TAXONOMIC REVISION OF THE *SCHENCKI*-GROUP OF THE ANT GENUS *MYRMICA* LATREILLE (HYMENOPTERA: FORMICIDAE) FROM THE PALAEARCTIC REGION

ALEXANDER RADCHENKO[1], GRAHAM W. ELMES[2] and ANTONIO ALICATA[3]

[1]*Museum and Institute of Zoology, Polish Academy of Sciences, 64, Wilcza str., 00-679 Warsaw, Poland; e-mail: agradchenko@hotmail.com*
[2]*Centre for Ecology & Hydrology, Winfrith Technology Centre, Winfrith Newburg, Dorchester, Dorset DT2 8ZD, United Kingdom; e-mail: gwe@ceh.ac.uk*
[3]*Dipartimento di Biologia Animale, Universita di Catania, via Androne 81, 95124 Catania, Italy; e-mail: antonal@mail1.dba.unict.it*

Abstract.— A taxonomic revision is made of the Palaearctic species of *Myrmica* belonging to the *schencki*-group. Three new species are described: *M. siciliana* (all castes) from Sicily, *M. onoyamai* (all castes) from Japan and *M. inucta* (workers only) from northwest Kazakhstan; also first descriptions are made of the sexual castes for two species: *M. caucasicola* (queen) and *M. koreana* (queens and males). Keys to the identification of both workers and males of all species, and maps of their distributions are provided. The distribution of the various species is discussed and it is suggested that the origins of extant Palaearctic *schencki*-group species is linked to the development of the Steppe Zone during the last 10 million years.

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Key words.— Ants, Formicidae, taxonomy, *Myrmica*, *schencki*-group, new species, key.

INTRODUCTION

When Radchenko (1994a) formalised the concept of species-group of the genus *Myrmica* he placed 4 species within the *schencki*-group: excluding synonyms (see below) these were *M. schencki* Viereck, *M. lacustris* Ruzsky, *M. ravasinii* Finzi and *M. caucasicola* Arnoldi. During the next decade another two species attributed to this group were described, one from Korea – *M. koreana* Elmes *et al.*, 2001 and another from southern Greece – *M. pelops* Seifert, 2003; Seifert took the opportunity to make a taxonomic review of the *schencki*-group. Although this review contained much important information, it concentrated mainly on the workers and provides no Keys to the identification of the reviewed species. Very recently a presumed socially parasitic and closely related species of *M. schencki*

has been described – *M. schenckioides* Boer et Nordijk, 2005.

During the last few years we have obtained additional *schencki*-group material from various parts of the Palaearctic that was collected mostly by the authors (GWE and AA). This contained specimens from three undescribed species and the previously unknown males and queens of *M. koreana* and queens of *M. caucasicola*; we describe them here. This makes a further revision of the *schencki*-group necessary in which we include tables of morphometrics, Keys for the identification of workers and males, and distribution maps for all species. We have been fortunate that museums have allowed us to investigate the extant type specimens of all previously described species and infraspecific forms of the *schencki*-group (except *M. schenckioides*, which has a very full recent

description). Based on original descriptions and specimens in our collections, several Nearctic species appear to belong to the *schencki*-group (see discussion). However, we restrict this revision to the Palaearctic fauna because the North American species of *Myrmica* require a full generic revision based on all castes. When this is done we expect it to comprise a set of species-groups distinct from the Palaearctic fauna with few groups in common, one such might be the *schencki*-group.

The *schencki*-group is defined by a combination of features of both male and female castes (see Radchenko 1994a, c, Seifert 2003). Males always have short antennal scape (< half the head width); if taken without workers, males of some species can be confused with those from the *scabrinodis*-group, which also have short scape, while males of *lobicornis*-group species have much longer scape (> 60% of head width). Workers and queens have two distinct features. First, the antennal scape is strongly curved at the base with a vertical lobe or dentiform ridge of various sizes on the bend; the lobe or ridge always forms a wide, shield-like plate on the short, vertical face (or foot – see below and Fig. 1) of the scape (see Figs 3–6, 11, 12, 24–27, 32, 33, 44–47, 52–54, 61–64, 70–73, 78–80, 85–87, 92–95, 98, 99, 110–113). Although the vertical lobes or dentiform ridges on the scape bends of *lobicornis*-group species

are generally of a different shape, superficially by this feature alone it is easy to confuse some of the *schencki*-group species with some from the *lobicornis*-group. The second important indicator of *schencki*-group species is a widely rounded and medially notched anterior margin of the clypeus (Figs 2, 10, 23, 31, 43, 51, 60, 69, 77, 84, 91, 97, 109).

Seifert (2003) additionally used the larger size of workers as one of the definitive features of the *schencki*-group, particularly CS (arithmetic mean of HL and HW) which he found ranged from 1.186–1.344 mm in the *schencki*-group species *versus* 1.056–1.116 mm in the *lobicornis*-group. Generally, workers of the *schencki*-group species are indeed larger than those of the *lobicornis*-group, but the CS of many specimens of our newly described species is smaller than 1.10 mm, therefore in the light of our new material a large CS remains a useful indicator of *schencki*-group species, but a small CS no longer definitively excludes the *schencki*-group.

MATERIAL AND METHODS

This revision is based on personal examination of the existing types of all described species and infraspecific forms belonging to the *schencki*-group from the
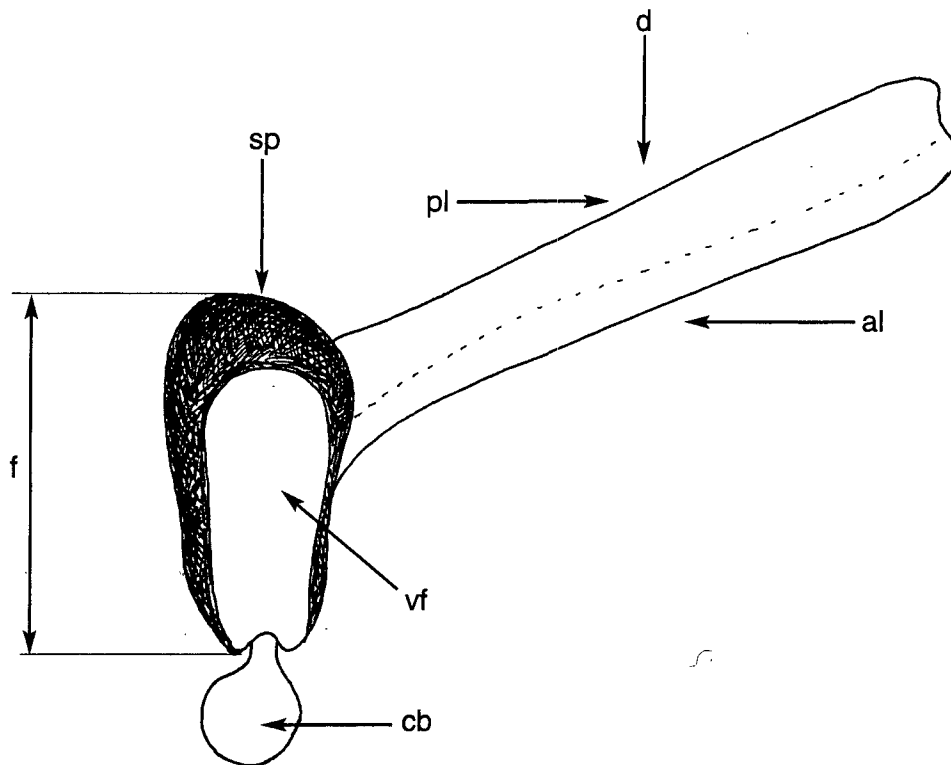

Figure 1. Schematic details of the left scape structure (workers and queens) of the species from the *schencki*-group; al – anterolateral view; cb – condylar bulb; d – dorsal view; f – foot of scape; pl – posteriolateral view; sp – shield-like process; vf – vertical face of foot.

Palaearctic Region, and on non-type material (more than 1000 specimens) both collected by the authors and preserved in different Museums and private collections:

IZK – Institute of Zoology of the Ukrainian National Academy of Sciences, Kiev, Ukraine;

ZMMU – Zoological Museum of Moscow State University, Russia;

ZISP – Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia;

BPI – Biological and Soil Institute of the Russian Academy of Sciences, Vladivostok, Russia;

BMNH – The Natural History Museum, London, UK;

MHNG – Museum d'Histoire Naturelle, Geneva, Switzerland;

SMN – Staatliches Museum für Naturkunde, Görlitz, Germany;

MCSN – Museo Civico di Storia Naturale, Milano, Italy;

MCZ – Museum of Comparative Zoology of Harvard University, USA;

ELMES – collections of Graham Elmes, UK;

ALICATA – Antonio Alicata, Italy;

SCHULZ – Andreas Schulz, Leilingen, Germany;

WERNER – Petr Werner, Prague, Czech Republic.

In the descriptions of the sharply angled antennal scape we use the term "foot" for the shorter upright (relative to head) part of the scape (Fig. 1). The following morphometrics were measured to the nearest 0.01 mm.

Morphometrics

HL – maximum length of head in dorsal view, measured in a straight line from the anteriormost point of clypeus (including any carinae or rugae, if they protrude over the anterior margin) to the mid-point of the occipital margin;

HW – maximum width of head in dorsal view behind (above) 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 from its articulation with condylar bulb to the proximal edge of scape;

AL – diagonal length of the alitrunk seen in profile, from the neck shield to the posterior margin of metapleural lobes (workers) and from the anterodorsal point of alitrunk to posterior margin of metapleural lobes (queens and males);

HTL – maximal length of hind tibia, measured from the junction with the femur to the junction with the first tarsal joint;

PNW – maximum width of pronotum from above in dorsal view (workers);

PL – maximum length of petiole from above, measured from the posterodorsal margin of petiole to its anterior edge at the articulation with propodeum; petiole should be positioned so that measured points lay on the same plane;

PW – maximum width of petiole from above;

PH – maximum height of petiole in profile, measured from the uppermost point of the petiolar node perpendicularly to the imaginary line between the anteroventral (just behind the subpetiolar process) and posteroventral points of petiole;

PPL – maximum length of postpetiole, measured from above from its anterior to posterior margins;

PPW – maximum width of postpetiole from above;

PPH – maximum height of postpetiole in profile from its uppermost to lowermost points, measured perpendicularly to the linear component of the lateral postpetiolar suture;

ESL – maximum length of propodeal spine in profile, measured along the spine from its tip to the deepest point of the propodeal constriction at the base of spines;

ESD – distance between tips of propodeal spine from above;

SCW – maximum width of scutum from above (queens and males);

SCL – length of scutum+scutellum from above (queens and males);

AH – height of alitrunk, measured from upper level of mesonotum perpendicularly to the level of lower margin of mesopleura (queens and males).

The mean values ± SD for workers, queens and males of each species are presented in Tables 1–3 (95% confidence limits being approximately the mean ± twice the SD). Traditionally a variety of indices calculated from the above morphometrics has proved useful in discriminating between various *Myrmica* species (e.g., Radchenko and Elmes 2001, 2004). Generally, for any group of species, the most useful indices for discrimination are those calculated from a combination of morphometrics that show the least correlation between the mean values for species. For example, using the data for *schencki*-group queens (Table 2) FW has no statistically significant correlation with any other morphometrics (generally $P > 0.40$). Discrimination between species was made on the full data sets standardised for size(s) by dividing by HW (e.g., sFW = FW/HW); in this group of species HW is so highly correlated with HL that using CS (Seifert 2003) had no advantage, furthermore morphometrics standardised

by HW equate to many of the traditional indices. Standardisation more or less eliminates size differences that might be due to chance, especially when sample sizes are small, but has the disadvantage of masking genuine differences in size between the species. Linear discriminant analyses were made on the standardised data using the MINITAB© statistical package to estimate the probability of misclassification. The most powerful discriminators were sFW, sFLW and sESL for female castes. Note that sFW = Frontal index (FI = FW/HW) and sESL = Propodeal spines index (ESLI = ESL/HW) while sFLW/sFW = Frontal lobe index (FLI) used traditionally. In the case of males the most powerful discriminator was sSL = Scape-length index2 (SI$_2$ = SL/HW) the next most important were sPL = Petiole index2 (PI$_2$ = PL/HW) and sPH (note: the traditional Petiole Iindex1 is a combination of these last two, PI$_1$ = PL/PH).

If required, mean values for the other traditional indices used elsewhere can be calculated from the means in Tables 1–3 (theoretically these are identical to means of indices calculated from individuals but in practise differ slightly due to rounding errors).

TAXONOMY

Description of the new species

Myrmica siciliana sp. nov.

Material examined. Holotype worker, Italy, Sicily, Monti Nebrodi, Piano Menta, 1500 m a.s.l., grassland in a damp area, 2.X.2004, leg. A. Alicata (AA 3/04), Museo Civico di Storia Naturale, Milano, Italy (MCSN); paratypes: 5 workers, 9 males from the nest of the holotype, (Isc 20 – Elmes coll.); 1 queen, Italy, Sicily, Monti Nebrodi, Piano Menta, 1500 m a.s.l., grassland in a damp area, 2.X.2004, leg. A. Alicata (AA 2/04, Isc 18 in Elmes coll.); 17 workers, 40 males, the same locality, date and collector as previous (AA 3/04, Elmes Isc 21); 5 workers, 1 male, Italy, Sicily, Monti Nebrodi, Portella Scafi, 1450 m a.s.l., grassland near pond, 2.X.2004, leg. A. Alicata (AA 6/04, Elmes Isc 23); 8 workers, 6 males, Italy, Sicily, Monti Nebrodi, near Pizzo Scavello, 1575 m a.s.l., bare patch in a beech wood, 1.X.2004, leg. A. Alicata (AA 5/04, Elmes Isc 22); 28 workers, 2 queens, 5 males, same locality and collector as previous, but date 2.X.2004 (AA 1/04, Elmes Isc 19); 4 workers, 1 queen, 2 males, Italy, Sicily, Monti Nebrodi, Serra del Re (pond), 1710 m a.s.l., bare patch in a beech-wood, 19.IX.2002, leg. A. Alicata (AA 4/03, Elmes Isc 17); 15 worker, 5 males, Sicily, reg. Monti Nébrodi, Mt. Soro, Piano Menta ca. 1550 m. N facing escarp. grazed open place among trees. nest in soil. 28-VIII-2005. leg. Elmes (Isc24); 33 workers, 9 males (Isc25), (same collection details); 48

workers, (Isc26), (same collection details); 24 workers, (Isc27), (same collection details); 3 queens, (Isc15), mating swarm just ending, taken from random sample of 3 *Myrmica* spp. and *Lasius* and *Aphaenogaster* running on the ground, (same site details); 30 workers, 4 males, NE Sicily, reg. Monti Nébrodi, Mt. Soro, Piano Menta, ca. 1450 m. N facing escarp. grazed damp "lawn", nest in soil at edge of damp place, 28-VIII-2005. leg. Elmes (Isc28) (MCSN, BNMH, IZK, ELMES, ALICATA).

Workers. (Figs 2–9, Table 1).

Head longer than broad, with slightly convex sides, straight occipital margin, and quite broadly rounded occipital corners. Anterior clypeal margin broadly rounded and distinctly notched medially. Frontal carinae not strongly curved, frons relatively wide and frontal lobes not proportionately extended (compared to *M. schencki*, see Table 1 and Key). Scape strongly angled at the base, with only a moderately developed, somewhat oblique vertical lobe (Figs 3–5), forming a small shield the on vertical face of antennal foot (Fig. 6).

Alitrunk with convex promesonotal dorsum; promesonotal suture indistinct from above; metanotal groove distinct, but not deep. Propodeal spines long, acute, almost straight, divergent (seen from above), projecting backwards at an angle less than 45°. In profile, anterior surface of petiole concave, meets with dorsal surface at a blunt angle, dorsal surface gradually sloping posteriorly, at most slightly flattened. Postpetiole distinctly shorter than high, with convex dorsum. Spurs on middle and hind tibiae well developed and pectinate.

Only frons with sinuous longitudinal rugae, remainder part of head dorsum with reticulation. Antennal sockets surrounded by concentric rugae. Clypeus with longitudinal rugae, frontal triangular striated. Sides of alitrunk with moderately coarse sinuous rugae, pronotum with reticulation. Sides of petiolar node with longitudinal rugosity, its dorsum with reticulation. Postpetiole with longitudinally-concentric rugae. Surfaces between rugae on the body smooth and shiny.

Hairs on the head margins and alitrunk dorsum abundant, erect to suberect, quite long and slightly curved; scape with suberect, and tibiae with subdecumbent hairs. The overall colour reddish-brown, appendages somewhat lighter.

Queens. (Figs 10–15, Table 2).

Generally like workers in shape of head and scape, colour and pilosity of the body except they have coarser sculpture, especially on the alitrunk, petiole and postpetiole. Frons relatively slightly wider and propodeal spines shorter and wider at their base.

Males. (Figs 16–21, Table 3).

Head slightly longer than broad, with convex sides and occipital margin, and gradually rounded occipital corners; anterior clypeal margin widely rounded and

