the propodeal spines are described as blunt, but in Figs 120, 127 (ibid.) they are distinctly pointed and (iii) under "collected material" the specimen was noted as a worker although the description and photograph are clearly that of a queen.

For the time being, we suggest that the pragmatic solution to this problem is to accept Kutter's treatment of *M. lemasnei*. When it is certain that Bernard's original holotype is lost, a neotype from Kutter's later series could be designated. If someone should find the holotype and demonstrate that it is not "*M. lemasnei*" sensu Kutter, then Bernard's holotype of *M. lemasnei* should be redescribed and the Kutter's material would be an un-named species.

**Distribution.** Pyrenees.

**Biology.** Workerless social parasite. In France this species was found in pine forest, at altitude 900 m, under a granite stone in a soil, in the nest of *M. sabuleti*; in Spain found in oak forest, at altitude 800 m in a *M. sabuleti* nest (Espadaler 1981). In the region of the Pyrenees (both France and Spain) where *M. lemasnei* has been found, there also lives a different form of *M. sabuleti*, the so-called "West-Mediterranean form" of *M. sabuleti* (Seifert 1988). Possibly, the West-Mediterranean form of *M. sabuleti* is the host of *M. lemasnei*, rather than "typical" *M. sabuleti*.

### *Myrmica kabylica* (Cagniant, 1970)

(Figs 102–114)

*Sifolinia kabylica* Cagniant, 1970: 40, q, m, Figs 1–6, Algeria; Kutter 1973: 256, 267 (misspelled as *S. cabylica*).

*Myrmica kabylica*: Bolton 1988: 4; 1995: 280.

*Symbiomyrma kabylica*: Seifert 1993b: 17.

**Material examined** Syntypes queen and male, Tala Guilief, Algeria (Kabylia), 17.vii.1966 (CAGNIANT).

**Measurements and indices.** Queen (syntype): HL 0.84; HW 0.75; SL 0.73; AL 1.21 mm; FI 0.45; FLI 1.06; SI<sub>1</sub> 0.87; SI<sub>2</sub> 0.97; PPI 0.60; ESLI 0.31; male (syntype): HL 0.79; HW 0.73; SL 0.74; AL 1.36 mm; SI<sub>1</sub> 0.94; SI<sub>2</sub> 1.01; PPI 0.62; ESLI 0.15.

**Taxonomic notes.** In most major features *M. kabylica* is most similar to *M. karavajevi* and *M. lemasnei* (see above), but clearly differs on a combination of morphological features (see Table 2 and Key).

**Distribution.** Known only from the type locality in Algeria.

**Biology.** It is a workerless social parasite. It was taken from a nest of *M. cagnianti* Espadaler living in subalpine meadow, at altitude 1800 m. The host species is very similar to *M. aloba* Forel, indeed the host nest was originally determined as *M. aloba* (see Espadaler 1996). It is possible that this species parasitizes all *M. aloba*-like species and might be found in nests of *M. aloba* on the Iberian Peninsula.

### *Myrmica ereptrix* Bolton, 1988

(Figs 115–120)

*Myrmica ereptrix* Bolton, 1988: 2, q, India; 1995: 279; Radchenko and Elmes 2001a: 250.

**Material examined.** Holotype queen, Kashmir, Gulmarg, 20.vii.1986, 2800 m, leg. Williams (LONDON).

**Measurements and indices** (holotype queen). HL 1.20; HW 1.06; SL 0.86; AL 1.96 mm; FI 0.53; FLI 1.02; SI<sub>1</sub> 0.72; SI<sub>2</sub> 0.81; PPI 0.92; ESLI 0.36.

**Taxonomic notes.** This species is known only from the single holotype queen. It has extremely exaggerated parasitic characteristics, especially a very conspicuous, extremely wide petiole and postpetiole, with well-developed, large ventral lobes. Bolton (1988) gave *M. rugosa* as the host species, but following our revision of the Himalayan species of *Myrmica* we identified the host as *M. aimonissabaudiae* (Radchenko and Elmes 2001a). *M. ereptrix* is quite distinctive from all other known Palaearctic *Myrmica* social parasites. This is not surprising if it follows Emery's rule because the Himalayan *Myrmica* fauna differs from all other Palaearctic *Myrmica* with almost the entire fauna being endemic to the region (Radchenko and Elmes 2001a).

### *Myrmica microrubra* Seifert, 1993

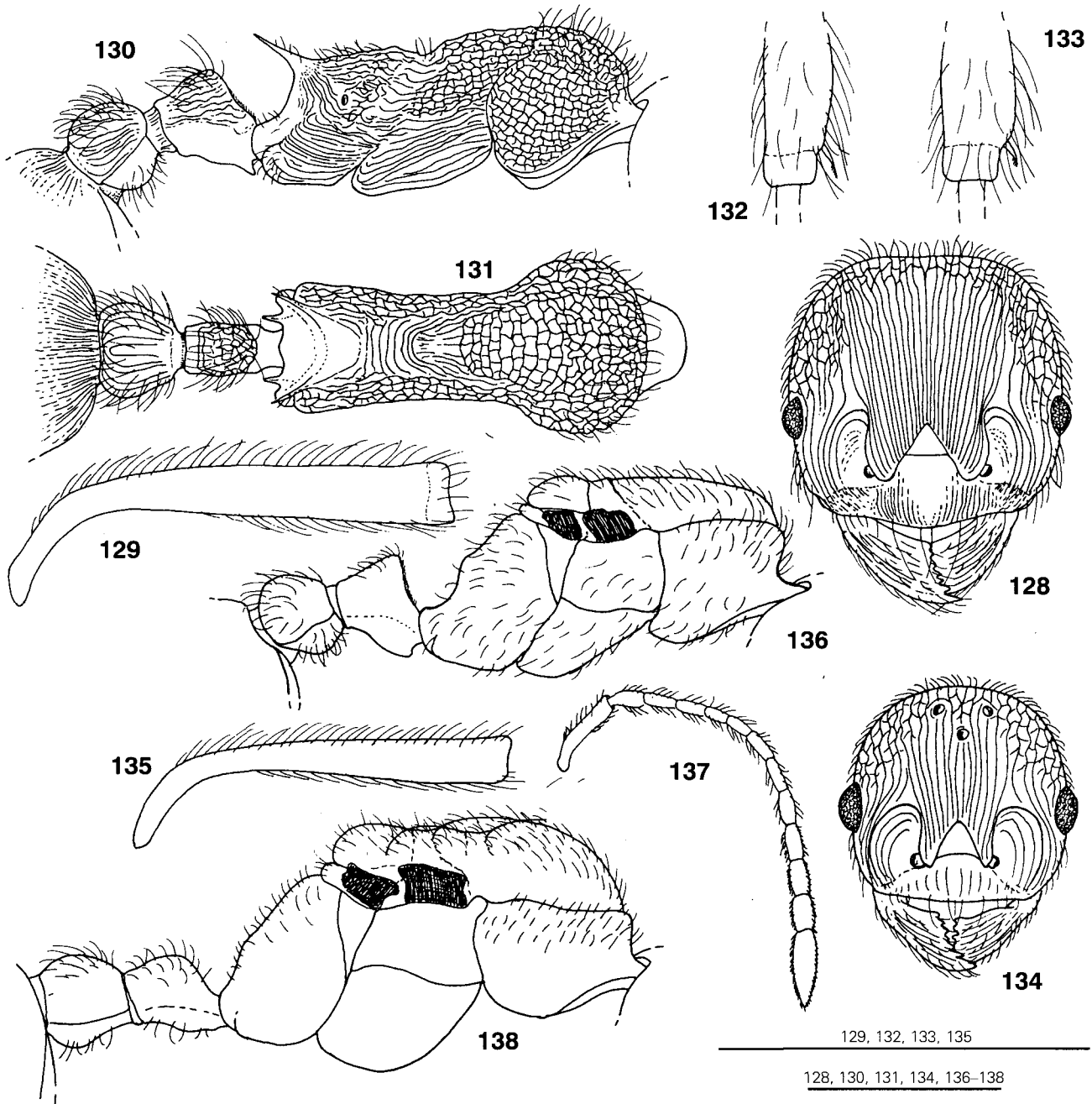
*Myrmica microrubra* Seifert, 1993a: 10, q, m, Figs 1, 4, Germany; 1993b: 14; 1996: 230; Czechowski et al. 1999: 123; 2002: 19.