2, 7–9

3–6
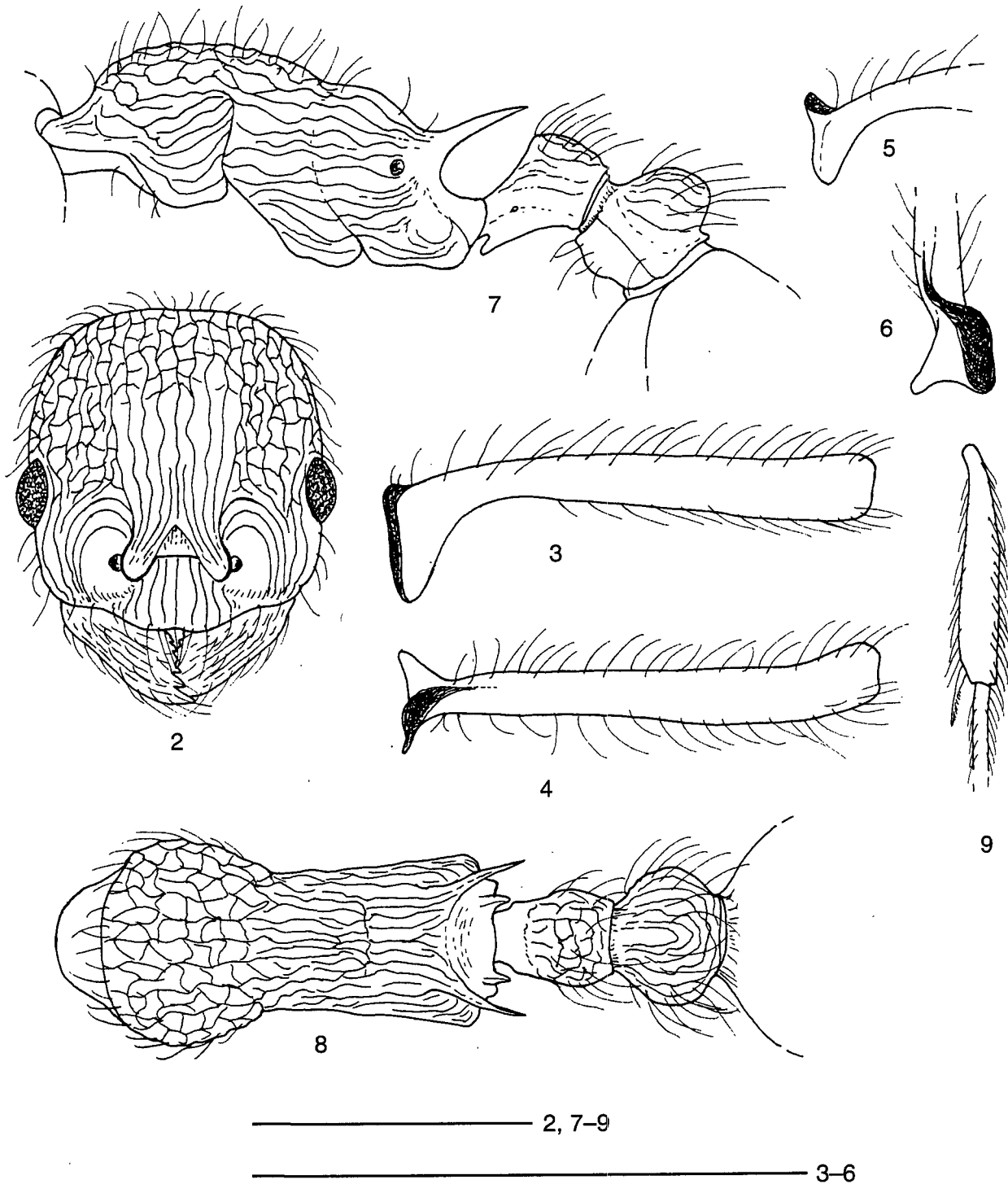
Figures 2–9. Details of structure of *Myrmica siciliana* (holotype, worker). (2) Head, dorsal view; (3) scape, posteriolateral view; (4) scape, dorsal view; (5) base of scape, anterolateral view; (6) vertical face of antennal foot; (7) alitrunk and waist in profile; (8) alitrunk and waist from above; (9) tibia and base of first tarsal joint of hind leg. Scale bars: 1 mm.
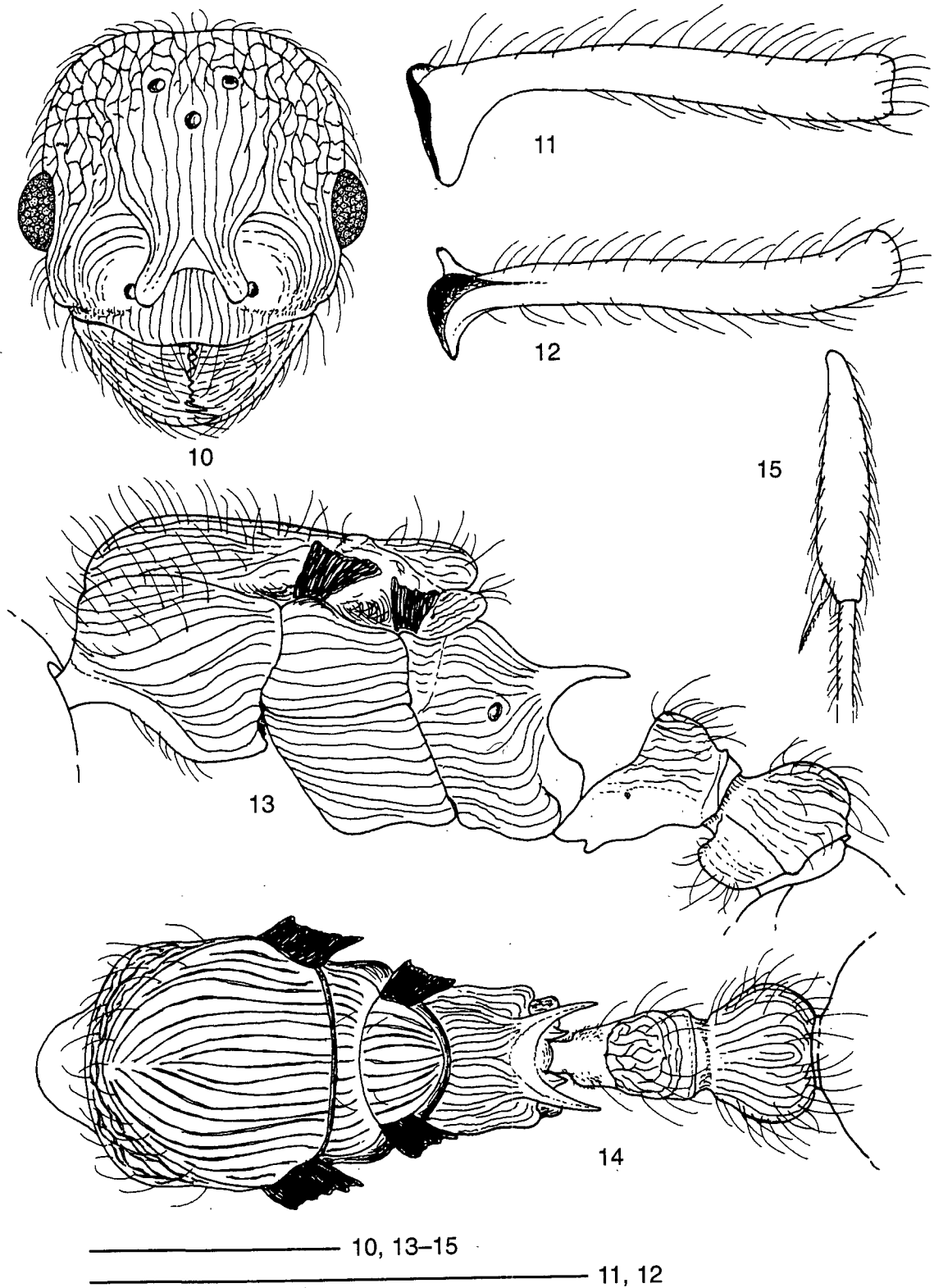
Figures 10–15. Details of structure of *Myrmica siciliana* (paratype, queen). (10) Head, dorsal view; (11) scape, posteriolateral view; (12) scape, dorsal view; (13) alitrunk and wais in profile; (14) alitrunk and waist from above; (15) tibia and base of first tarsal joint of hind leg. Scale bars: 1 mm.
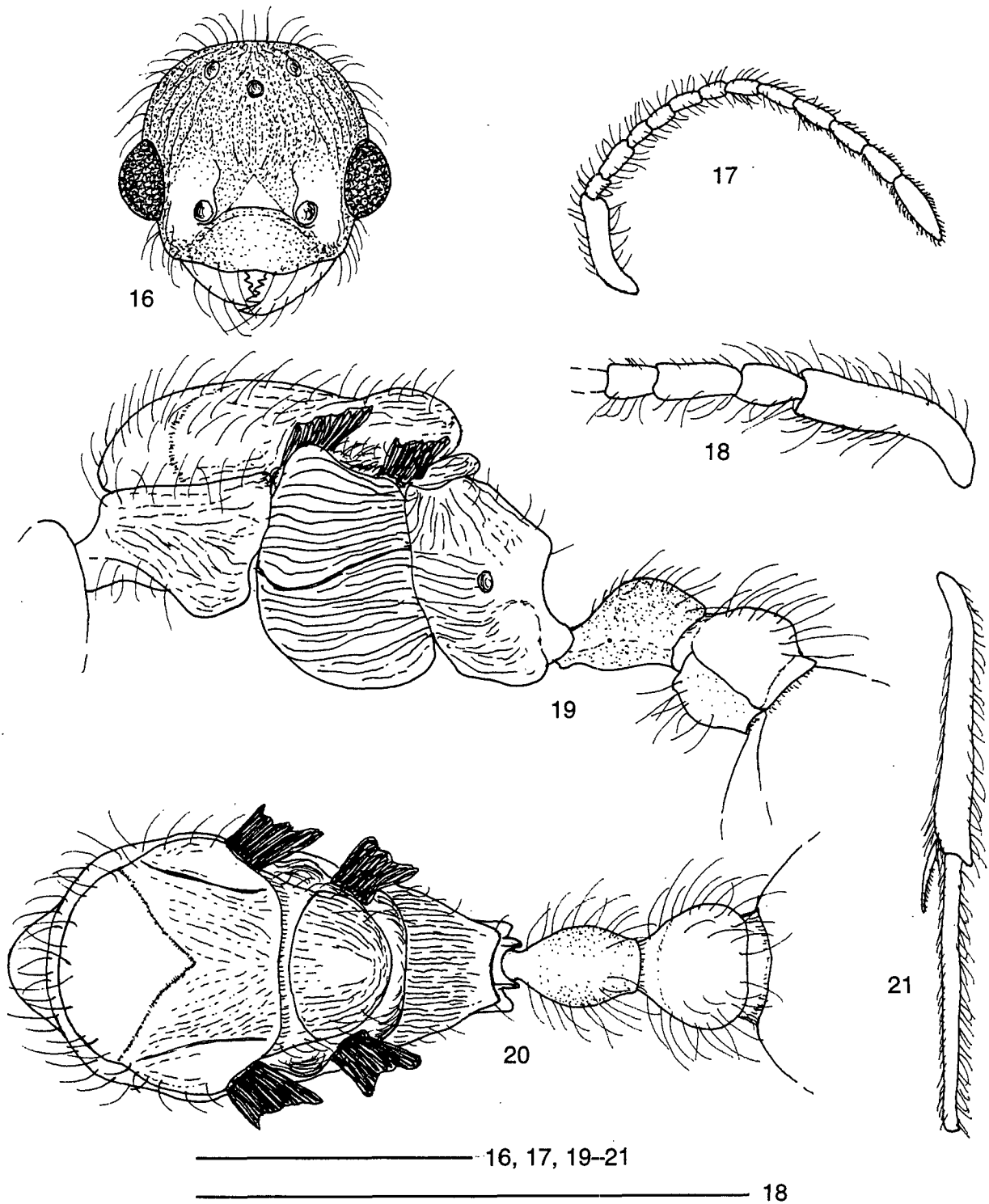
Figures 16–21. Details of structure of *Myrmica siciliana* (paratype, male). (16) Head, dorsal view; (17) antenna; (18) scape and three basal antennal joints, lateral view; (19) alitrunk and waist in profile; (20) alitrunk and waist from above; (21) tibia and first tarsal joint of hind leg. Scale bars: 1 mm.

shallowly notched medially. Scape short, but distinctly longer than first and second funicular segments together, distinctly curved at the base though not sharply angled. Antennae 13-segmented, with 5-segmented club.

Alitrunk relatively long, scutum slightly convex, scutellum does not project dorsally above scutum when seen in profile. Propodeum with blunt rounded tubercles. In profile, petiole relatively long and low, with widely rounded dorsum of node, its anterior surface slightly concave, not steep; postpetiole distinctly higher than long, with weakly convex dorsum.

Head dorsum finely but densely punctured, frons with fine striation, temples with coarser rugulae. Central part of scutum behind Mayr's furrows, and scutellum with fine longitudinal striation. Propleura with fine striation and rugulosity, mesopleura and propodeum coarsely rugulose. Sides of petiole finely punctured, petiolar dorsum and postpetiole smooth and shiny. Surface of alitrunk between striation and rugae smooth and shiny.

Head margins with long, curved erect hairs. Alitrunk, petiole and gaster with somewhat shorter erect to suberect hairs, postpetiole with longer hairs. Tibiae and tarsi with short subdecumbent to suberect hairs; scape and first 7 funicular segments with relatively long hairs, segments of antennal club with very short subdecumbent hairs. Colour of body dark brown to black, appendages somewhat lighter.

Ecology. Known only from Sicily (see Fig. 22): most specimens were found on Mt. Nebrodi in Sicily and they were believed absent from the neighbouring Mt. Etna region until we recently found two specimens (queen and worker foraging in mature woodland – see above). On Nebrodi they live at quite high altitudes (about 1500 m) where they sometimes nest in open areas or bare

patch in beech-wood, they are most abundant in damp areas of open grazed grassland. They do not require permanently wet soil, rather they live on the drier margins of ponds and areas that are temporarily flooded following heavy rain. Nests are in the soil with small entrance holes, we did not note the presence of woven funnel entrances typically associated with both *M. schencki* and *M. koreana* nests. However, they face quite strong competition from *M. sabuleti* Meinert and *Tetramorium* Mayr, *Lasius* F., *Formica* L. and *Aphaenogaster* Mayr species. Like many other species of *Myrmica* living in such circumstances foraging appeared restricted to the early morning and early evening.

When collecting on August 28th 2005 we encountered the end of a nuptial flight in the area of damp grassland (ca. 0.5 ha) among open mixed woodland where the holotype nest had been taken. Males of both *M. siciliana* and *M. sabuleti* were still leaving the nests and both winged and wingless queens were running on the ground. The actual swarm was not found but we guess it was a fairly local affair probably centred on one of the trees in the small meadow. A single *M. lobicornis*-group male and several queens of *M. lobulicornis* Nylander were found, and based on other male swarms (unpublished observations) the *Myrmica* species almost certainly formed a common male-swarm. Males and queens of *Aphaenogaster* were also found and it would have been interesting to know if they also swarmed with the more numerous *Myrmica*.

Comparative diagnosis. Although *M. siciliana* shares many features with various species of the *schencki*-group, it well differs from all others by its particular combination of characters. The distinctly wider frons of the workers and queens (mean FI in
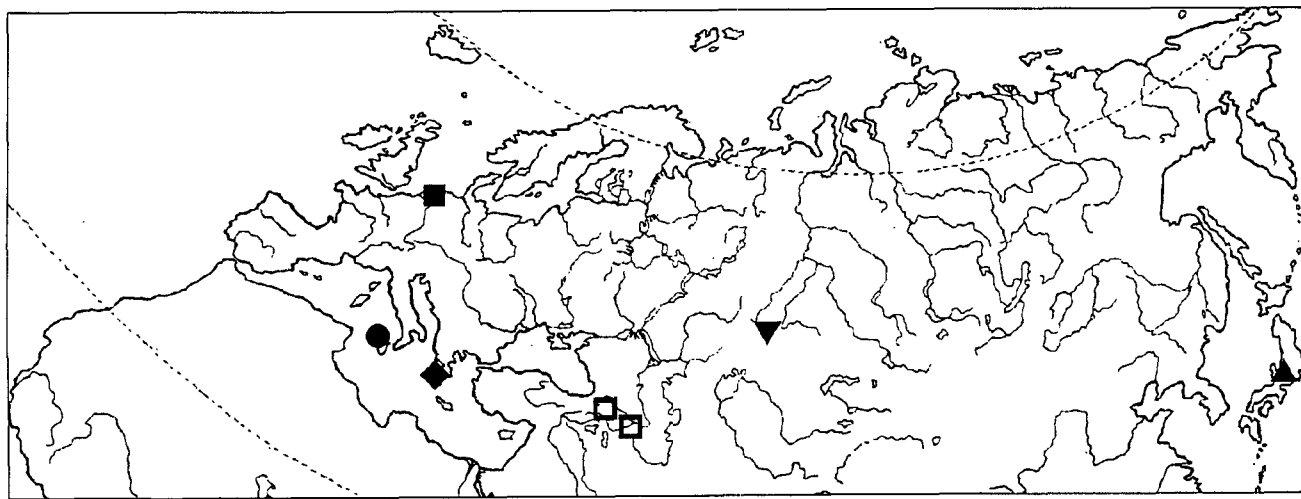

Figure. 22. Map of distribution of ● – *Myrmica siciliana*, ▲ – *M. onoyamai*, ▼ – *M. inucta*, □ – *M. caucasicola*, ◆ – *M. pelops* and ■ – *M. schenckioides*.

workers 0.295, in queens – 0.301; see also Tables 1 and 2) well separates *M. siciliana* from *M. ravasinii*, *M. schencki* and *M. pelops* (mean FI < 0.250 in both castes). In addition, workers well differ from any other species of the *schencki*-group (except of *M. onoyamai*, see below) by their less extended frontal lobes (mean FLI 1.291 *versus* > 1.400); this difference is somewhat less pronounced in queens (Table 2). In both female castes the FLI of *M. siciliana* is distinctly larger than that of *M. onoyamai* (mean 1.291 and 1.232 *versus* 1.202 and 1.151 for workers and queens respectively). The much reduced sculpture of the head and alitrunk in *M. inucta* (described below) prevents its confusion with *M. siciliana*. Finally and not least, the shape of the lobe at the base of scape of workers and queens of *M. siciliana* subjectively appear very different to that of the other species (compare Figs 3–6, 11, 12 and 24–27, 32, 33, 44–47, 52–54, 61–64, 70–73, 78–80, 85–87, 92–95, 98, 99, 110–113).

Males of *M. siciliana* well separate from those of *M. ravasinii* and *M. caucasicola* by the short standing hairs on legs and antennae (compare Figs 17, 18, 21 and 74, 75, 82, 83). They differ from *M. lacustris* by distinctly longer scape (SI$_1$ > 0.38, mean 0.423 *versus* SI$_1$ < 0.36, mean 0.335; SI$_2$ > 0.40, mean 0.445 *versus* SI$_2$ < 0.37, mean 0.339), and from *M. onoyamai* and *M. koreana* – by somewhat longer scape that are distinctly curved at their base (see Table 3 and compare Figs 17, 18 and 38, 39, 104, 105). Males of *M. siciliana* most resemble those of *M. schencki* and differ from them by a relatively longer and lower petiole (mean PI$_1$ 1.625, PI$_2$ 0.657 *versus* mean PI$_1$ 1.477, PI$_2$ 0.606) and by a distinctly less angled curve at the base of the scape (compare Figs 17, 18 and 56, 57).

Etymology. This species is named after Sicily, where it was collected.

Myrmica onoyamai Radchenko et Elmes, sp. nov.

Material examined. **Holotype** worker, Japan, Isl. Honshu, Nagano Pref., about 11 km E of Matsumoto on road to Tobira pass, ca. 1400 m a.s.l., No. J-99, 24.VII.2002, leg. G. W. Elmes (BMNH); **paratypes:** 25 workers, 10 queens, 1 male from the nest of the holotype (BMNH, IZK, ELMES).

Workers. (Figs 23–30, Table 1).
Head longer than broad, with slightly convex sides, straight occipital margin, and quite broadly rounded occipital corners. Anterior clypeal margin broadly rounded and shallowly notched medially. Frontal carinae feebly curved, frons wide (the widest among all known species of the *schencki*-group), frontal lobes narrow, not extended. Scape strongly angled at the base, with small vertical dentiform ridge (Figs 24–26) forming a small shield on the vertical face of foot (Fig. 27).

Alitrunk with weakly convex promesonotal dorsum; promesonotal suture visible from above; metanotal groove very shallow. Propodeal spines long, acute, straight, not widened at the base, slightly divergent (seen from above), projecting backwards at an angle less than 45°. In profile, anterior surface of petiole slightly concave, meeting the dorsal surface at a blunt rounded angle; dorsal surface convex and gradually sloping posteriorly, without dorsal plate. Postpetiole somewhat shorter than high, with convex dorsum. Spurs on middle and hind tibiae well developed and pectinate.

Only frons with sinuous longitudinal rugae, remainder part of head dorsum with reticulation. Antennal sockets surrounded by concentric rugae. Clypeus with longitudinal rugae, frontal triangle smooth. Sides of alitrunk with quite coarse sinuous rugae, promesonotal dorsum with reticulation. Petiolar node with sinuous longitudinal rugae, its dorsum also has reticulation, postpetiole with longitudinally-concentric rugae. Surfaces between rugae on head and alitrunk smooth and shiny, those on petiole and postpetiole punctured.

Head margins with fairly short suberect hairs, hairs on alitrunk and waist erect, longer and more abundant; scape with suberect, and tibiae with subdecumbent hairs. The overall colour brown, head dorsum blackish-brown, appendages yellowish-brown.

Queens. (Figs 31–36, Table 2).
Generally like workers in shape of head and scape, colour and pilosity of the body except they have coarser sculpture, especially on the alitrunk, petiole and postpetiole. The frons is slightly relatively wider and the propodeal spines are blunter and wider at their base.

Male. (Figs 37–42, Table 3).
Head longer than broad, with convex sides and occipital margin, and gradually rounded occipital corners; anterior clypeal margin widely rounded and shallowly notched medially. Scape short, but longer than first and second funicular segments together, very feebly and gradually curved. Antennae 13-segmented, with 5-segmented club.

Alitrunk relatively long, scutum slightly convex, scutellum does not project dorsally above scutum when seen in profile. Propodeum with blunt rounded tubercles. In profile, petiole relatively long and low, with rounded dorsum of node, its anterior surface almost straight and quite steep; postpetiole higher than long, with weakly convex dorsum.

Head dorsum finely but densely punctured, frons and temples with very fine striation. Scutum and scutellum smooth and shiny, only posterior part of scutum and posteriolateral parts of scutellum with very fine striation. Propleura smooth and shiny, only with fine striation on their posterior parts; mesopleura and propodeum not coarsely rugose. Petiole and postpetiole smooth and shiny.
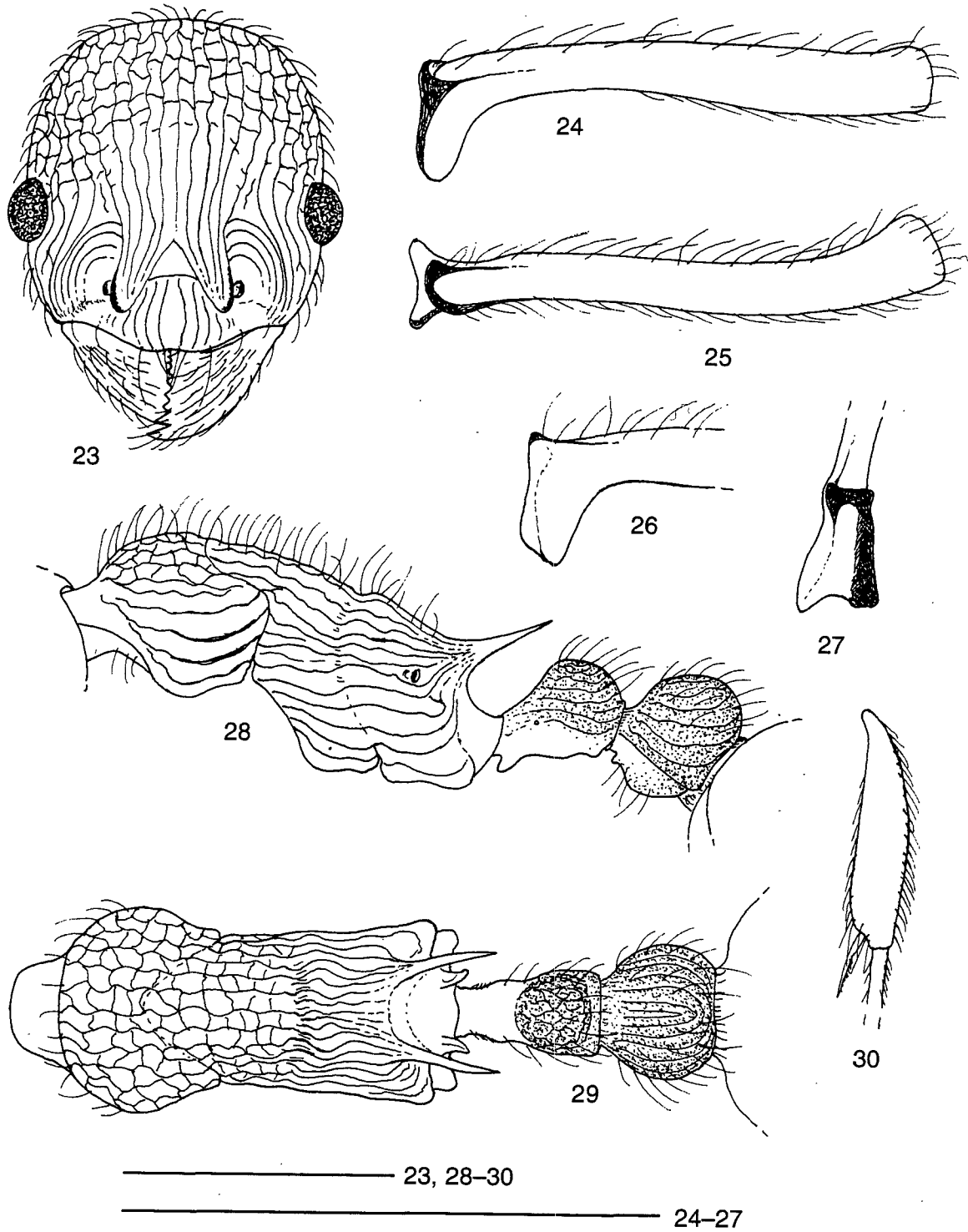
Figures 23–30. Details of structure of *Myrmica onoyamai* (holotype, worker). (23) Head, dorsal view; (24) scape, posteriolateral view; (25) scape, dorsal view; (26) base of scape, anterolateral view; (27) vertical face of antennal foot; (28) alitrunk and waist in profile; (29) alitrunk and waist from above; (30) tibia and base of first tarsal joint of hind leg. Scale bars: 1 mm.
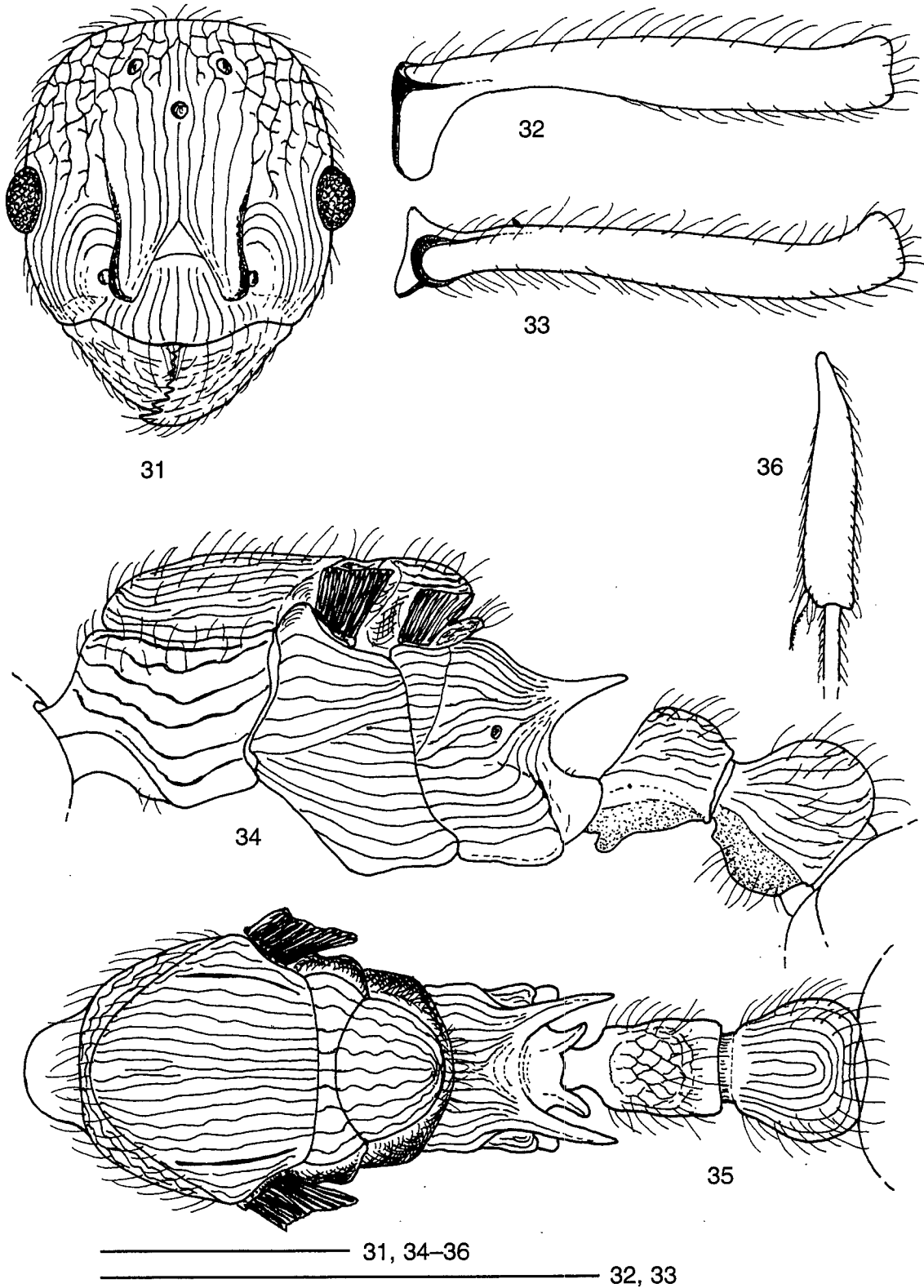
Figures 31–36. Details of structure of *Myrmica onoyamai* (paratype, queen). (31) Head, dorsal view; (32) scape, posteriolateral view; (33) scape, dorsal view; (34) alitrunk and waist in profile; (35) alitrunk and waist from above; (36) tibia and base of first tarsal joint of hind leg. Scale bars: 1 mm.
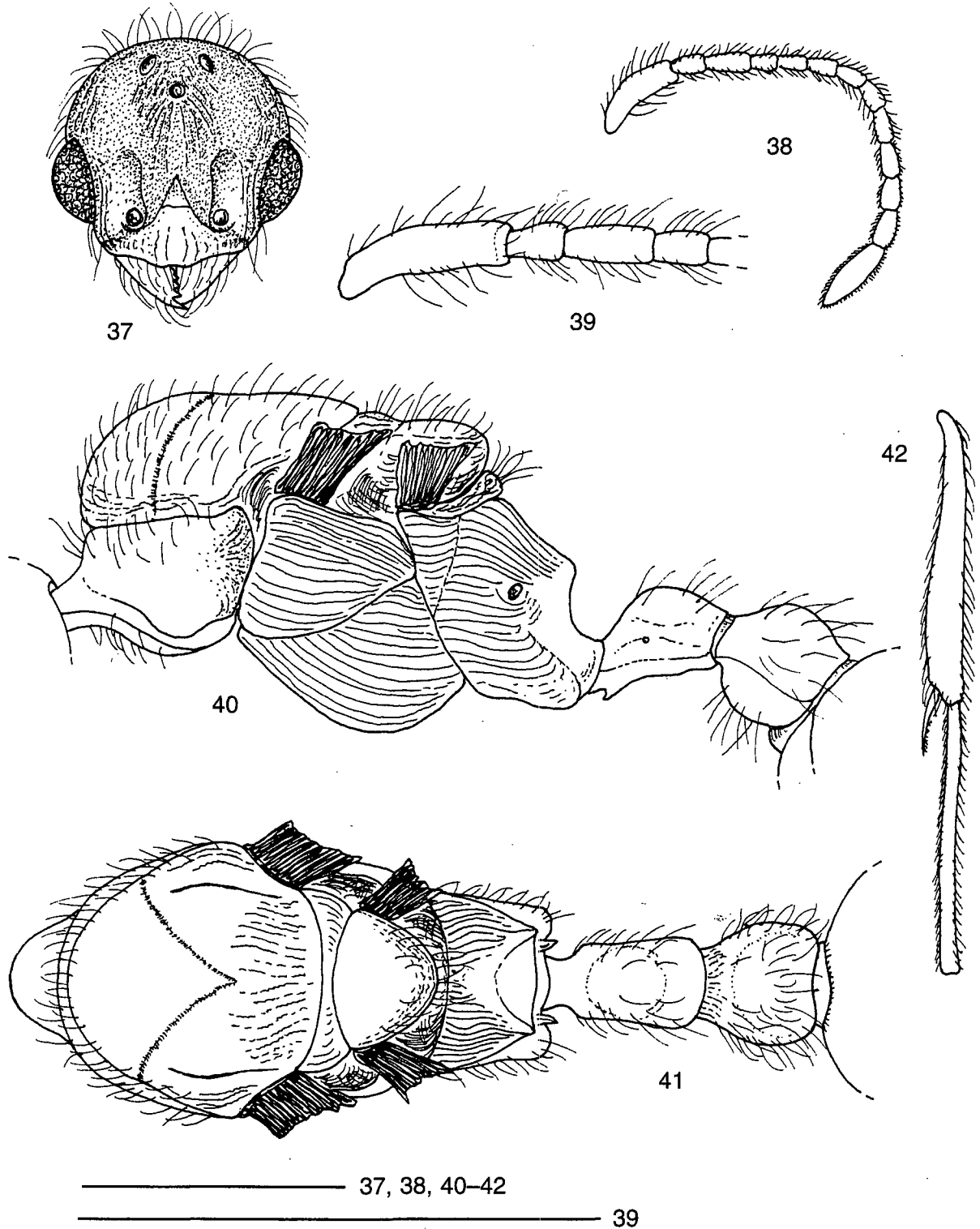
Figures 37–42. Details of structure of *Myrmica onoyamai* (paratype, male). (37) Head, dorsal view; (38) antenna; (39) scape and three basal antennal joints, lateral view; (40) alitrunk and waist in profile; (41) alitrunk and waist from above; (42) tibia and first tarsal joint of hind leg. Scale bars: 1 mm.

Head margins, alitrunk and waist with quite long erect hairs. Tibiae and tarsi with short subdecumbent to suberect hairs; scape and first seven funicular segments with longer hairs, segments of antennal club with very short subdecumbent hairs. Body colour black, appendages lighter.

Ecology. This species is known only from a single colony from Honshu, Japan (see Fig. 22). The nest of this species was found under a small stone in pile of sandy gravel dumped by the side of the road, possibly to grit the road in icy conditions. It had been there some time because the surface had been stabilised by moss and lichens. The road followed the course of a river and the site was an area of mixed woodland at an altitude ca. 1400 m a.s.l., about 10 m from the river. This anthropogenic nest-site was quite exposed, hot and dry compared to general area. Therefore the location may not be typical for this species. We guess that it naturally should be associated with warmer exposed biotopes such as sub-alpine grassland and sandy screes at the base of cliffs.

Comparative diagnosis. Workers and queens of *M. onoyamai* well differ from those of all other members of *schencki*-group by the a relatively wide frons with proportionally less extended frontal lobes: in workers mean FI 0.353, mean FLI 1.202 *versus* mean FI < 0.320, mean FLI > 1.280. The single known male of *M. onoyamai* well separates from males of *M. ravasinii* and *M. caucasicola* by the short standing hairs on legs and antennae (compare Figs 38, 39, 42 and 74, 75, 82, 83); it differs from males of *M. lacustris* by its longer scape (SI$_1$ 0.371 *versus* SI$_1$ < 0.360, mean 0.335 and SI$_2$ 0.394 *versus* SI$_2$ < 0.370, mean 0.339), and from *M. siciliana* and *M. schencki* – by the base of the scape being only very feebly and gradually curved (compare Figs 38, 39 and 17, 18, 56, 57). The male of *M. onoyamai* most resembles males of *M. koreana* but differs from it by shorter hairs on the head margins, by the much less sculptured, almost smooth scutum and scutellum, by the not angled dorsal plane of the scape, by wider postpetiole (PPH/PPW=PPI$_2$ 1.225 *versus* PPI$_2$ < 1.050 (compare also Figs 37–41 and 103–107).

Etymology. The species is dedicated to Prof. Keiichi Onoyama, Obihiro University, Japan, famous Japanese myrmecologist, with whom we collaborate on the investigation of the genus *Myrmica*.

Myrmica inucta Radchenko et Elmes, sp. nov.

Material examined. Holotype worker, Kazakhstan, Naurzumsky Natural reserve, No 625, leg. T. Bragina (IZK); **paratypes**: 3 workers from the nest of the holotype (IZK, ELMES).

Workers. (Figs 43–50, Table 1).

Head longer than broad, with subparallel sides, slightly convex occipital margin, and quite narrowly rounded occipital corners. Anterior clypeal margin rounded and notched medially. Frontal carinae not strongly curved, frons relatively wide, but frontal lobes distinctly extended. Scape strongly angled at the base, with small vertical lobe (Figs 44–46) that forms only a very small shield on the vertical face of foot (Fig. 47).

Alitrunk with convex promesonotal dorsum; promesonotal suture visible from above; metanotal groove shallow, but distinct. Propodeal spines long, acute, straight, not widened at the base, subparallel when seen from above, projecting backwards at an angle less than 45°. In profile, anterior surface of petiole concave, meeting the dorsal surface at a blunt angle; dorsal surface convex and gradually sloping posteriorly, without distinct dorsal plate. Postpetiole somewhat shorter than high, with convex dorsum. Spurs on middle and hind tibiae well developed and pectinate.

Whole body with reduced sculpture, shiny. Head dorsum at most with fine longitudinal striation, antennal sockets do not surrounded by rugae, clypeus completely smooth. Sides of alitrunk with fine sinuous striation, alitrunk dorsum with somewhat coarser striation and fine rugulosity. Petiole and postpetiole finely punctured.

Head margins with quite short subdecumbent hairs, alitrunk dorsum (except of propodeum) and waist with relatively long erect to suberect hairs; scape with suberect, and tibiae with subdecumbent hairs. The overall colour black.

Queens and males are unknown.

Ecology. The type specimens were collected in a nature reserve noted for its salted marshes, and we speculate that *M. inucta* may be a local species of the relict salted steppes, at one time more common in northwest Kazakhstan. The type specimens were found in a salted depression on tall-grass halophytous meadow-steppe. Such depressions are typically filled with water after rain, which evaporates in dry periods, over many years these depressions become very salted with salt deposited on the soil surface. The margins form distinct habitats for many plants and animals, including some *Myrmica* species, e.g., *M. bergi* Ruzsky (Bondar' *et al.* 1998).

Comparative diagnosis. Workers of *M. inucta* well differ from all other *schencki*-group species by its reduced body sculpture and entirely black body. Generally, reduced sculpture of the body is very rare in the genus *Myrmica*: previously only one species with reduced sculpture was known from the Old World – *M. nitida* Radchenko et Elmes from the Himalaya.

For the time being we place *M. inucta* in the *schencki*-group because its workers possess all the main diagnostic features of that group, however, we
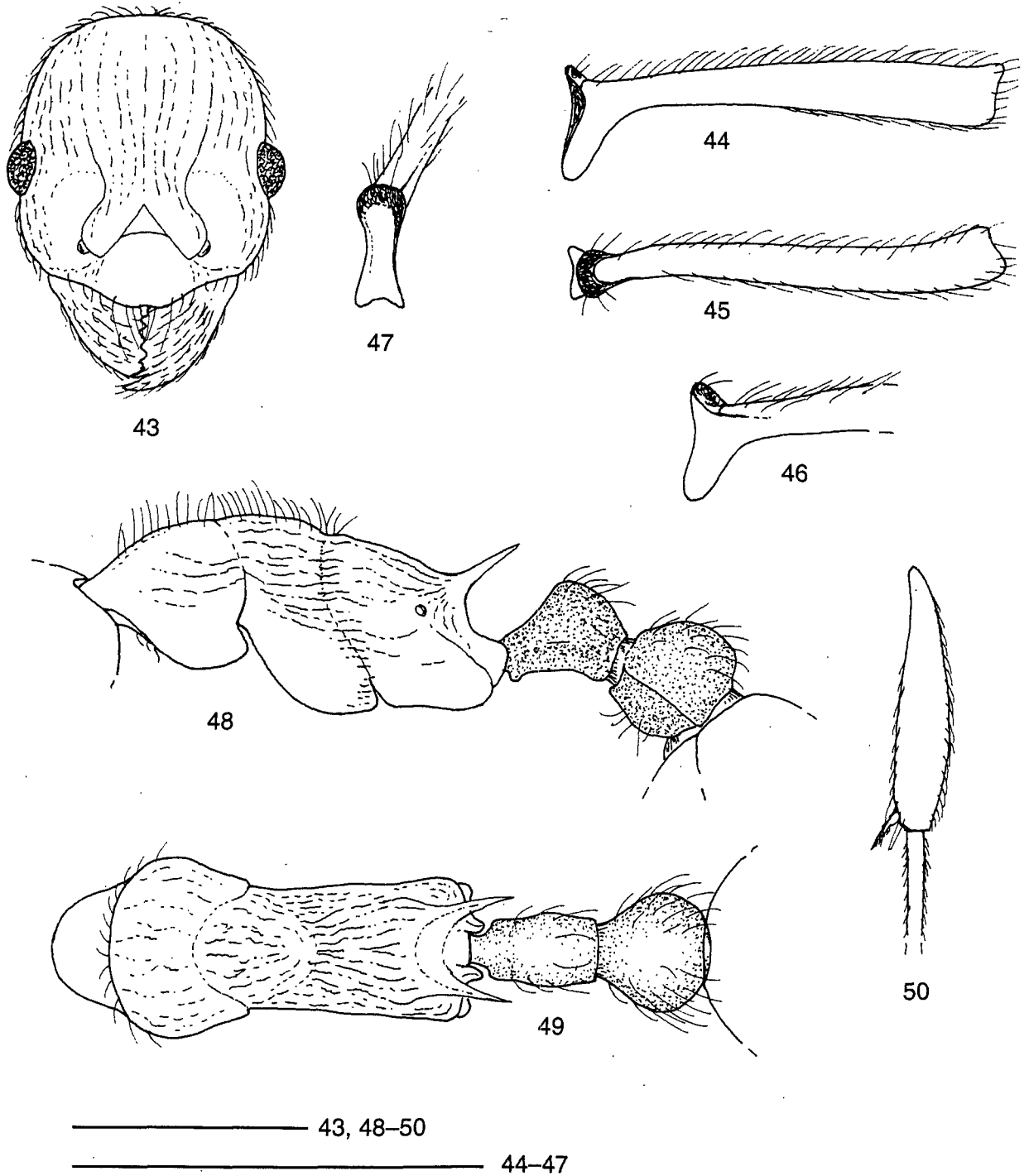
Figures 43–50. Details of structure of *Myrmica inucta* (holotype, worker). (43) Head, dorsal view; (44) scape, posteriolateral view; (45) scape, dorsal view; (46) base of scape, anterolateral view; (47) vertical face of antennal foot; (48) alitrunk and waist in profile; (49) alitrunk and waist from above; (50) tibia and base of first tarsal joint of hind leg. Scale bars: 1 mm.

can not exclude the possibility that it may belong to the *lobicornis*-group. This can only be resolved when males are found.

Etymology. This species is named after Latin word *"inuctus"* – oily-sheen, which indicates the appearance of the body surface.