= *Myrmica rubra microgyna*: Elmes and Keller 1993: 295, not Brian and Brian 1949: 397.

= *Myrmica microgyna* Pearson, 1981: Buschinger 1990: 255 (see note below).

**Material examined.** About one hundred of queens and males from Britain, Denmark, Sweden, Finland, Slovakia, Ukraine and Russia (ELMES, KIEV, WARSAW).

**Measurements and indices** (Note: specimens measured were reared in the laboratory from four infested colonies collected in Dorset, England and two from near St. Petersburg, Russia. Ten "normal" *M. rubra* males reared from infested colonies from the same regions were measured for comparison). Queens (n=15): HL 1.00–1.12; HW 0.84–0.96; SL 0.78–0.88; AL 1.64–1.88 mm; FI 0.48–0.54; FLI 1.02–1.07; SI<sub>1</sub> 0.75–0.85; SI<sub>2</sub> 0.89–1.05; PPI 0.47–0.55; ESLI 0.16–0.24; males (n=20 of *M. microrubra*; n=10 of *M. rubra* from same sites, in



Figures 128–138. Details of structure of *Myrmica luteola*. 128–133. Paratype worker. 134–135. Queen. 137, 138. Male. (128, 134) Head, dorsal view; (129, 135) antennal scape, lateral view; (130, 136, 138) alitrunk and waist in profile; (131) alitrunk and waist from above; (132) distal part of tibia of hind leg; (133) distal part of tibia of middle leg; (137) antenna.

brackets); HL 0.74–0.98 (0.88–1.02); HW 0.66–0.84 (0.76–0.86); SL 0.57–0.78 (0.76–0.88); AL 1.40–1.92 (1.80–2.14) mm; SI<sub>1</sub> 0.70–0.91 (0.79–0.96); SI<sub>2</sub> 0.76–1.03 (0.93–1.07); PPI 0.59–0.70 (0.62–0.70); ESLI 0.00–0.01 (0.0–0.06).

**Taxonomic notes.** This species used to be considered a microgyne morph of its host until Seifert (1993a) described it as a separate socially parasitic species. Using allozyme analysis Pearson (1981) suggested that

*M. rubra* microgynes are sufficiently isolated from *M. rubra* to be considered as a separate species, but he never formally named it [even though Buschinger (1990) ascribed the authorship of the species “*M. microgyna*” to him]. There remains the possibility (favoured by Elmes in several experimental reports) that queens of *M. microrubra* are intraspecific inquillines or microgynes. These possibilities were discussed by Bourke and Franks (1991) and the exact status of *M. microrubra* is