Review of species

Myrmica schencki Viereck, 1903
(Figs 51–58, Tables 1–3)

Myrmica rubra var. *schencki* Viereck 1903: 72, w, q, m, Europe (see also Baroni Urbani 1971: 35, note) [first available use of *Myrmica rubra* subsp. *scabrinodis* var. *schencki* Emery, 1895: 315, unavailable name]; lectotype and paralectotypes in MHNG, examined.

Myrmica scabrinodis lobicornis var. *schencki*: Ruzsky 1905: 699 [unavailable name].

Myrmica scabrinodis schencki: Emery 1908: 178.

Myrmica schencki: Bondroit 1911: 11 (for details see Radchenko 1994c, Bolton 1995, Seifert 2003).

Myrmica schencki var. *kutteri* Finzi, 1926: 111, w, Switzerland, synonymy of Bernard 1967: 118, Radchenko 1994c: 77, Bolton 1995: 280, Seifert 2003: 145, confirmed here; syntypes in ZMMU, examined.

Myrmica schencki var. *obscura* Finzi, 1926: 111, w, q, m, Italy; Baroni Urbani 1971: 36. Junior synonym of *schencki*: Bernard 1967: 118, Radchenko 1994c: 77, Seifert 2003: 145; of *lobicornis* (part.): Seifert 1988: 38; confirmed here, syntypes in MCZ, examined.

Myrmica schencki nat. *subopaca* Arnoldi, 1934: 172, w, Ukraine [Bolton (1995) erroneously recorded type locality as Russia] [also described as new by Arnoldi, in Karawajew 1934: 96] [unresolved junior primary homonym of *Myrmica subopaca* F. Smith 1858: 127], synonymy of Arnoldi 1970: 1843, Radchenko 1994c: 77, Seifert 2003: 145, confirmed here; syntypes in ZMMU and IZK, examined.

Myrmica betuliana Ruzsky, 1946: 70, w, Russia (West Siberia), synonymy of Radchenko 1994c: 77, types lost.

Material examined. Type material of *M. schencki*: lectotype worker (upper specimen on the pin with 2 workers, designated by Seifert 2003), "Graten?", "*Myrmica lobicornis* Nyl.", "*M. scabrinodis* var. *Schencki* Emery (*lobicornis Schencki*)", "Lectotype (top specimen) *Myrmica rubra scabrinodis* var. *schencki* Emery, 1895, designated by Seifert", "Museo Civico di Genova" (MHNG); paralectotypes: 1 worker (bottom specimen) on the pin with lectotype; 1 worker and 1 queen (damaged) on the same pin, "w♀Ex", "Paralectotypus var. *schencki* Emery, 1895"; 1 worker and 1 male (damaged); "♂wEx", "Paralectotypus var. *schencki* Emery, 1895" (MHNG); Type material of *Myrmica schencki* var. *kutteri*: 3 workers, syntypes, "Cotypus", "*M. schencki* var. *kutteri* Finzi", "Zermatt ca. 1750 m VII.17" (ZMMU); syntypes of *Myrmica schencki* var. *obscura*: 2 workers "M. Nanos V.23 Finzi, typo" (red pen), "B. Finzi coll.", "Pur. 1950", "MCZ type 28794", 2 workers (same, but no red type label), 1 queen (same labels as first, but date 15.9.24), 1 male (same labels as queen, but no red type label)

(MCZ); syntypes of *Myrmica schencki* nat. *subopaca*: 19 workers, "Proval'e, Donets, vi. 928, Medvedev" [original labels written in Russian; correct place: south-eastern Ukraine, Donetsk Prov., Natural Reserve "Proval'skaya Step"], Nos 3687, 3688, 3691, 3692, 3693, 3694, 3695; 3665 (ibid., 20vi.928); 3670 (ibid., 18.VI.928); 3671 (ibid., 19.V.928); 2 workers, "Proval'e, Donets, VII.31, S. Medvedev", "5632 Coll. Karawajew", "*Myrmica schencki* Em. n. *subopaca* Arnoldi typ.", "Syntypus *Myrmica schencki subopaca* K. Arnoldi" (ZMMU, IZK).

Non-type material: several hundred workers, several tens males and queens of *M. schencki* from Europe, Caucasus, Siberia, Northern Kazakhstan and Tien-Shan' (ZMMU, ZISP, IZK, BMNH, ELMES).

Distribution. (Fig. 59). Europe (northern limit: central England and Ireland, southern Norway, Sweden and Finland; southern limit: northern Spain and Italy, Balkans), Caucasus, north-eastern Turkey, south of West Siberia, northern Kazakhstan, Tien-Shan', Altai Mts; the easternmost known locality is vicinity of Krasnoyarsk (East Siberia, material in ZMMU, examined).

Ecology. Throughout most of its northern distribution, *M. schencki* is associated with hot, dry grassland habitats including calcareous grassland, glacial sand deposits (e.g., Jensen 1976) and seaboard sand-dunes. In its southern distribution it is a species of sub-alpine grassland. Much of its distribution seems to coincide with species of *Tetramorium*, which is a dominant species in such habitats. The common factor appears to be the need for relatively high soil temperatures but not completely arid conditions. In biotopes where the soil is potentially very arid, e.g., the sand-dunes of NW Europe, the sub-alpine pastures of the Southern Alps and limestone pavement as in the Burren, Ireland, there is a relatively high rainfall, which stops complete desiccation of the soils. *M. specioides* Bondroit is the only other European *Myrmica* species that can tolerate similarly hot habitats. In many places it faces as much competition from ants from other genera as from *Myrmica* species, and we believe that this contributes to its habit of building a small woven funnel at its nest entrance in which a "guard-worker" sits with its head more or less blocking the entrance. One of us (GWE) has often recorded and excavated *M. schencki* nests from the middle of *Tetramorium caespitum* (L.) nests, a species that can be quite aggressively territorial. Its habitat requirements in the east of its range are less well known but we have recorded it from locally hot exposed microhabitats in open forest.

M. schencki has been well studied during the last two decades because it is a primary host of the larvae of the parasitic butterfly *Maculinea rebeli* (Hir.) that has a very high nature conservation value throughout Europe (see numerous papers in Settele *et al.* 2005), models of its population structure have
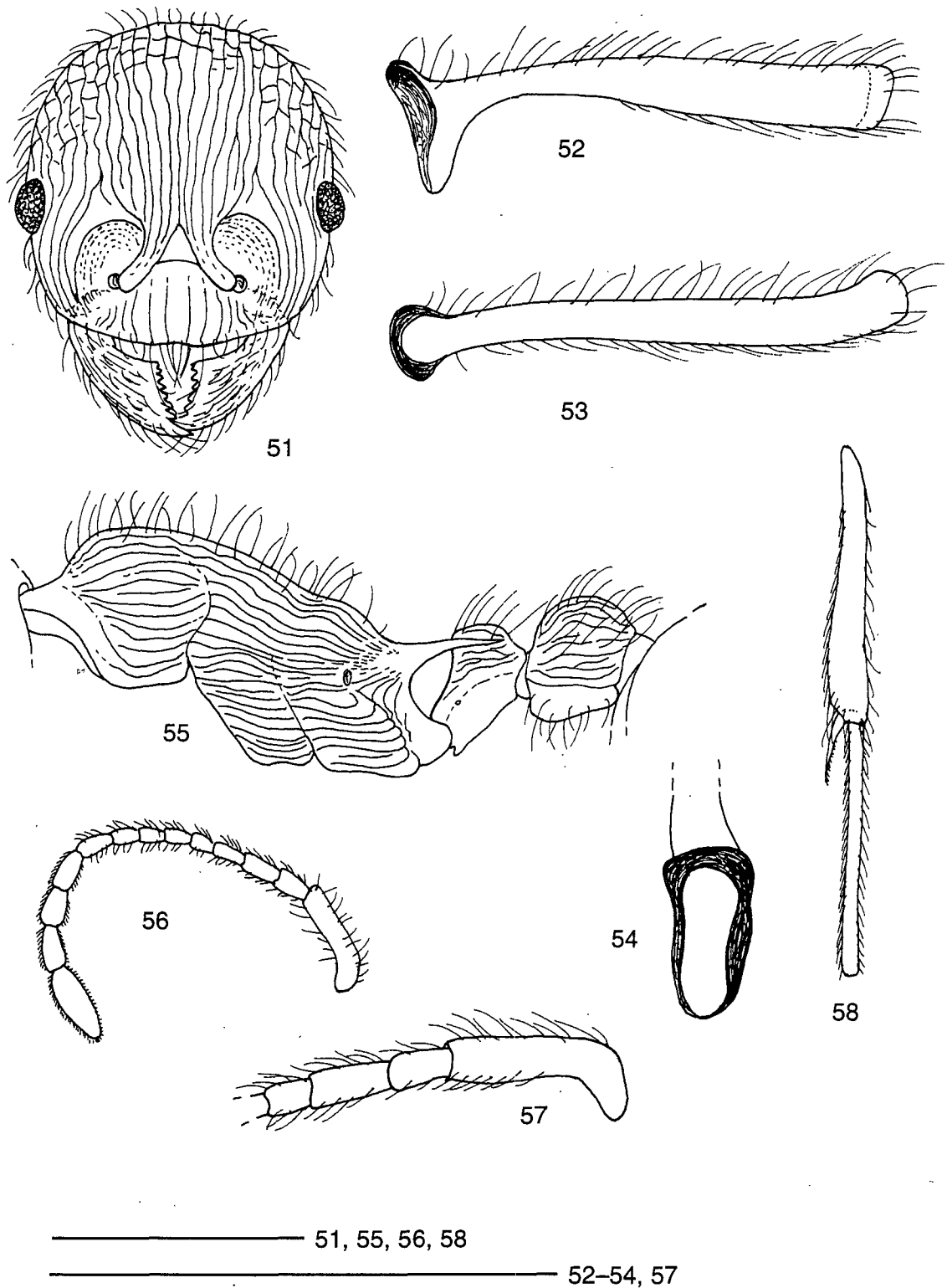
Figures 51–58. Details of structure of *Myrmica schencki* (51–55 – lectotype, worker; 56–58 – paralectotype, male). (51) Head, dorsal view; (52) scape, posteriolateral view; (53) scape, dorsal view; (54) vertical face of antennal foot; (55) alitrunk and waist in profile; (56) antenna; (55) scape and three basal funicular joints, lateral view; (58) tibia and first tarsal joint of hind leg. Scale bars: 1 mm.

been developed (Hochberg *et al.* 1994) and its characteristic cuticular hydrocarbons have been determined (Elmes *et al.* 2002). Its nest populations vary from less than a hundred to several thousands of workers and although many nests are monogynous, colonies with two, sometimes many more queens are not uncommon.

Notes. The authorship of this common species was ascribed to Emery by almost all subsequent authors, however based on the paragraphs 10.2, 45.5.1 and 50.3.1 of the 4th edition of the International Code of Zoological Nomenclature (1999) the author of *M. schencki* is really Viereck, who made the first available use of the name (see Bolton 1995, Seifert 2003).

Emery (1895) described var. *schencki* based on material from both the USA (Maine and New Jersey) and Europe. Later Forel (1914) separated the North American populations as var. *"emeryana"* from the European populations, for which he used the name *"schencki"*. Baroni Urbani (1971: 35) believed this was probably technically wrong and the name *"schencki"* should appertain to the North American species, however, because "the name had so long been employed incorrectly" he would leave any decision on this to "future revisers" (loc. cit.). Seifert (2003) tried hard but failed to find the original North American type series, but located in Emery's collection (MHNG) the specimens from Europe labelled *"schencki"* in Emery's own hand, from which he designated a lectotype. Even if the original series were to be located and Baroni Urbani's view was correct, we believe that Forel's treatment of *Myrmica emeryana* and Seifert's treatment of *M. schencki* should stand (see paragraph 24 the International Code... 1999). There have been so many recent publications relating to *M. schencki* (see Settele *et al.* 2005 for a few) that to attempt to change these names would cause untold confusion in both Europe and North America.

Seifert (2003) noted that the material, which includes the lectotype, fully corresponds with the characters of West Palaearctic *M. schencki* as recognised by many authors for more than 50 years (we completely agree with his view that *M. schencki* has only a Palaearctic distribution). Seifert noted that the original locality label of the lectotype specimen is quite illegible but read it as "Graten" and attributed this material to Europe on the grounds that if the material had a North American origin Emery would have "surely stated". We made a search for this name and found nothing fully corresponding to it, either in North America or Europe, however if this label were "Graben" it could one of several places in regions of Germany and Austria where *M. schencki* is common.

Almost certainly the original American part of the type material, that was collected from Maine, USA by Pergande, belongs to *Myrmica emeryana*. Support for this view came when we examined specimens, recently collected in Maine by one of us (GWE), of a quite widespread species recognised as *"Myrmica emeryana"* by local entomologists. Our specimens are morphologically very similar to the species from the *schencki*-group and either belongs to that or to another closely related species-group, but they absolutely could not be confused with Palaearctic *M. schencki*.

M. schencki is fairly stable morphologically, specimens having quite constant characters. The primary diagnostic characteristics of its workers is a narrow frons (mean FI 0.233) and well-developed vertical lobe at the scape bent (Figs 52–53) with a distinct shield-like appearance on the vertical face of the foot (Fig. 54). *M. koreana* is the most similar species though *M. schencki* differs from it by its smaller FI (mean FI in *koreana* 0.294), bigger scape lobe and deeper metanotal groove (see Table 1, Figs 51–54 and 91–95; for more detail see Elmes *et al.* 2001). Queens of
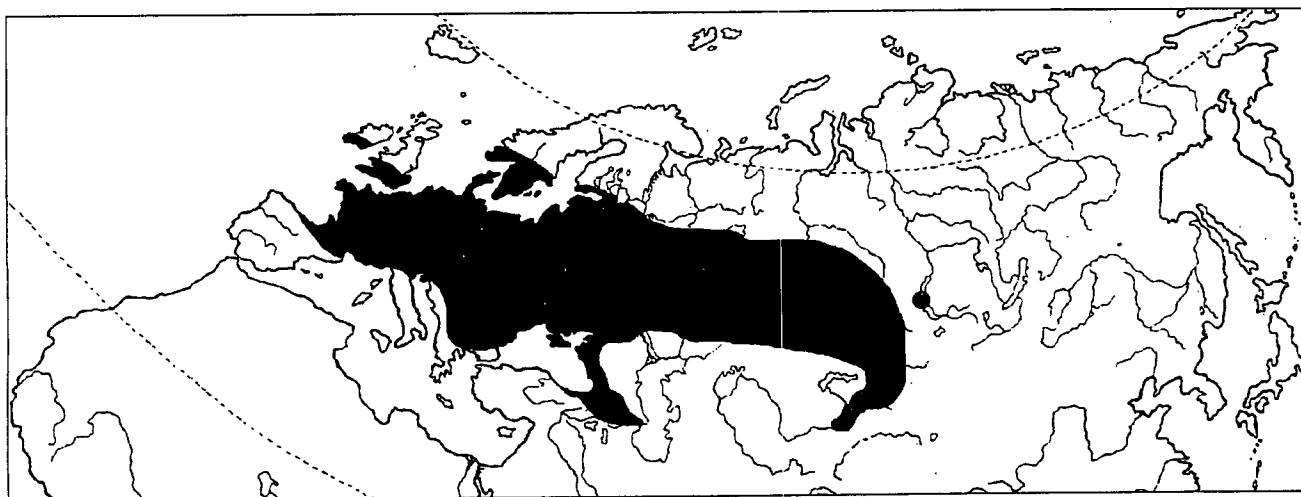

Figure 59. Map of distribution of *Myrmica schencki*.

M. schencki are much larger than those of *M. koreana* (mean HW 1.226 *versus* 1.024 mm). Although the female castes of *M. schencki* can usually be distinguished those of *M. lobicornis* and related species on scape-shape alone, i.e. the presence of the shield-like plate on the vertical face of the foot of the scape (compare Figs 54 and 117) a few individuals might be confused. However, apart from their narrower frons (means FI 0.233 of workers *versus* > 0.265) they have a quite different shape of petiole seen in profile, which has a well-developed anterior peduncle and concave anterior face, which meets with the dorsal surface to form a blunt angle. This feature has long been used in European keys (e.g., Collingwood 1958, 1979, Kutter 1977, Arnoldi 1970, Arnoldi and Dlussky 1978, Czechowski *et al.* 2002, Radchenko *et al.* 2004). The short scape of males makes it impossible to confuse them with males of the *lobicornis*-group (for their separation from the other species of the *schencki*-group see Key below).

Eight infraspecific forms of *M. schencki* have been described from the Palaearctic Region. Three of them (*Myrmica schencki* var. *brunescens* Karawajew, 1929 from Caucasus; *Myrmica schencki* var. *burtshakabramovitshi* Karawajew, 1929 from Ukraine, and *Myrmica schencki* var. *starki* Karawajew, 1929 from northern Russia, Kola Peninsula) are now considered as synonyms of *M. lobicornis* (or related species) (Arnoldi 1970, Seifert 1988, Radchenko 1994d, Bolton 1995). *Myrmica lobicornis* var. *plana* Karawajew, 1927 from Ukraine, was considered to be subspecies of *M. schencki* by Karawajew (1929); this was synonymised with *M. deplanata* (Karawajew 1934, Arnoldi 1970, Seifert 1988), now itself synonymised with *M. lacustris* (Radchenko 1994c). A fifth form, *M. caucasicola* Arnoldi is considered to be a good species (Radchenko 1994a, c, Bolton 1995, Seifert 2003).

Only three forms (*Myrmica schencki* var. *kutteri*, *M. schencki* nat. *subopaca* and *M. schencki* var. *obscura*) remain synonyms of *M. schencki*. We investigated the type specimens of all these taxa and confirm the earlier established synonymies (see above). We measured the types of var. *obscura* and found slight differences from typical *M. schencki*, most obviously the male has a relatively shorter scape (SI$_2$ 0.40) and the workers – a slightly wider frons (FI > 0.26). The workers and queen are somewhat intermediate to *M. caucasicola*. Based on discriminators calculated from the morphometric discrimination analysis (below), three workers and the queen were assigned *M. schencki* with a high confidence and only a small chance of being *M. caucasicola* although one worker had only a 13% probability of being clustered with *M. schencki* and an 86% chance of being identified as *M. caucasicola*. We would not be surprised if these specimens eventually are shown to represent

a different Central Italian form (perhaps even species), but unless more material is obtained the name *obscura* best remains synonymised with *M. schencki*.

We formally propose that *M. betuliana* Ruzsky, 1946 should be considered as a junior synonym of *M. schencki*. Despite the type specimens of *M. betuliana* being most probably lost, there exists a fairly good description. This species was described from West Siberia, where it was found in small birch woods (Barabinskaya Step': station Tajga; Bogorodskoe on Ob' river, Vershinino; Basandaika; now – Novosibirsk and Tomsk Provinces, Altai Region). The main diagnostic features of this species (workers), pointed by Ruzsky (1946: 70–71) are: "Resembles *lobicornis* (by the shape of scape); by the shape of alitrunk and waist it is similar to *M. ruginodis*. Scape at the base curved, almost right angled, with a wide shovel-like lobe (which is big and well defined)... Propodeal spines long, thin, straight and acute; ... metanotal groove weak. Petiolar and postpetiolar dorsum ovally rounded, not shiny, submat, with fine longitudinal reticulation and rugulosity. Head and alitrunk with quite coarse longitudinal rugulosity... Colour rather light, brownish-reddish-yellow or brownish-yellow. 5.0–5.5 mm" (translation from Russian by AR). In our opinion all the main diagnostic features of Ruzsky's description (except perhaps only weakly developed metanotal groove) conform to those of *M. schencki*. The only other candidates for its identity are *M. koreana* from which it differs by its "wide shovel-like lobe", and *M. lobicornis*, which apart from the lobe shape, has quite another shape of petiole (see above).

Myrmica lacustris Ruzsky, 1905
(Figs 60–67, Tables 1–3)

Myrmica scabrinodis var. *lacustris* Ruzsky 1905: 686, w, Russia (West Siberia) and northern Kazakhstan; Emery 1908: 177, 1921: 40, Weber 1950: 206, neotype in ZMMU, examined.

Myrmica lacustris: Radchenko 1994a: 44, 1994b: 140, 1994c: 77, Bolton 1995: 280, Seifert 2003: 150.

Myrmica lobicornis var. *deplanata* Emery 1921: 38, w, Russia (Saratov and Orenburg Gubernies, now – Volgograd and Cheliabinsk Provinces), Georgia, Ukraine (Crimea), types lost [first available use of *Myrmica scabrinodis* subsp. *lobicornis*. var. *deplanata* Ruzsky 1905: 700, unavailable name], synonymy of Radchenko 1994c: 77.

Myrmica lobicornis subsp. *deplanata*: Weber 1948: 276.

Myrmica schencki var. *deplanata*: Finzi 1926: 111.

Myrmica deplanata: Arnoldi 1934: 169, m, *et auct.* (for details see Radchenko 1994c, Seifert 2003).

Myrmica moravica Soudek 1922: 45, w, q, Czechia (Moravia) [also described as new by Soudek 1923: 107], 1925: 35, m, Finzi 1926: 104, Weber 1950: 213, synonymy of Karawajew 1934: 83, Seifert 1988: 36, Bolton 1995: 281 (as synonym of *deplanata*); Radchenko 1994c: 78, Seifert 2003: 150 (as synonym of *lacustris*).

Myrmica deplanata moravica: Novák and Sadil 1941: 80, Kratochvíl, in Kratochvíl, Novák and Snoflák 1944: 40, Sadil 1940: 102, 1952: 263, Arnoldi 1970: 1843.

Myrmica lobicornis var. *plana* Karawajew 1927: 283, w, Ukraine,
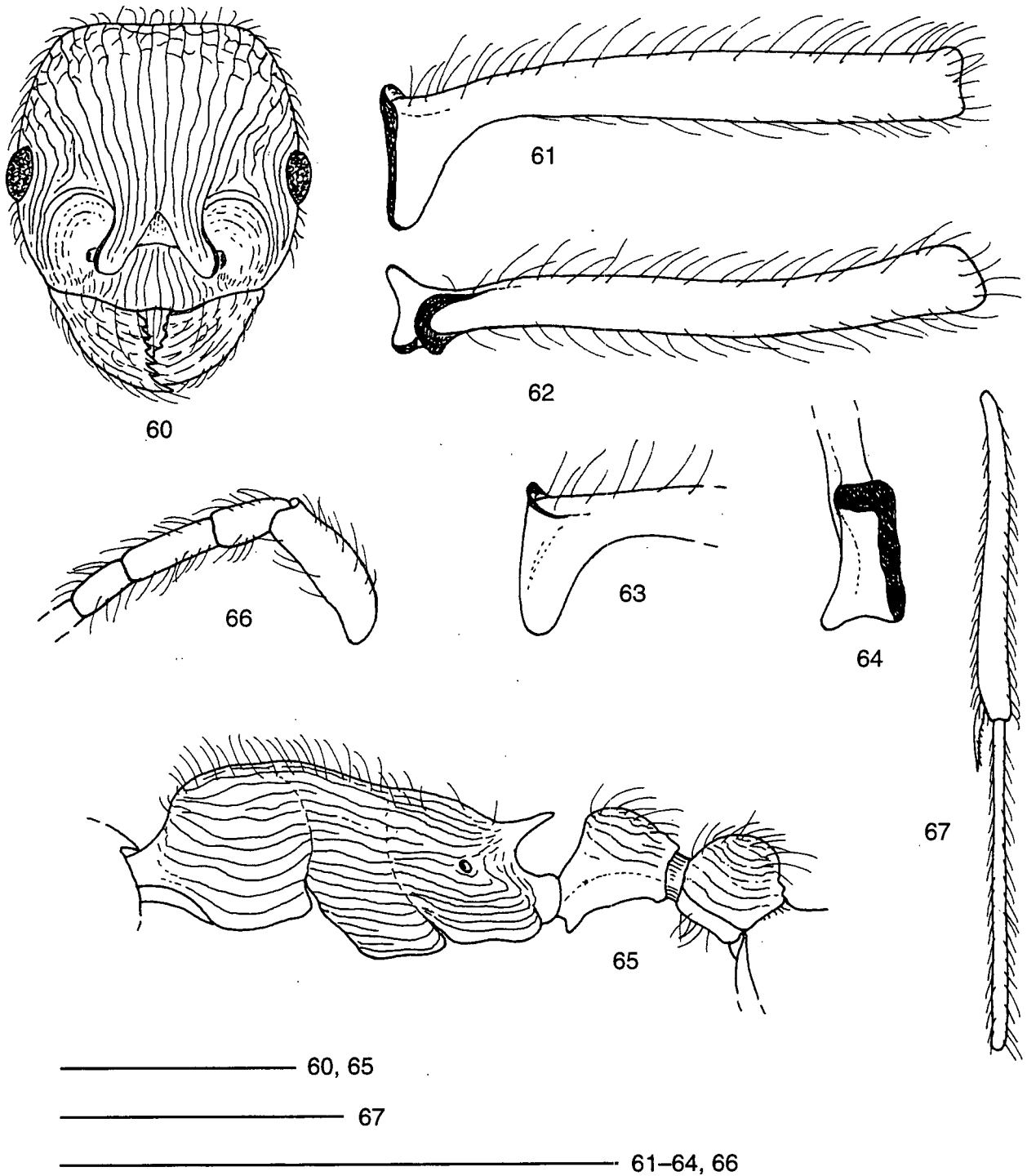
Figures 60–67. Details of structure of *Myrmica lacustris* (60–65 – worker; 66, 67 – male). (60) Head, dorsal view; (61) scape, posteriolateral view; (62) scape, dorsal view; (63) base of scape, anterolateral view; (64) vertical face of antennal foot; (65) alitrunk and waist in profile; (66) scape and three basal funicular joints, lateral view; (67) tibia and first tarsal joint of hind leg. Scale bars: 1 mm.

syntypes in IZK and ZMMU, examined, synonymy of Karawajew 1934: 83, Arnoldi 1970: 1843, Seifert 1988: 36 (as synonym of *deplanata*); Radchenko 1994c: 78, Bolton 1995: 282, Seifert 2003: 150 (as synonym of *lacustris*).

Myrmica schencki var. *plana*: Karawajew 1929: 208, Weber, 1948: 302.

Myrmica deplanata nat. *plana*: Arnoldi 1934: 170, q, m, Karawajew 1936: 276.

Myrmica deplanata subsp. *plana*: Sadil 1940: 102.

Material examined. Type material: neotype queen of *M. lacustris*, "N.-Petrovskij, Akmolinskij uezd" (now – Akmola Province of Kazakhstan) (label in Russian), designated by Radchenko 1994c, (ZMMU); 4 workers, syntypes of *Myrmica lobicornis* var. *plana*, "Askania-Nova, Dobrschanskiy, 1923" (IZK, ZMMU). Non-type material: more than one hundred workers, several tens of males and queens from Czechia, Ukraine, Russia, Bulgaria, Transcaucasus, Kazakhstan, Tien-Shan' and Turkmenistan (IZK, ZMMU, ZISP, MIZ, ELMES).

Distribution. (Fig. 68). Central and southern Europe (Austria, Czech Republic, Slovakia, former Yugoslavia, Romania, Bulgaria, Trace), southern Ukraine and south of European part of Russia, Transcaucasus, Turkmenistan, Iran, south of West Siberia, northern Kazakhstan, Tien-Shan', to the east as far as the Altai Mts. Ruzsky (1925, 1936) recorded *M. lacustris* (under the name *M. scabrinodis lobicornis* var. *deplanata* and *M. lobicornis* var. *deplanata* respectively) for Transbaikalia [Verhneudinsk (now – Buryatia, Ulan-Ude), vil. Kudara; vicinity of Chita]; we can find no trace of this material in FSU collections and based on our current understanding of the distribution of *M. lacustris* these identifications seem doubtful.

Ecology. *M. lacustris* is one of the truly thermoxerophilous *Myrmica* species. It inhabits mainly steppes and steppe-like open mountain slopes at a low altitude, prefers stony places with low, often sparse vegetation. Nests are built in the soil or often under stones in places that become very hot in summer months. Although it is reportedly tolerant of high soil salinity it is not particularly associated with the damper steppe areas that can become quite salted (see ecology of *M. inucta*). Generally, *M. lacustris* colonies are widely and sparsely distributed, even in localities where it has been frequently recorded its nests are never abundant.

Notes. The junior synonym *M. deplanata* was widely used in myrmecological literature until Radchenko (1994c) showed that Ruzsky's (1905) *deplanata* is conspecific with another previously forgotten form, described by him in the same monograph – *M. scabrinodis* var. *lacustris*, and that the latter name has priority. While arguably it might have been better for stability of nomenclature to retain the name *M. deplanata*, the synonymy was valid and must stand (see also Seifert 2003). Based on examination of the type specimens of *Myrmica lobicornis* var. *plana* we confirm the earlier established synonymy, first with *M. deplanata* and now – with *M. lacustris*.

Despite our best efforts we can not find the type specimens of *M. moravica*. In the ZMMU there 2 workers labelled as "Hubochepy, Praha, Bohemia, J. Sadil, 1938", "*Myrmica moravica* Soud., var. n., cotype", however they really do not belong to the type series, because were collected later (in 1938). We also examined 6 workers from IZK with the label "Morava, Sadil leg.", "*Myrmica moravica* Soud. Karawajew det.". All these specimens assuredly belong to *M. lacustris* indicating that the synonymy is correct.

Arnoldi's (1948) *M. deplanata* subsp. *lulakeranica* is a *nomen nudum*. However, we examined corresponding material from Talysh (SE Azerbaijan), and similar nest series from Kopet Dagh, preserved in
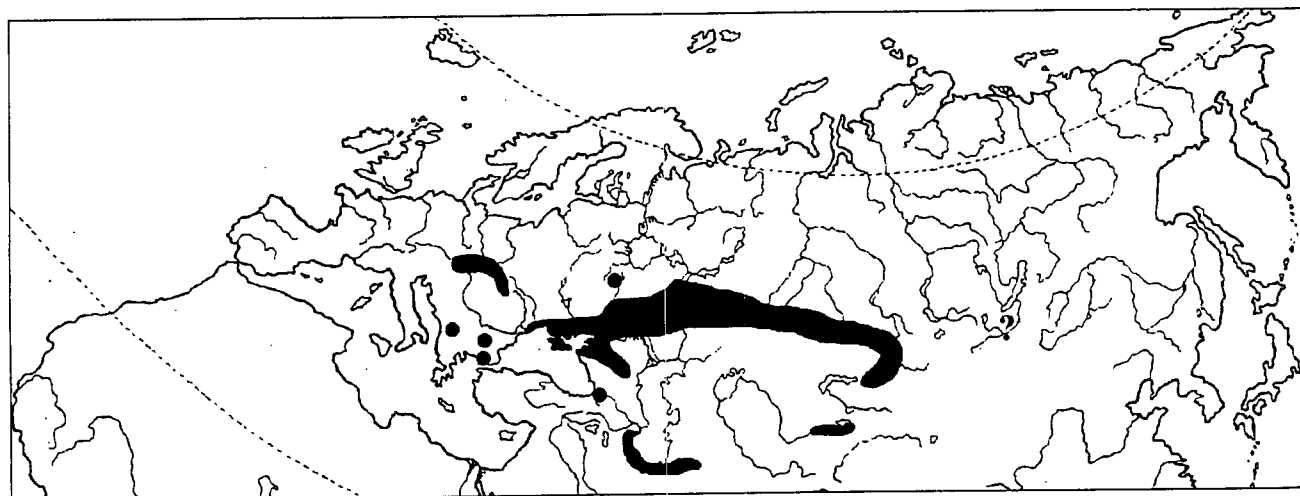

Figure 68. Map of distribution of *Myrmica lacustris*.

ZMMU. These series are quite typical of *M. lacustris*, though in this region, workers have very small, reduced vertical dentiform lobe on the scape bend. Radchenko (1994c) also attributed to *M. lacustris* the unavailable name *M. scabrinodis* subsp. *lobicornis* var. *grandis* Kuznetsov-Ugamsky, 1927, described from Osh Province, Kyrgyzstan.

Based on Ruzsky's (1905) somewhat ambiguous description of *Myrmica scabrinodis* var. *salina*, Radchenko (1994c) considered it to be a synonym of *M. lacustris*. However, Seifert (2002, 2003) disagreed with this opinion, designated the neotype of *M. salina*, and proposed that it is a species from *scabrinodis*-group and is the senior synonym of *M. slovaca* Sadil. In the absence of original type specimens we accepted this opinion (Radchenko and Elmes 2004).

Workers and queens of *M. lacustris* well differ from those of sympatric *M. schencki*, *M. caucasicola* and *M. koreana* by a wider frons (mean FI of workers 0.308 *versus* < 0.30), by short propodeal spines (mean ESLI of workers 0.242 *versus* > 0.300), by the coarser and less sinuous rugosity on alitrunk, etc. (compare Figs 60, 65 and 51, 55, 77, 81, 91, 96); their workers well differ from *M. inucta* by the body sculpture (see above).

Males of *M. lacustris* clearly separate from those of any other species of *schencki*-group by their very short scape, which is shorter than 1st and 2nd funicular segments together (mean SI_1 0.335, mean SI_2 0.339 *versus* mean SI_1 > 0.375, mean SI_2 > 0.390) (compare Figs 66 and 17, 18, 38, 39, 56, 57, 74, 82, 104, 105).

Myrmica ravasinii Finzi, 1923
(Figs 69–75, Tables 1–3)

Myrmica ravasinii Finzi 1923: 2, w, Albania, syntypes in ZMMU, MIZ and IZK examined; Müller 1923: 39, Finzi 1926: 112, Weber 1950: 212, Zhizhilashvili 1967: 53, 1974: 193, Arnoldi 1970: 1843, Arnoldi and Dlussky 1978: 535, Agosti and Collingwood 1987a: 53, 1987b: 268, Seifert 1988: 37, Arakelyan 1989: 733, q, m, Radchenko 1994a: 44, 1994b: 140, 1994c: 79, Bolton 1995: 282, Seifert 2003: 150.

Material examined. 3 workers, syntypes "Albania, Tomor, 1600 m, 1922" (ZMMU, MIZ, IZK); non-type material: about one hundred workers, more than 20 males and queens from Georgia, Armenia and Turkey (ZMMU, IZK, ELMES).

Distribution. (Fig. 76). Albania, former Yugoslavia, Greece, Georgia, Armenia, and Turkey.

Ecology. This is a semi-xerophilous species. The regions where it lives are very hot in summer therefore it is a mountain species usually being found between 800 and 1800 m a.s.l.. Generally it lives in fairly open forests (fir, pine, beech), where presumably it benefits from warmth in spring but shade in summer, though occasionally it has been found on mountains meadows.

In very dry mountains it is often associated with the edges of small gullies where the sub-soil may be a little moist. Nests are built in the soil and it may live under stones in shaded places.

Notes. Although it is probably the most morphologically unusual among the West Palaearctic *Myrmica* species, it appears to have a quite stable morphology. Its extremely narrow frons (mean FI of workers 0.166) and extraordinarily enlarged lobe on the scape bend (see Figs 69–73) well distinguish it from all other known *Myrmica*. Males well differ from those of the other species of the *schencki*-group (except *M. caucasicola*) by the presence of long erect hairs on the scape, tibiae and tarsi (compare Figs 74, 75 and 17, 18, 21, 38, 39, 42, 56–58, 66, 67, 104, 105, 108).

Myrmica caucasicola Arnoldi, 1934
(Figs 77–90, Tables 1–3)

Myrmica schencki nat. *caucasicola* Arnoldi 1934: 172, w, m, Armenia, Azerbaijan, lectotype in ZMMU, paralectotypes in ZMMU and ZISP.
Myrmica schencki var. *caucasicola*: Weber 1948: 298.
Myrmica schencki subsp. *caucasicola*: Arnoldi 1970: 1838.
Myrmica caucasicola: Radchenko 1994a: 44, 1994b: 140, 1994c: 79, Arakelyan 1994: 24, Bolton 1995: 278, Seifert 2003: 147 (redescription of workers).

Material examined. Lectotype worker (examined before its designation), " Azerbaijan, Tallish, Mt. Nudis-galasi, 14.VII.1929, No A 4286, leg. K. Arnoldi" (designated by Seifert 2003: 147 who erroneously noted the type locality as "Tallish Mountains, Nodus-galasi"), ZMMU; paralectotypes: 39 workers, "Mt. Nudis-galasi, Tallish, VI.1929, leg. K. Arnoldi", Nos A 4224, A 4232, A 4237, A 4240, A 4242, A 4282A 4286, A 4294; 3 workers, "Alazapin, Tallish, 800–1000 m, No A 4240 (Sic!), VI.1929, leg. K. Arnoldi"; 3 males, "Armenia, Karaulis, IX.30, No 4680, leg. A. Avetisian" (ZMMU, ZISP). Non-type material: about 30 workers and 1 queen from Tallish (ZMMU, IZK).

Queen. (first description) (Figs 84–90, Table 2).

This description is based on single queen with the label: "137, USSR, Caucasus, Azerbaijan, Tallish Mts., Lerik, 1200 m, xerophitous canyon, 8.X.83, Golovatsch" (ZMMU).

Generally like workers in shape of head and scape, colour and pilosity of the body, except it has coarser sculpture on the head and alitrunk, and propodeal spines that are wider at their base and shorter.

Distribution. (Fig. 22). It seems to an endemic species of southern Transcaucasus.

Ecology. Little is known about ecology of *M. caucasicola* except that it inhabits mainly dry mountain forests at an altitude 700–1600 m a.s.l.
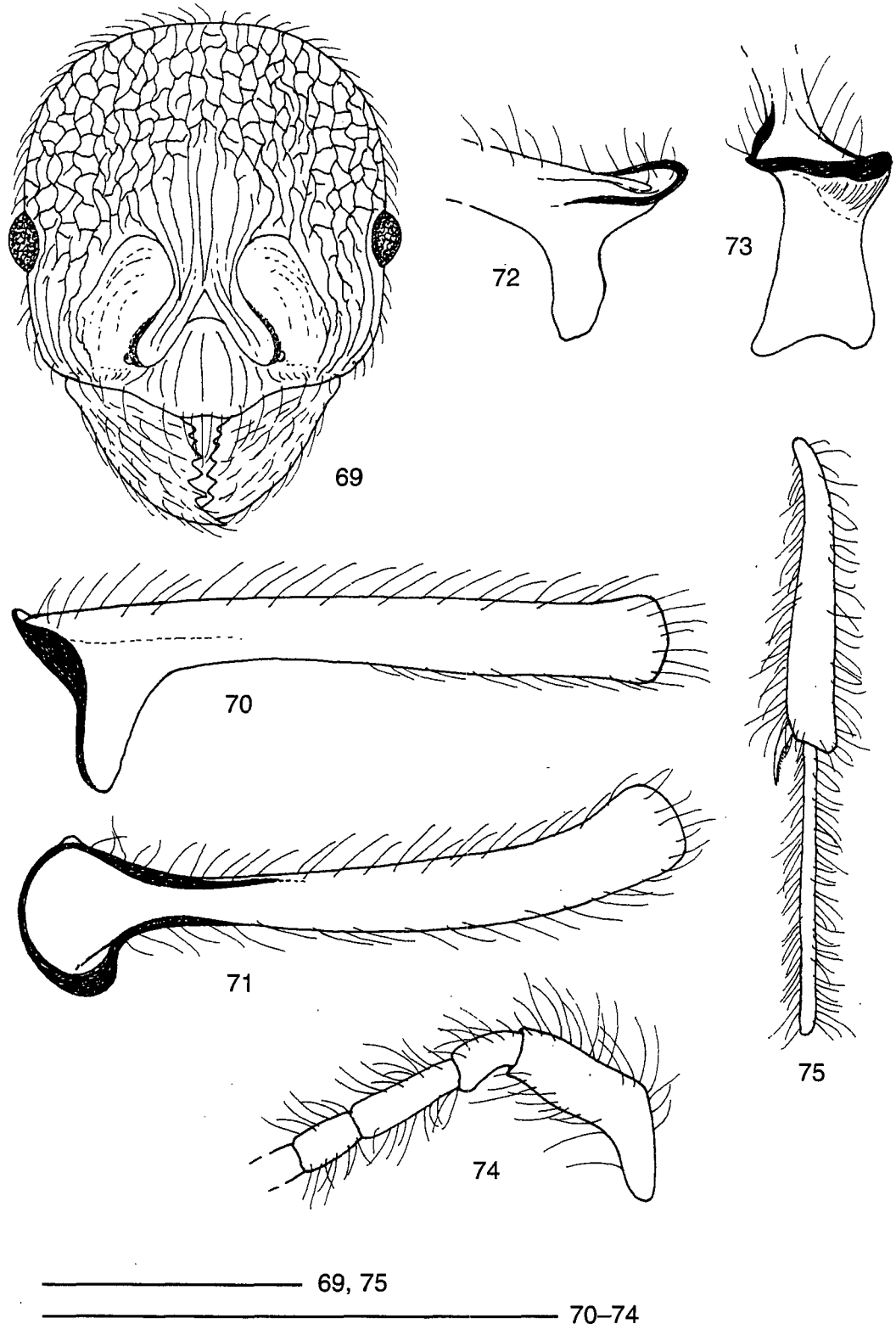
Figures 69–75. Details of structure of *Myrmica ravasinii* (69–73 – syntype, worker; 74, 75 – male). (69) Head, dorsal view; (70) scape, posteriolateral view; (71) scape, dorsal view; (72) base of scape, anterolateral view; (73) vertical face of antennal foot; (74) scape and three basal funicular joints, lateral view; (75) tibia and first tarsal joint of hind leg. Scale bars: 1 mm.
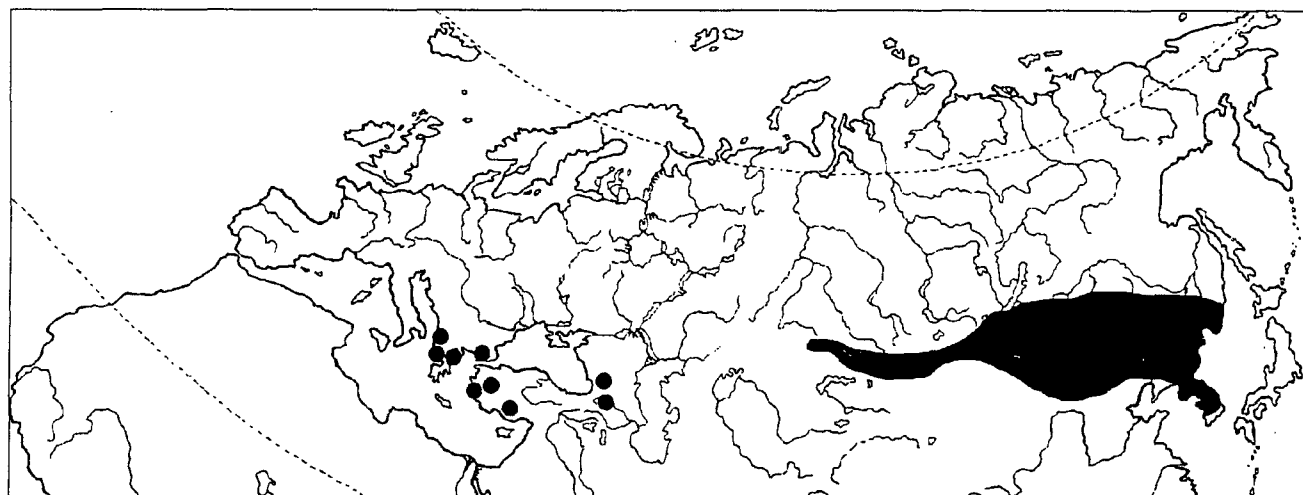
Figure 76. Map of distribution of *Myrmica ravasinii* (spots) and *M. koreana* (black area).