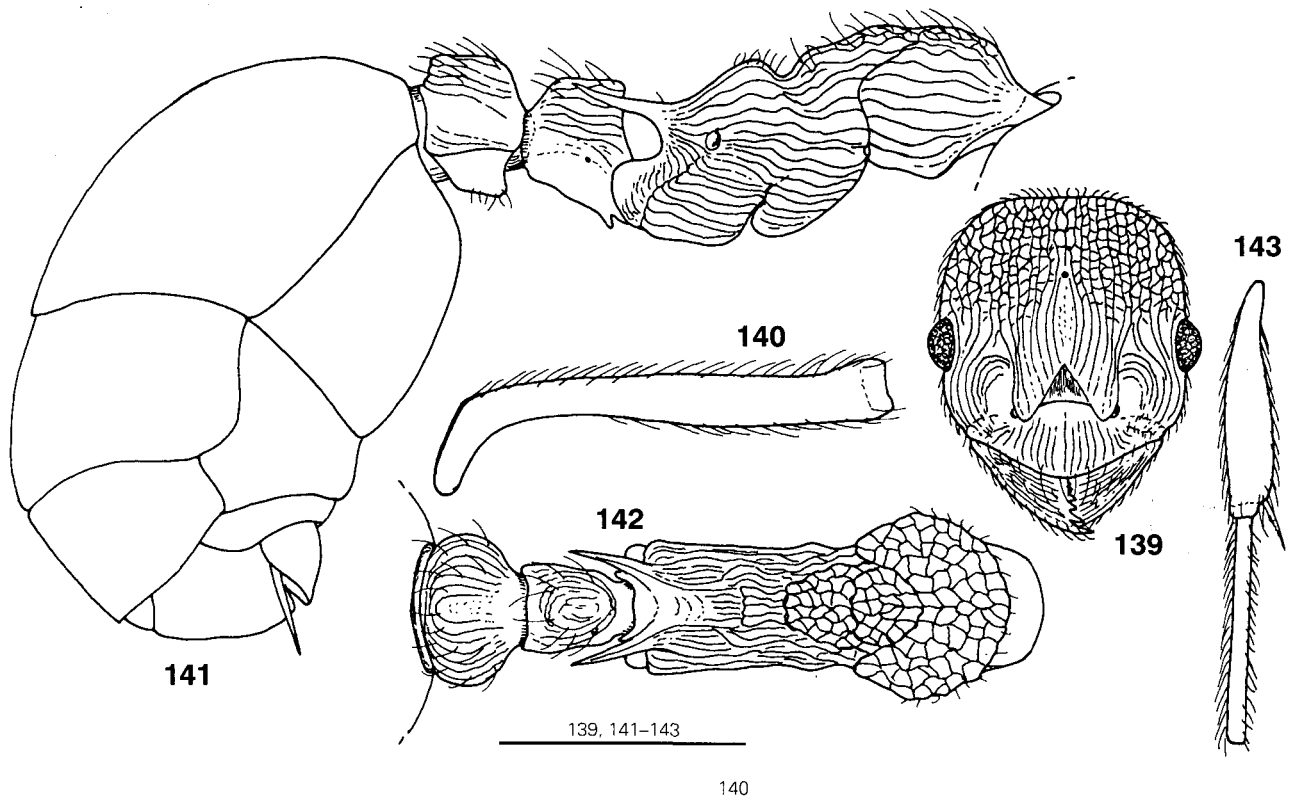
still under discussion (Buschinger 1997). Thus the question of *M. microrubra* remains open and can only be resolved by more modern genetic studies combined with experimental biological investigations.

Generally, *M. microrubra* queens clearly differ from normal *M. rubra* queens by size; any queen, found in a *M. rubra* colony, having HW < 1.05 mm is very probably *M. microrubra*. Separation of males from those of *M. rubra* is more problematic and one can only be certain of the parentage of males when they are reared from eggs laid by *M. microrubra* queens and/or pseudogynes. Males found in wild colonies infested with *M. microrubra* cannot be assigned to either of the two species with much confidence. *M. microrubra* males reared in the laboratory were smaller than those of *M. rubra*, in particular they were visibly smaller because of a shorter AL while HW and HL more or less overlapped the range of *M. rubra* males bred from the host populations. Two other features which might possibly assist in their separation are i) the antennal scape of *M. rubra* males are on average, significantly longer (T test on data above,  $P < 0.001$ ) than those of *M. microrubra* from the same sites (mean  $SI_1$  0.86 v 0.78), and ii) the blunt denticles on the propodeum are more or less absent on *M. microrubra* males and usually cannot be measured whereas those of *M. rubra* are usually, but not always, visible (mean ESL = 0.026 mm). Although

these comparisons were made only on two infested populations they were geographically well-separated so that these differences might hold throughout the range of *M. microrubra*.

**Distribution.** *M. microrubra* has so far been reported formally as a separate species only from Great Britain, Germany, Austria, Finland and Poland. However, in the literature there are many reports of microgynes in colonies of *M. rubra*, which almost certainly all refer to *M. microrubra*. Thus the range of this species at least includes the entire European part of the range of its host species.