Notes. M. caucasicola was first considered as variety/subspecies of *M. schencki* and was raised to species by Radchenko (1994a, b, c). Its workers and queens most resemble *M. schencki* and differ from it mainly by their somewhat wider frons (FI of workers 0.25–0.29, mean 0.260 *versus* FI 0.20–0.26, mean 0.233 in *M. schencki*), and by a much smaller lobe at the scape bend (compare Figs 77–80 and 51–54).

Males of *M. caucasicola* have very long, erect hairs on the tibiae and tarsi and are hardly distinguishable from those of *M. ravasinii* (compare Figs 83 and 75). On the other hand, this feature well discriminates males of both species from all other species of the *schencki*-group.

Myrmica koreana Elmes, Radchenko et Kim, 2001
(Figs 91–108, Tables 1–3)

Myrmica koreana Elmes, Radchenko and Kim 2001: 108, w, Korean Peninsula; Seifert 2003: 153.
Myrmica schencki: Ruzsky 1936: 94, Kupyanskaya 1986: 87, 1990: 109 (part., only material from Russian Far East), not Viereck 1903 et auct.

Material examined. Holotype, worker, South Korea, unknown location, in pitfall traps, leg. B.-J. Kim (BMNH). Paratypes: 13 workers the same series as holotype; 1 worker, South Korea, Gechon-ri, near Pyongang, Pyong chang-gun, in pitfall traps, c. 1970, leg. B.-J. Kim; 4 workers (1 without gaster), South Korea, mountains, locality not known, leg. B.-J. Kim; 1 worker, South Korea, mountains, locality not known, leg. B.-J. Kim; 7 workers, South Korea, Sunchon City, 300 m a.s.l.., in soil, 2.vii.1982, leg. B.-J. Kim; 4 workers (1 without gaster) North Korea, Pyongyang, 21.vii.1959, leg. B. Pisarski and J. Prószyński, (ELMES, BMNH, IZK, KIM, MIZ); non-type material: about

one hundred workers, 20 queens and 19 males from South Siberia, Mongolia, Russian Far East and North Korea.

Queens. (first description) (Figs 97–102).
Generally like workers in shape of head and scape, colour and pilosity of the body except they have coarser sculpture, especially on the alitrunk, petiole and postpetiole, and propodeal spines that are wider at their base and shorter. They are small (mean HW 1.02 mm) even relative to the workers, which are small for *schencki*-group species (mean HW 1.01 mm).

Males. (first description) (Figs 103–108).
Head slightly longer than broad, with convex sides and occipital margin, and gradually rounded occipital corners; anterior clypeal margin widely rounded and notched medially. Scape short but longer than 1st and 2nd funicular segments together, feebly curved though with distinctly angled dorsal plane. Antennae 13-segmented, with 5-segmented club.

Alitrunk quite long, scutum convex, scutellum does not project dorsally above scutum when seen in profile. Propodeum with blunt rounded tubercles. In profile, petiole relatively long and low, with narrowly rounded dorsum of node, its anterior surface almost straight but not steep; postpetiole higher than long, with weakly convex dorsum.

Head dorsum densely punctured and with very fine striation. Scutum and scutellum longitudinally rugulose, only anterior part of scutum finely striated. Propleura smooth and shiny, only with fine striation on their posterior parts; mesopleura and propodeum not coarsely rugose. Petiole finely striated, postpetiole smooth and shiny.

Head margins with very long curved standing hairs, alitrunk and waist with shorter hairs. Tibiae and tarsi with short subdecumbent to suberect hairs; scape and first 7 funicular segments with longer hairs,

segments of antennal club with very short subdecumbent hairs. Body colour black, appendages somewhat lighter.

Distribution. (Fig. 76). South-eastern part of West Siberia, north-eastern Kazakhstan, south of East Siberia, Mongolia, South Siberia, Russian Far East and Korea; almost certainly it will be found in northern China.

Ecology. M. koreana inhabits mainly steppes and steppe-like habitats both on planes and mountains up to 1700 m a.s.l., rarely it has been found living in light deciduous and mixed forests. Michał Woyciechowski of Kraków, Poland collected many nests from steppe-like habitat in northern Mongolia. Here, nests were in the soil and most had small woven funnel-like entrances, very similar to those typical of *M. schencki*

——————————— 77, 81, 83

————————————————— 78–80, 82
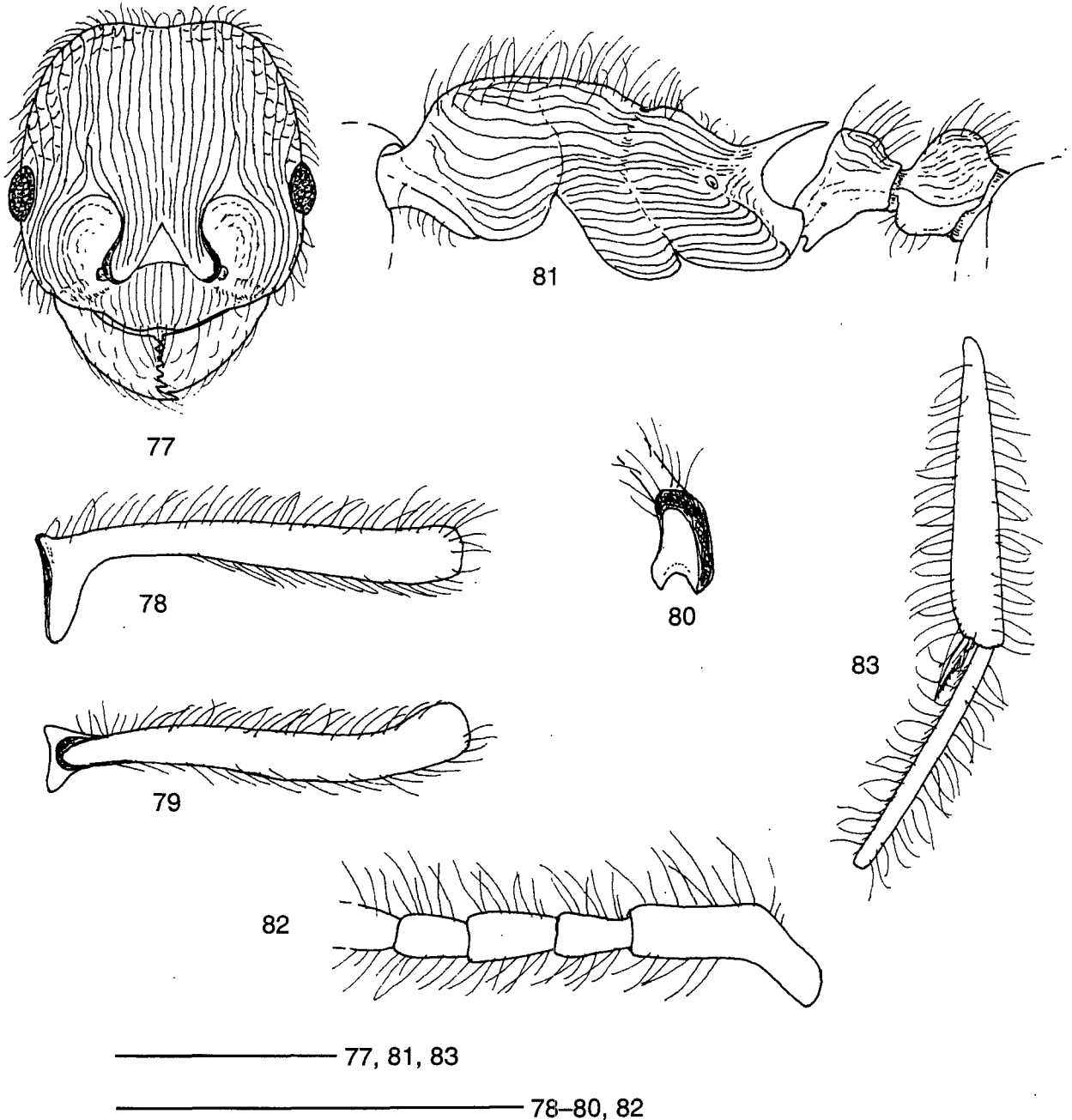
Figures 77–83. Details of structure of *Myrmica caucasicola* (77–81 – paralectotype, worker; 82, 83 – paralectotype, male). (77) Head, dorsal view; (78) scape, posteriolateral view; (79) scape, dorsal view; (80) vertical face of antennal foot; (81) alitrunk and waist in profile; (82) scape and three basal funicular joints, lateral view; (83) tibia and first tarsal joint of hind leg. Scale bars: 1 mm.
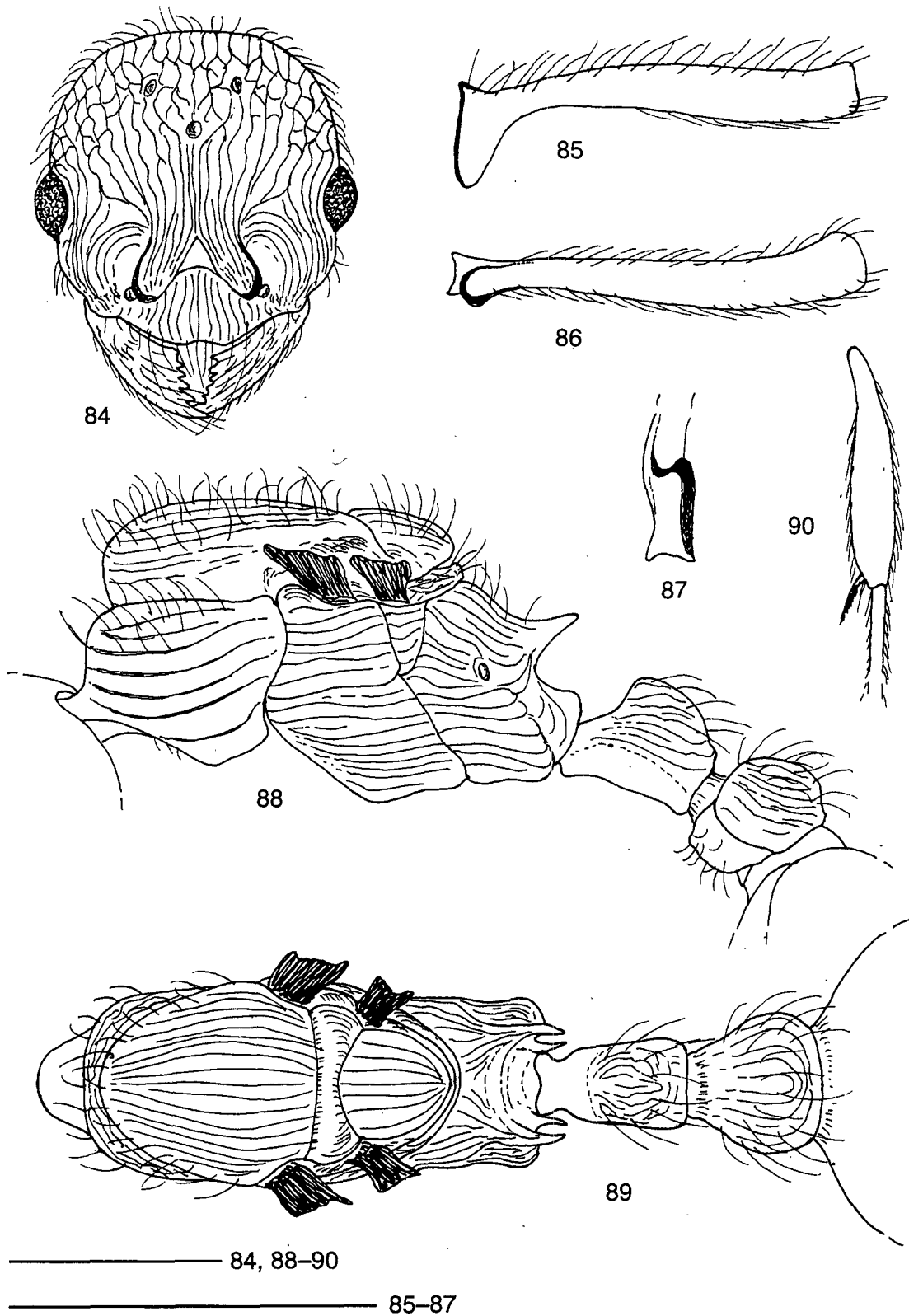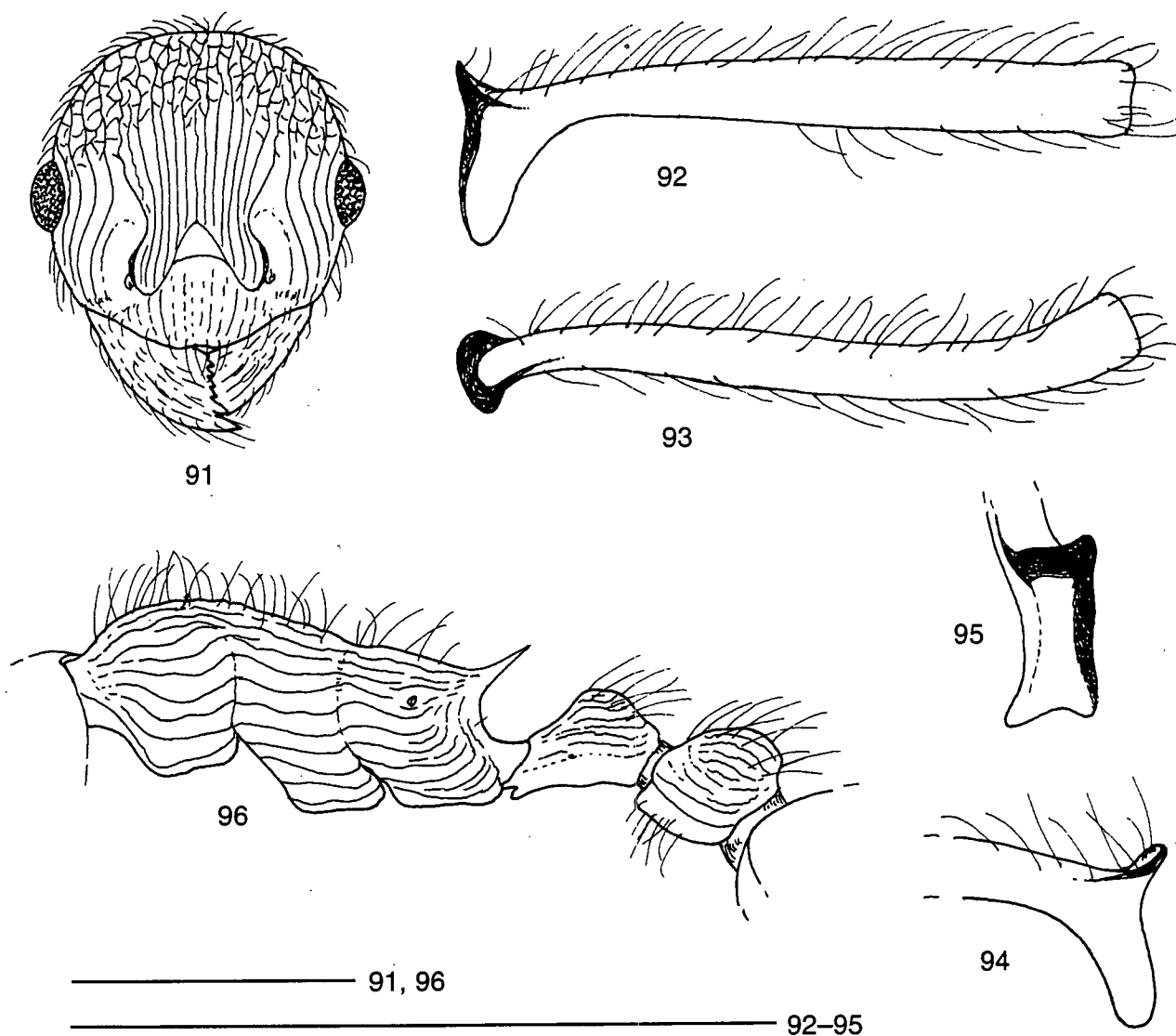
Figures 84–90. Details of structure of *Myrmica caucasicola* (queen). (84) Head, dorsal view; (85) scape, posteriolateral view; (86) scape, dorsal view; (87) vertical face of antennal foot; (88) alitrunk and waist in profile; (89) alitrunk and waist from above; (90) tibia and base of first tarsal joint of hind leg. Scale bars: 1 mm.

but perhaps somewhat shorter (though length may depend upon the vegetation structure to some extent).

Notes. Queens of *M. koreana* are considerably smaller than those of all other known queens of the *schencki*-group species (see Table 2). Workers and queens of *M. koreana* most resemble those of *M. schencki* and partly – *M. lacustris*. They differ from *M. lacustris* by distinctly longer propodeal spines (mean ESLI 0.313 *versus* 0.242 in workers and 0.292 *versus* 0.248 in queens) and in queens – by relatively more extended frontal lobes (mean FLI 1.549 *versus* 1.280), also by less coarse rugosity on the alitrunk and

a different body colour (compare also Figs 91, 96 and 60, 65). Workers of *M. koreana* clearly differs from *M. schen-cki* by having a much shallower metanotal groove and by the smaller lobe on the scape bend (compare Figs 91–96 and 51–54); also *M. koreana* has a distinctly wider frons (both queens and workers mean FI about 0.30 *versus* about 0.24, see Tables 1 and 2).