**Biology.** *M. microrubra* queens ("microgynes") generally co-occur in their host colonies with *M. rubra* queens ("macrogynes"), where they produce nearly forty times as many queens as do the host queens (probably due to social manipulation – see Elmes and Brian 1991). Although considered to be workerless social parasites of *M. rubra*, they frequently produce many pseudogynes in early summer from "rapid brood" (Elmes 1976); such individuals generally have wings, but reduced thoraxes and are infertile, without a spermatheca. Elmes (1978) considered them as a first step in the "sympatric evolution" of a social parasite (see Bourke and Franks 1991). These are among the easiest of the social parasites to find and the species will be quite tractable to further detailed experimental study.



Figures 139–143. Details of structure of *Myrmica myrmecophila* (holotype worker). (139) Head, dorsal view; (140) antennal scape, lateral view; (141) alitrunk, waist and gaster in profile; (142) alitrunk and waist from above; (143) tibia and first tarsal joint of hind leg.

*Myrmica luteola* Kupyanskaya, 1990  
(Figs 128–138)

*Myrmica luteola* Kupyanskaya, 1990: 103, w, q, Figs 16, 5, 21; 17, 3, 7, Russia; Radchenko 1994a: 44; 1994b: 136, Figs 1k, 3b; 1994c: 75, m, Figs a–d; Bolton 1995: 281.

**Material examined.** Holotype worker, Kurily Islands, Isl. Kunashir, Lake Goriachee, 24.viii.1975, leg. Kupyanskaya (MOSCOW); paratypes: 8 workers from the nest of holotype; 11 workers, 1 queen, Primorsky province, Kedrovaya Pad', 18.ix.1973, leg. Kupyanskaya (MOSCOW, VLADIV, KIEV). Non-type material: about 50 workers, 6 males, 9 queens from Primorsky province, Isl. Kunashir, Korea and Japan (MOSCOW, KIEV, WARSAW, ELMES).

**Taxonomic notes.** Queens of this species are not very obvious being hardly larger, or even somewhat smaller, than their workers. The queen differs from her workers by an absence of propodeal spines (or at most with short denticles), while the workers have long propodeal spines. Although some reduction of the propodeal spines in relation to those of workers is not unusual for queens, the reduction shown by *M. luteola* is unique for all other known *Myrmica* species. *M. luteola* also possess several "socially-parasitic" features, such as reduced spurs on mid- and hind tibiae, slightly developed ventral petiolar and postpetiolar processes and a very hairy body. In addition, the first gastral tergite of workers and queens is distinctly longitudinally-striated basally; this unusual feature for Palaearctic *Myrmica* is known only from the Nearctic *M. striologaster* Cole.

**Distribution.** Primorsky province of Russia, Isl. Kunashir, Korea, Japan.

**Biology.** There are very few published accounts of the biology of this unusual *Myrmica* species. Kupyanskaya (1990) described how, in Far Eastern Russia, *M. luteola* usually lives in open places in spruce and southern-type mixed forest, generally preferring forest glades and the meadows bordering rivers and lakes; she noted that it usually builds its nests in decaying wood and that sexuals are present in the nest from June-September. In Japan, *M. luteola* inhabits sparsely forested rocky sites and builds nests under stones or around tree roots; nuptial flight take place from September to mid-October (Masuko and Terayama 2002).

Based entirely on morphological characteristics, Elmes and Radchenko (1998) speculated that *M. luteola* might be a microgyne form, derived from a species such as *Myrmica mirabile* Elmes and Radchenko, or might be a temporary social parasite. Very recently Masuko and Terayama (2002) showed that *M. luteola* could be temporary social parasite of *Manica yessensis* Azuma. While their evidence is open to several other interpretations, if they are correct then *M. luteola* would provide the first example of intergeneric parasitism by a *Myrmica* species. On the another hand,

there are no *Manica* species in the Russian Far East, therefore *M. luteola* either parasitises several different hosts or is a facultative social parasite.

**Addendum**

*Myrmica myrmecophila* Wasmann, 1910  
(Figs 139–143)

This species was described from the single "ergatoid queen" found in the nest of *M. sulcinodis* in Tyrol (Austria). Van Boven (1970) synonymised it with *M. sulcinodis* and guessed it to be an "ergatoid queen".