Males of *M. koreana* well differ from those of *M. ravasinii* and *M. caucasicola* by the much shorter hairs on their tibiae and tarsi. They clearly separate from *M. schencki* and *M. siciliana* by a shorter and much less curved scape. They most resemble

Figures 91–96. Details of structure of *Myrmica koreana* (holotype, worker). (91) Head, dorsal view; (92) scape, posteriolateral view; (93) scape, dorsal view; (94) base of scape, anterolateral view; (95) vertical face of antennal foot; (96) alitrunk and waist in profile. Scale bars: 1 mm.
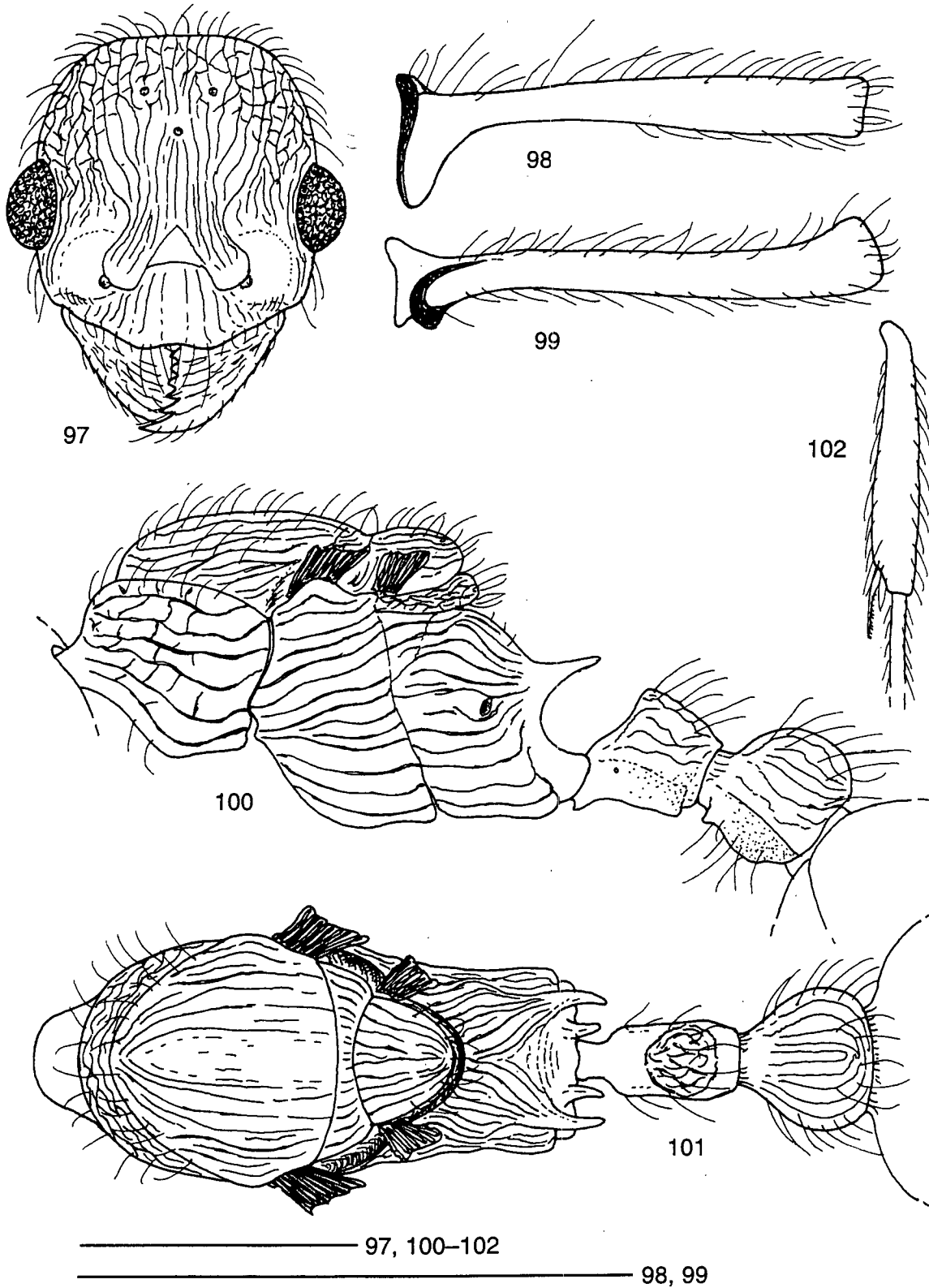
Figures 97–102. Details of structure of *Myrmica koreana* (queen). (97) Head, dorsal view; (98) scape, posteriolateral view; (99) scape, dorsal view; (100) alitrunk and waist in profile; (101) alitrunk and waist from above; (102) tibia and base of first tarsal joint of hind leg. Scale bars: 1 mm.
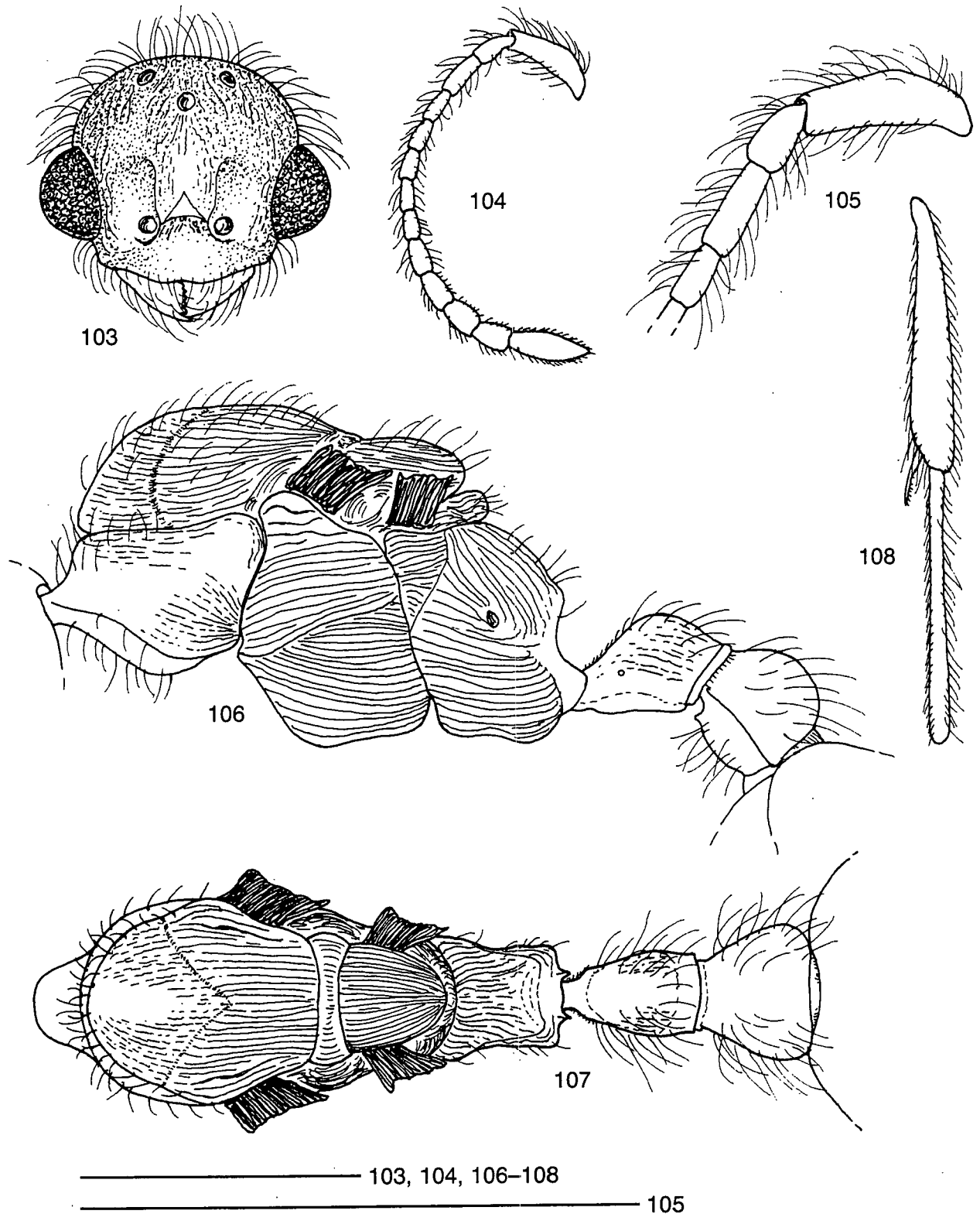
Figures 103–108. Details of structure of *Myrmica koreana* (male). (103) Head, dorsal view; (104) antenna; (105) scape and three basal antennal joints, lateral view; (106) alitrunk and waist in profile; (107) alitrunk and waist from above; (108) tibia and first tarsal joint of hind leg. Scale bars: 1 mm.

M. onoyamai having a differently shaped scape (compare Figs 104, 105 and 38, 39) and distinctly lower postpetiole (see Table 3).

Records of *M. schencki* (Ruzsky 1936, Kupyanskaya 1986, 1990) from the Russian Far East actually should be referred to *M. koreana* (corresponding material of Kupyanskaya is in ZMMU and BPI, examined).

Myrmica pelops Seifert, 2003
(Figs 109–116, Table 1)

Myrmica pelops Seifert 2003: 148, workers, Greece, holotype in SMN, paratypes in SMN, SCHULZ, IZK, ELMES, WERNER.

Material examined. Paratypes: 4 workers (nest of the holotype): "Greece, Peloponnesus, Taigetos Mts., Laganda Pass (20 km E Kalamata) 1.6.1994, 1100–1400 m A. Schulz leg."; 3 workers, "Greece, Peloponnisos, Taigetos Oros, unterhalb des Profitis Ilias, 1800–2000 m, No 1368, 02.VI.1994, leg. Schulz and Vock" (IZK, SCHULZ, IZK, ELMES, WERNER).

Distribution. (Fig. 22). The species is known only from the type series from Greece (Peloponnese Peninsula).

Ecology. Is poorly known. Seifert noted that all samples of *M. pelops* were found in very light, devastated coniferous forests.

Notes. Seifert stated that *M. pelops* relates to *M. ravasinii*, based on its quite large size, a somewhat similar kind of scape structure and the shape and sculpture of its petiole. However, it clearly differs from *M. ravasinii* by a much wider frons (FI > 0.22 *versus* < 0.20) and a clearly much smaller lobe at the scape bend (compare Figs 109–113 and 69–73). On the other hand, the FI of *M. pelops* is similar to that of *M. schencki* (see Table 1), but it well differs from this species by a distinctly different shape of scape lobe, by coarser rugae on the body, and by a shorter and stouter petiole with a short anterior peduncle (compare Figs 110–115 and 52–55).

Myrmica schenckioides Boer et Noordijk, 2005
(Figs 118–121, after Boer and Noordijk 2005)

Myrmica schenckioides Boer et Noordijk 2005: 120, ♀, The Netherlands.

Notes. This species was described from a single winged gyne, found by the roadside in The Netherlands. By its general size and by the shape of its head, frons and scape it is very similar to normal gynes of *M. schencki*, but it has a peculiar combination of features on the propodeum, petiole and postpetiole; in particular, the postpetiole has a large ventral lobe or

process more normally associated with the socially parasitic *Myrmica* species (Radchenko and Elmes 2003). This led its authors (loc. cit.) to assume that it is a social parasite of *M. schencki*. We agree with them that it is either a social parasite or some sort of aberration of *M. schencki* and therefore include *M. schenckioides* in the *schencki*-group.

Morphometric discrimination

One hundred percent discrimination between the measured workers of nine species was achieved when using all the standardised morphometrics; standardising by HW eliminates size differences so that the discrimination more or less reflected real differences in shape. However, 96% discrimination could be achieved using only three standardised measurements sFW = FI, sFLW and sESL = ESLI (Fig. 122). The clustering method used produces a dendrogram of similarities (Fig. 123) that reflects the distance between the means for the species (clusters). When only 3 variables are used it is easy to see how this works, the method first searches for the two closest means (in this case *M. caucasicola* and M. *schencki* see Fig. 122) groups them together and then searches again for the closest pair (in this case the new group and *M. siciliana*, these are grouped again but the next closest pair is a new cluster comprising *Myrmica pelops* and *M. ravasinii*) and so on until the least similar is found (in this case *M. inucta*). Adding extra variables provides little extra discrimination power so that a dendrogram based on all the morphometrics is little different from Fig. 123. Discrimination using the 3 variables is least successful in identifying *M. schencki*: 3 individuals being identified as *M. caucasicola* and 2 as *M. pelops*, the only other misidentifications were 1 *M. caucasicola* placed to *M. lacustris* and 1 *M. siciliana* placed to *M. caucasicola*. Using the linear discriminant functions calculated from all the variables three from four type specimens of *M. schencki* var. *obscura* were identified as *M. schencki* (see above).

The same three variables produced 100% discrimination between the measured queens (Table 2). As is apparent from the above descriptions, males are generally harder to discriminate, only 95% successful discrimination could be achieved using all the standardised morphometrics, even so 90% discrimination could be achieved using just 3 of these, sSL = SI2, sPL = PI2 and sPH (note the last two are often combined as PI1 = PL/PH); misclassifications were 1 *M. koreana* as *M. ravasinii*, 1 *M. schencki* as *M. ravasinii* and 1 as *M. siciliana*, and 3 *M. siciliana* as *M. schencki*. Thus on morphometrics alone *M. siciliana* and *M. schencki* males are most likely to be confused, which accords with the more subjective analysis (above).

DISCUSSION

The species of the *schencki*-group have fairly distinctive morphological features compared to most Eurasian *Myrmica* species and it is not surprising that this is reflected in similarly distinctive ecological and zoogeographical traits. Males have short antennal scape, which is believed to be plesiomorphic condition of this feature in the genus *Myrmica* (Radchenko and Elmes 2001). On the other hand, the scape of the female castes appear highly derived from the presumed ancestral, simply-curved shape: the scape of the *schencki*-group are strongly angled at the base with a distinctive vertical lobe on the bend, that appears shield like on the vertical face of the foot (see above). In some species (especially *M. ravasinii*) this can be extraordinarily well-developed. In the *schencki*-group it is particularly clear that scape-lobe size is inversely correlated with a relative frons width (similar correlations exist in other groups, e.g., *scabrinodis*-group). Thus within a group, scape-lobe size and frons width are different measures of the same structure. We are sure the
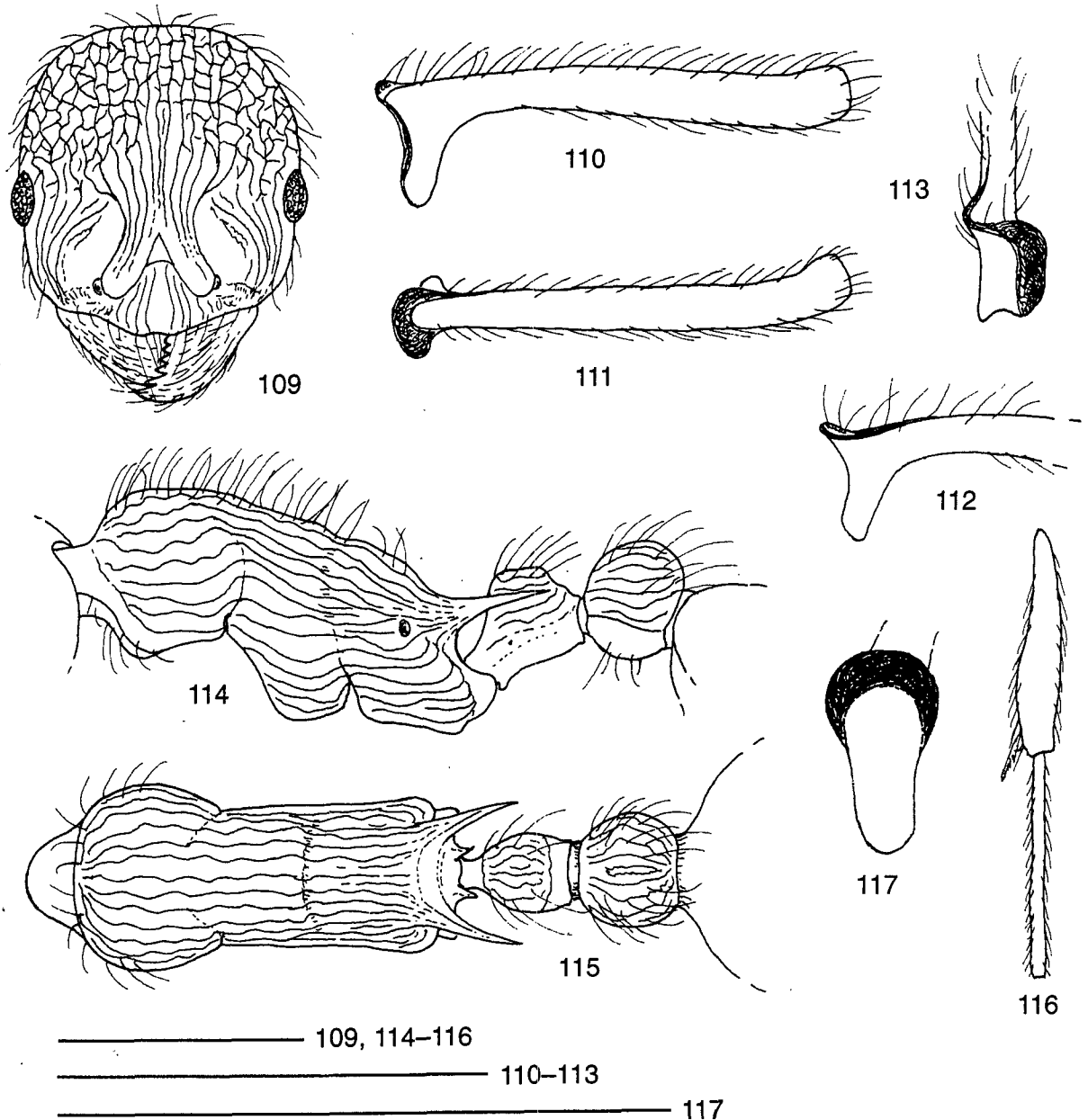
Figures 109–117. Details of structure of *Myrmica pelops* (109–116, paratype, worker) and *M. lobicornis* (117, lectotype, worker). (109) Head, dorsal view; (110) scape, posteriolateral view; (111) scape, dorsal view; (112) base of scape, anterolateral view; (113, 117) vertical face of antennal foot; (114) alitrunk and waist in profile; (115) alitrunk and waist from above; (116) tibia and base of first tarsal joint of hind leg. Scale bars: 1 mm.

explanation for the correlation must be biomechanical, probably related to counterbalance and musculature attachments as determined by the normal orientation and movement requirements of behaviour, most probably foraging behaviour. So far, this theory remains untested but if correct, the basic shape for any species group would be ancestral, maybe differences evolved due to different mechanical requirements or possibly simply being alternative solutions to the same mechanical problem. In either event, the extent to which lobes are developed in living species would have an ecological basis.