We investigated the holotype worker ("ergatoid queen" sensu Wasmann) with the labels "Arlberg 27.8.91 G.E. Hol.", "*Myrmica myrmecophila* Wasm. sp. n.", "= ergatoide ouvrière de *M. sulcinodis* Nyl. det. Van Boven, 1969"; on the same pin there is 1 specimen (bottom) of "normal" *M. sulcinodis* (MAASTRICHT).

The holotype worker has a grossly enlarged gaster and minute central ocellum; by all other features it is indistinguishable from *M. sulcinodis*. We believe that most probably it is ordinary worker of *M. sulcinodis*, infested by *Mermis*. It is not a social parasite and is not considered further here.

**KEY FOR IDENTIFICATION OF PALAEARCTIC SOCIALLY PARASITIC MYRMICA**

**Workers**

1. Antennal scape angulate at the base, with longitudinal lobe or carina (Figs 31, 32, 38, 39, 59, 60, 68, 69) ..... **2**
- . Antennal scape only curved at the base, without angle and carina (Figs 122, 129) ..... **5**
- 2(1). Clypeus with big foveolate impression basally (Fig. 30). Less hairy species, petiole with 6 long standing hairs (Figs 30, 33, 34). Italy ..... **M. symbiotica** (Menozzi)
- . Clypeus without foveolate impression basally (Figs 37, 58, 67). More hairy species, petiole with more than 10 (usually with 12–20) long standing hairs (Figs 37, 40, 41, 58, 61, 62, 67, 70, 71) ..... **3**
- 3(2). Postpetiole narrower (PPI < 0.45). Head and alitrunk with longitudinal, slightly sinuous rugae, without reticulation, only extreme upper and lateral parts of head dorsum with reticulation (Figs 67, 70, 71). Central Europe, Great Britain ..... **M. vandeli** Bondroit
- . Postpetiole wider (PPI > 0.50). Head and alitrunk at least partly with reticulation (Figs 37, 40, 41, 58, 61–63) ..... **4**
- 4(3). Frons narrower (FI 0.34–0.35). Whole head dorsum with coarse reticulation, only lower part of frons

- with sinuous rugae (Fig. 37). Switzerland, Germany  
 ..... *M. bibikoffi* Kutter
- Frons wider (FI 0.40–0.42). Head dorsum with longitudinal, slightly sinuous rugae, only its rear third with reticulation (Fig. 58). Central and North Europe, Great Britain ..... *M. hirsuta* Elmes
- 5(1). Smaller species (HW < 1.0, AL < 1.5 mm). Antennal scape relatively short ( $SI_1 < 0.75$ ,  $SI_2 < 0.80$ ), weakly curved at the base (Fig. 122). Frontal carinae not curved outwards posteriorly but merge with the longitudinal rugae running towards the occipital margin of the head; antennal sockets surround by concentric rugae, which about the frontal carinae; frontal carinae quite strongly curved anteriorly to form widely extended frontal lobes (FLI > 1.20) (Fig. 121). Much less hairy species, petiolar node with less than 10 standing hairs (Fig. 123, 124). 1st gastral tergite completely smooth. South Siberia, Mongolia ..... *M. arnoldii* Dlussky
- Bigger species (HW > 1.3, AL > 1.8 mm). Antennal scape relatively long ( $SI_1 > 0.80$ ,  $SI_2 > 0.85$ ), more strongly curved at the base (Fig. 129). Frontal carinae curved outwards posteriorly to merge with the rugae, which surround antennal sockets; frontal carinae weakly curved anteriorly to form narrow frontal lobes (FLI < 1.10) (Fig. 128). Much more hairy species, petiolar node with about 10 long standing hairs and with numerous shorter hairs; 1st gastral tergite finely but distinctly striated at the base (Figs 130, 131). Russian Far East, Korea, Japan ... *M. luteola* Kupyanskaya
- ### Queens
1. Bend of antennal scape usually angled (in *M. laurae* only curved), but always with a longitudinal lobe, or at least a visible carina at the base (Figs 18, 19, 45, 46) ..... 2
- Bend of antennal scape only curved and always with no lobe or carina at the base (Figs 6, 16, 78, 91, 103, 116, 135) ..... 5
- 2(1). Eyes with conspicuous hairs, length of the longest hairs 0.035 mm (Fig. 17). Antennal scape gradually curved at the base, with narrow longitudinal ridge (Figs 18, 19). Italy ..... *M. laurae* (Emery), = *M. sannitica* Mei
- Eyes usually with no hairs, or if present, they are inconspicuous and very short, length  $\leq 0.01$  mm (Figs 44, 66). Antennal scape angled at the base, with a more developed longitudinal carina or lobe (Figs 45, 46) ..... 3
- 3(2). Petiolar node with coarse longitudinally-concentric sculpture, without reticulation (Fig 76). Postpetiolar narrower (PPI 0.50–0.58, mean = 0.54). Central Europe, Great Britain ..... *M. vandeli* Bondroit
- Petiolar node with coarse reticulation (Figs 49, 50). Postpetiolar wider (PPI 0.58–0.68, mean = 0.63) .... 4
- 4(3). Bigger species (HW 1.22–1.24 mm). Frons narrower (FI 0.34–0.35). Only frons with longitudinal sinuous rugae, remainder part of head dorsum with coarse reticulation (Fig. 44). Switzerland, Germany ..... *M. bibikoffi* Kutter
- Smaller species (HW 0.80–1.10 mm). Frons wider (FI 0.39–0.46). Head dorsum mainly with longitudinal, slightly sinuous rugae, only its rear third with reticulation (Fig. 66). Central and North Europe, Great Britain ..... *M. hirsuta* Elmes
- 5(1). Shape of petiole and postpetiole very unusual, both being very wide (PPI 0.92), and with very big ventral processes (Figs 117, 118). Himalaya ..... *M. ereptria* Bolton
- Petiole and postpetiole much narrower (PPI < 0.70) ..... 6
- 6(5). Frontal carinae curved outwards posteriorly to merge with the rugae, which surround antennal sockets (Fig. 134) ..... 7
- Frontal carinae not curved outwards posteriorly but merge with the longitudinal rugae running towards the occipital margin of the head; antennal sockets surround by concentric rugae, which about the frontal carinae (Figs 5, 77, 90, 102) ..... 8
- 7(6). Propodeum with at least a short, but always sharply pointed spine (like in *M. rubra*). Europe (probably the entire range of *M. rubra*) ..... *M. microrubra* Seifert
- Propodeum only angulate or at most with short blunt denticles (Fig. 136). Russian Far East, Korea, Japan ..... *M. luteola* Kupyanskaya
- 8(6). Antennal scape relatively short ( $SI_1 < 0.76$ ,  $SI_2 < 0.70$ ). Petiolar node (seen in profile) subtriangular (Figs 7, 15) ..... 9
- Antennal scape longer ( $SI_1 > 0.80$ ,  $SI_2 > 0.85$ ). Petiolar node (seen in profile) with broadly rounded dorsum (Figs 79, 92, 104) ..... 10
- 9(8). Frontal carinae somewhat strongly curved, frons narrower (FI 0.45–0.46, FLI 1.16–1.21). Slightly smaller species (HW 0.93–0.97, AL 1.50–1.58 mm). Switzerland ..... *M. myrmicoxena* Forel
- Frontal carinae somewhat less curved, frons wider (FI 0.47–0.50, FLI 1.15–1.17). Slightly bigger species (HW 1.04–1.08, AL 1.68–1.76 mm). South Siberia, Mongolia ..... *M. arnoldii* Dlussky
- 10(8). The basal half of the first gastral tergite with conspicuous, fairly-long, suberect hairs; postpetiolar dorsum with distinct reticulation (Figs 92, 93). France, Spain ..... *M. lemasnei* Bernard
- First gastral tergite with only sparse, short, decumbent pubescence; postpetiolar dorsum without reticulation (Figs 79, 80, 104, 105) ..... 11
- 11(10). Surface of head, alitrunk and waist finely but densely punctured, appears dull (Figs 102, 104, 105). Petiolar and postpetiolar nodes with relatively short, straight or slightly downward-curved



hairs (Figs 104, 105). Cubital cell of forewing closed and partly separated by a short vein. Algeria . . . . .  
 . . . . . *M. kabylica* (Cagniant)  
 - Surface of head, alitrunk and waist smooth or at most superficially punctured, appears shiny (Figs 77, 79, 80). Petiolar and postpetiolar nodes with fairly long, downward-curved hairs (Figs 79, 80). Cubital cell of forewing closed but usually not partly separated by a short vein (occasionally there is trace of such vein). East, Central and North Europe . . . . .  
 . . . . . *M. karavajevi* (Arnoldi), =*M. winterae* (Kutter), =*M. faniensis* van Boven

**Males**

- 1. Antennae 12-jointed . . . . . 2
- Antennae 13-jointed . . . . . 6
- 2(1). Antennal scape short ( $SI_1 < 0.40$ ,  $SI_2 < 0.45$ ) (Fig. 127). South Siberia, Mongolia . . . . . *M. arnoldii* Dlussky
- Antennal scape long ( $SI_1 > 0.70$ ,  $SI_2 > 0.80$ ) (Figs 26, 84, 97, 109) . . . . . 3
- 3(2). Eyes with conspicuous hairs, length of the longest hairs 0.04 mm (Fig. 25). Propodeum with pointed teeth (Figs 27, 28). Italy . . . . .  
 . . . . . *M. laurae* (Emery), =*M. samnitica* Mei
- Eyes usually with no hairs, or if present, they are inconspicuous and very short, length  $\leq 0.01$  mm (Figs 83, 96, 108). Propodeum with short blunt denticles (Figs 85, 86, 98, 99, 110, 111) . . . . . 4
- 4(3). Surface of alitrunk (especially of scutum and scutellum) finely but densely punctured, appearing dull (Figs 110, 111). Algeria . . . . . *M. kabylica* (Cagniant)
- Surface of alitrunk not punctured, smooth and appearing shiny (Figs 85, 86, 98, 99) . . . . . 5
- 5(4). First gastral tergite with only sparse short decumbent pubescence (Figs 85, 86). East, Central and North Europe . . . . . *M. karavajevi* (Arnoldi), =*M. winterae* (Kutter), =*M. faniensis* van Boven
- Basal half of the first gastral tergite with conspicuous, fairly long suberect hairs (Figs 98, 99). France, Spain . . . . . *M. lemasnei* Bernard
- 6(1). Propodeum (seen in profile) more or less rounded, at most with very short blunt tubercles ( $ESLI < 0.05$ ) (Fig. 138) . . . . . 7
- Propodeum (seen in profile) with distinct, short, usually blunt denticles ( $ESLI > 0.05$ ) (Figs 53, 54) . . . . . 8
- 7(6). Antennal scape much shorter ( $SI_1 < 0.50$ ,  $SI_2 < 0.55$ ) (Fig. 137). Russian Far East, Korea, Japan . . . . . *M. luteola* Kupyanskaya
- Antennal scape much longer (very similar to *M. rubra*) ( $SI_1 > 0.70$ ,  $SI_2 > 0.75$ ). Europe (probably the entire range of *M. rubra*) . . . . . *M. microrubra* Seifert
- 8(6). Head margins (seen in full-face view) with short hairs; antennal scape shorter ( $SI_1 = SI_2 = 0.35$ ) (Fig. 14). Switzerland . . . . . *M. myrmicoxena* Forel

- Head margins (seen in full-face view) with long hairs; antennal scape longer ( $SI_1 > 0.40$ ,  $SI_2 > 0.45$ ) (Figs 51, 52, 73, 74) . . . . . 9
- 9(8). Lateral and posterior parts of head dorsum with distinct reticulation (Fig. 51) Switzerland, Germany . . . . . *M. bibikoffi* Kutter
- Lateral and posterior parts of head dorsum without reticulation, at most with longitudinal striation or sometimes only punctured (Fig. 73) . . . . . 10
- 10(9). Postpetiole wider (PPI 0.64–0.70, mean = 0.66). Central and North Europe, Great Britain . . . . .  
 . . . . . *M. hirsuta* Elmes
- Postpetiole narrower (PPI 0.45–0.60, mean = 0.56). Central Europe, Great Britain . . . . .  
 . . . . . *M. vandeli* Bondroit

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