Ecologically all known *schencki*-group species differ from the majority of sympatric *Myrmica*, which more generally are indicators of mesophitous habitats. While many of the other species are relatively thermophilous within their preferred habitats, few are adapted to dry sunny conditions. In contrast, all the *schencki*-group species are semi-xerophilous and often somewhat halophilous. For example, *M. lacustris* and *M. koreana* are typical steppe-ant species, living in dry and hot habitats, whereas other *Myrmica* species of the Steppe Zone (such as *M. bergi*, *M. stangeana* Ruzsky, *M. salina*, etc.) dwell in intra-zonal, wet places (Bondar' *et al*. 1998, Radchenko *et al*. 2002, Bondar' and Rusina 2003). *M. inucta* may be more similar to these species in its habitat preferences (see above). *M. ravasinii*, *M. caucasicola*, *M. siciliana* and *M. pelops* are Mediterranean species that live mainly in open and warm, or even quite hot, mountain forests and, although only a single colony of *M. onoyamai* has been found to date, the strange anthropogenic
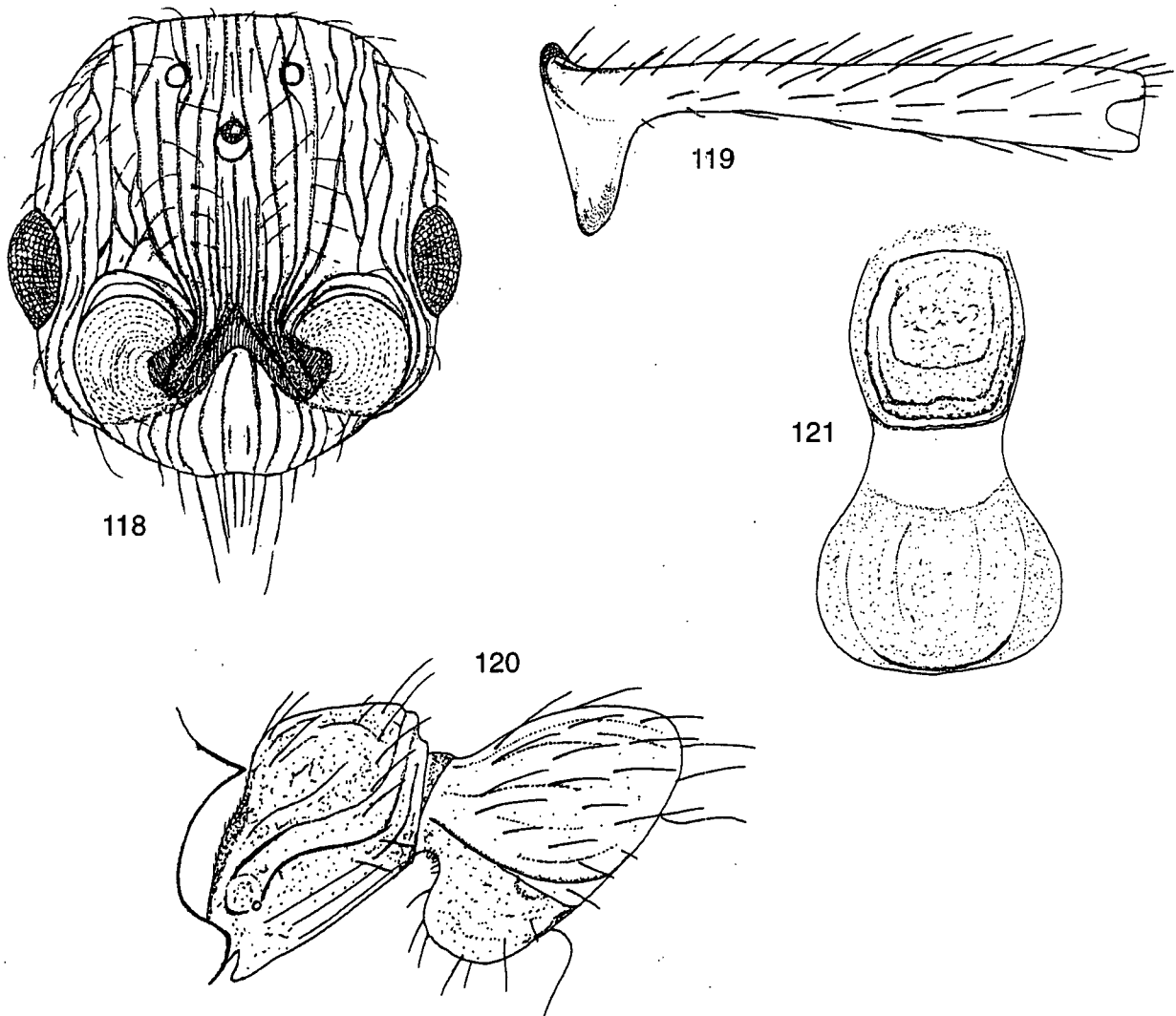
Figures 118–121. Details of structure of *Myrmica schenckioides* (holotype, queen; after Boer and Noordijk, 2005). (118) Head, dorsal view; (119) scape, lateral view; (120) propodeal spine and waist, lateral view; (121) waist from above. Scale bar is unknown.

location of its nest site in mixed mountain forest, suggests that it might also have similar natural requirements. *M. schencki* itself is the only ecologically-widely distributed species from this group, occupying several habitats ranging from coniferous forests to steppe but, as outlined above, it lives only in relatively dry, exposed, sunny places and never lives in cold grassland or dense forests.

Although, the distribution of the *schencki*-group is Transpalaearctic, maybe even Holarctic, no member

species is so widely distributed (Figs 22, 59, 68, 76). The three most widespread species are *M. schencki*, *M. lacustris* and *M. koreana*, whose ranges overlap to some extent. We consider *M. lacustris* and *M. koreana* to be ecologically vicarial species, i.e., probably using similar habitat and nest sites but living in the western and eastern parts of the Steppe Zone respectively. Similarly, *M. schencki* and *M. koreana* are geographically vicarial species, probably overlapping only in north-eastern Kazakhstan and the south-eastern
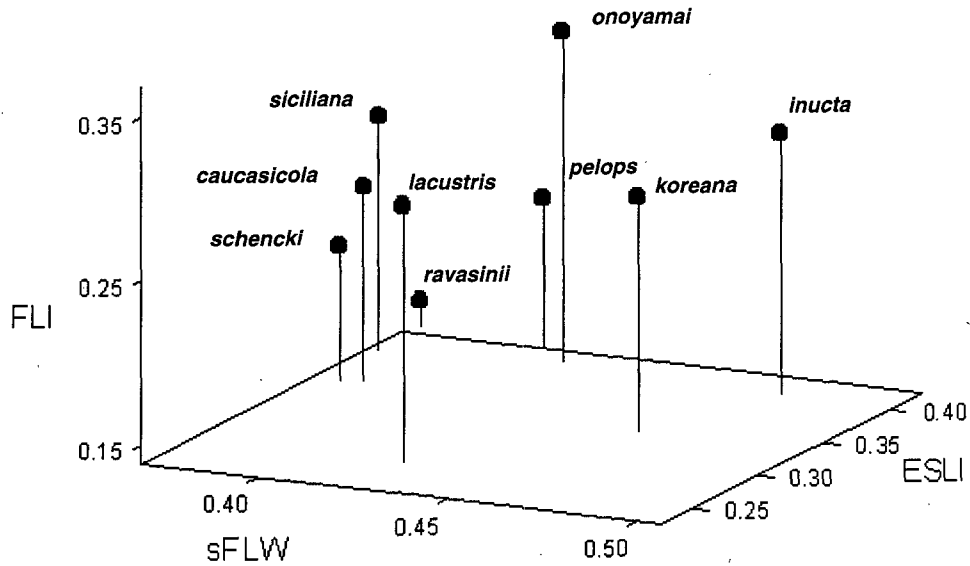
Figure 122. 3D plot of the mean values of measurements standardised (by HW) of frons width (sFW = Fi), frontal lobe width (sFLW = Fli) and propodeal spine length (sESL = ESLI) for workers of nine species from the *schencki*-group.
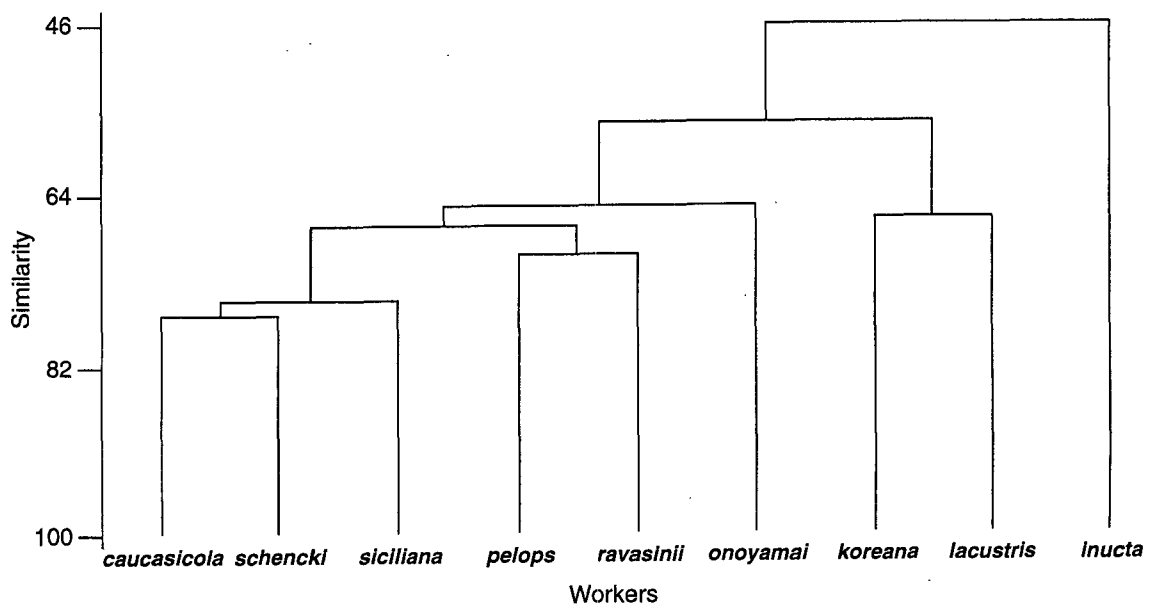
Figure 123. The clustering dendrogram for workers of nine species from the *schencki*-group based on similarities calculated from the data illustrated in Fig. 122.

part of West Siberia where a hybrid zone might exist. On the other hand, the geographic distribution of *M. schencki* encompasses almost the entire distribution of *M. lacustris* and these two species must be isolated mostly by ecology (see above).

All the other species have quite local distribution, and at least some of them are real endemics. Zoogeographically, the Peloponnese peninsula can be considered an island, thus *M. siciliana, M. pelops* and *M. onoyamai* may all be island endemics; although it is possible that *M. siciliana* might be found in southern Italy, and *M. pelops* – in north-western Greece. The region of northwest Kazakhstan, where *M. inucta* was collected, has been poorly studied for ants, and it may be more widespread. However, the current knowledge indicates that it might be well-separated ecologically from sympatric *M. lacustris*. Seifert (2003) suggested that *M. caucasicola* might be a very local endemic of the Talysh region and although we believe it is somewhat more widespread the Transcaucasus, it might be quite separated ecologically from *M. schencki* populations in this region.

The ecology and distributions the Palaearctic species of the *schencki*-group leads us to suggest that they are relict of an age prior to the Pleistocenic, probably with Miocenic origins (> 10 Mya), and by the time dry grassland habitats arose, their ancestors already had a Holarctic distribution. We suggest they were pre-adapted in someway to such habitat and thus in the Palaearctic their subsequent evolution was influenced by the history of the formation of the Steppe Zone. In North America similar evolutionary pressures might have occurred or perhaps the species remained associated with more ancestral habitat types.

In this paper we will simply note that there is a minimum of 3–4 American species, which, based upon our current knowledge of their morphology, we would place directly into the *schencki*-group (or a new very close sister group). Some habitats used by the species, collected in Main, are similar to some habitats of *M. schencki*, and other species are associated with hot, fairly dry sunny grassland where they construct woven nest entrances, albeit of a different design, but analogous to those of *M. schencki*. It seems almost certain these species had a common ancestry with the *schencki*-group species (remember, Emery even described *M. schencki* from American material – see above), there seem too many morphological similarities for them to have evolved convergently. However, further speculation is best left until at least the North American *Myrmica* have been revised and placed to the species-groups, or when some sort of genetically-based phylogenetic reconstruction is attempted.

After the development of steppe-like landscapes in Palaearctic (ca 10 Mya) their extent was geographically interrupted several times for long periods, leading to the evolution of some different species of plants and animals in some isolated regions (Lavrenko 1940, 1954, Lavrenko *et al.* 1991, Popov, 1983, Radchenko 1987, 2003, Kryzhanovsky 2002), including the ancestors of the modern *schencki*-group species. Despite the fact that the most drastic changes in environments took place later in Pleistocene, the steppe-zones were much less dramatically influenced by glaciation as were more northern territories; it is believed that many of the present steppe-zone regions were major refugia where pre-pleistocenic biota survived, some to the present day. We suggest that some *schencki*-group species had already developed their distinctive range of highly specialised morphology (see above) by the time Pleistocene isolation. In the different steppe-zone refugia some species survived almost unchanged, e.g., *M. lacustris* and *M. ravasinii*, whereas in other regions species retreated to more southern refugia where some local endemics, such as *M. siciliana, M. pelops* and *M. caucasicola,* might have evolved. Under this hypothesis the geographically vicarial pair *M. schencki* and *M. koreana* was already formed, living in cooler conditions in different steppe-zone regions. After the glaciation they moved northwards and adapted to exploit other hot, sunny but less steppe-like habitats, including recent anthropogenic grasslands favoured by *M. schencki* in the west. This might explain why this pair is morphologically more distinct than other west – east vicarial pairs, believed to have diverged relatively recently (see Radchenko 2005): for example, *M. ruginodis* Nyl. – *M. kotokui* Forel or from other ant genera *Myrmecina graminicola* (Latr.) – *M. nipponica* Wheeler; *Lasius fuliginosus* (Latr.) – *L. fuji* Radchenko; *Solenopsis fugax* (Latr.) – *S. japonica* Wheeler; *Liometopum microcephalum* (Panzer) – *L. orientale* Karaw.

Key for the identification of the Old World species of *schencki*-group

Workers

1. Frontal carinae very strongly curved, frons extremely narrow (FI 0.15–0.19, mean 0.166, FLI 1.96–2.56, mean 2.299) (Fig. 69). Scape with an extremely large lobe (Figs 70–73) .... *M. ravasinii* Finzi

–. Frontal carinae less curved, frons wider (FI > 0.20, FLI < 1.90) (Figs 2, 23, 43, 51, 60, 77, 91, 109). Scape either with smaller vertical lobe or with a vertical or sometimes transversely oblique dentiform carina (Figs 3–6, 24–27, 44–47, 52–54, 61–64, 78–80, 92–95, 110–113) 2

2(1). Head and alitrunk with very reduced sculpture, only with fine striation, surface between striae smooth and shiny, only petiole and postpetiole finely punctured (Figs 43, 48, 49). Whole body appears shiny black ....
.... *M. inucta* Radchenko et Elmes, sp. nov.

–. Head and alitrunk with well developed, often quite coarse rugosity, surface between rugae neither smooth nor shiny (Figs 2, 7, 8, 23, 28, 29, 51, 55, 60, 65, 77, 81, 91, 96, 109, 114, 115). Body never entirely black 3

3(2). Frontal carinae feebly curved, frons wide, frontal lobes not extended (mean FI 0.353, mean FLI 1.202) (Fig. 23). Scape with only small dentiform ridge (Figs 24–27) ....
.... *M. onoyamai* Radchenko et Elmes, sp. nov.

–. Frontal carinae strongly curved, frons narrower, frontal lobes more extended (mean FI < 0.310, mean FLI > 1.280) (Figs 2, 51, 60, 77, 91, 109). Scape either with a differently shaped dentiform ridge or lobe (Figs 3–6, 52–54, 61–64, 78–80, 92–95, 110–113) 4

4(3). Frontal carinae strongly curved, frons narrower (FI 0.20...0.29, means 0.233...0.260) (Figs 51, 77, 109) 5

–. Frontal carinae less curved, frons wider, (FI 0.26...0.32, means 0.294...0.308) (Figs 2, 60, 91) 7

5(4). Vertical face of foot of the scape strongly excavated (seen in profile, Figs 110, 112; for the shape of scape lobe see also Figs 111, 113). Alitrunk with fairly coarse, more or less straight longitudinal rugae (Figs 114, 115) .... *M. pelops* Seifert

–. Vertical face of foot of the scape not excavated (seen in profile, Figs 52, 78; for the shape of scape lobe see also Figs 53, 54, 79, 80). Alitrunk with finer sinuous longitudinal rugae (Figs 55, 81) 6

6(5). Scape with dentiform ridge (Figs 78–80). Frontal carinae less curved, frons wider (FI 0.25–0.29, mean 0.260) .... *M. caucasicola* Arnoldi

–. Scape with well developed, big lobe (Figs 52–54). Frontal carinae more strongly curved, frons narrower (FI 0.20–0.26, mean 0.233) ....
.... *M. schencki* Viereck

7(4). Frontal lobes not very extended (FLI 1.23–1.36, mean 1.291) (Fig. 2). Alitrunk with distinct metanotal groove, propodeal spines longer (ESLI 0.32–0.42, mean 0.376, Figs 7, 8). For shape of scape lobe see Figs 3–6 ... *M. siciliana* sp. nov.

–. Frontal lobes more extended (mean FLI > 1.400) (Figs 60, 91). Alitrunk often with no metanotal groove or at most with a very shallow one, propodeal spines shorter (ESLI ≤ 0.34, mean < 0.320) (Figs 65, 96). For shape of scape lobe see Figs 61–64, 92–95 8

8(7). Frontal lobes moderately extended (FLI 1.36–1.52, mean 1.406) (Fig. 60). Alitrunk with quite coarse, almost straight longitudinal rugae, propodeal spines shorter (ESLI 0.18–0.30, mean 0.242) (Fig. 65). Body colour usually dark reddish-brown .... *M. lacustris* Ruzsky

–. Frontal lobes well extended (FLI 1.50–1.67, mean 1.598) (Fig. 91). Alitrunk with finer sinuous longitudinal rugae, propodeal spines longer (ESLI 0.27–0.34, mean 0.313) (Fig. 96). Alitrunk yellowish-brown, head reddish-brown and gaster dark brown in colour ...... *M. koreana* Elmes *et al.*

Males (the males of *M. pelops* and *M. inucta* are currently unknown)

1. Middle and hind tibiae with very long semierect hairs (Figs 75, 83) ....
M. ravasinii Finzi and *M. caucasicola* Arnoldi

–. Middle and hind tibiae with short subdecumbent hairs (Figs 21, 42, 58, 67, 108) 2

2(1). Scape very short and not curved at the base, shorter than 1st and 2nd funicular segments together (SI_1 0.32–0.35, mean 0.335; SI_2 0.32–0.36, mean 0.339) (Fig. 66) ......*M. lacustris* Ruzsky

–. Scape distinctly longer and at least slightly curved at its base, longer than 1st and 2nd funicular segments together (mean SI_1 > 0.350, mean SI_2 > 0.390) (Figs 17, 18, 38, 39, 56, 57, 104, 105) 3

3(2). Scape weakly curved at the base and relatively short (SI_1 0.36–0.40, mean < 0.400, SI_2 0.38–0.42, mean < 0.410; see Figs 38, 39, 104, 105) 4

–. Scape strongly curved at the base and clearly longer (SI_1 0.39–0.49, mean > 0.420, SI_2 0.40–0.50, mean > 0.430; see Figs 17, 18, 56, 57) 5

4(3). Dorsal plane of scape (lateral view) distinctly angled (Figs 104, 105). Postpetiole almost as wide as high (PPH/PHW = PPI_2 < 1.05); scutum and scutellum longitudinally rugulose (Fig. 106, 107). Head margins with abundant, longer hairs (Fig. 103) .... *M. koreana* Elmes *et al.*

–. Dorsal plane of scape (lateral view) smoothly curved (Figs 38, 39). Postpetiole distinctly narrower than high (PPI_2 1.23); scutum and scutellum almost smooth, only with fine striations (Figs 40, 41). Head margins with sparser and shorter hairs (Fig. 37) ....
.... *M. onoyamai* Radchenko et Elmes, sp. nov.

5(3). Petiole relatively longer (mean PI_1 1.626, mean PI_2 0.657); petiolar node very finely punctured and at most with fine longitudinal striation ....
.... *M. siciliana* sp. nov.

–. Petiole relatively shorter (mean PI_1 1.479, mean PI_2 0.606); petiolar node usually densely punctured and longitudinally rugulose ....
.... *M. schencki* Viereck

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Table 1. Mean values (in mm) ± SD of morphometrics of WORKERS of the *schencki*-group species, number measured in parenthesis. The standardised values (i.e., divided by HW) and traditional indices most useful in discriminating between these species are also given (see methods).

morph.	ravasinii (21)	schencki (26)	caucasicola (9)	pelops (6)	siciliana (30)	lacustris (25)	inucta (4)	koreana (29)	onoyamai (14)
HL	1.347 ± 0.045	1.181 ± 0.061	1.218 ± 0.057	1.293 ± 0.062	1.179 ± 0.048	1.302 ± 0.056	1.180 ± 0.016	1.123 ± 0.063	1.197 ± 0.023
HW	1.244 ± 0.046	1.079 ± 0.063	1.070 ± 0.066	1.171 ± 0.076	1.073 ± 0.058	1.169 ± 0.061	1.025 ± 0.019	1.006 ± 0.055	1.085 ± 0.028
FW	0.207 ± 0.021	0.252 ± 0.024	0.289 ± 0.025	0.284 ± 0.018	0.317 ± 0.022	0.360 ± 0.020	0.319 ± 0.014	0.297 ± 0.020	0.383 ± 0.011
FLW	0.472 ± 0.018	0.415 ± 0.033	0.418 ± 0.025	0.485 ± 0.021	0.408 ± 0.024	0.506 ± 0.025	0.498 ± 0.005	0.473 ± 0.024	0.461 ± 0.012
SL	1.065 ± 0.021	0.940 ± 0.060	0.930 ± 0.041	1.038 ± 0.027	0.892 ± 0.047	1.041 ± 0.045	0.985 ± 0.010	0.954 ± 0.047	0.961 ± 0.019
AL	2.041 ± 0.063	1.656 ± 0.102	1.678 ± 0.090	1.906 ± 0.071	1.675 ± 0.091	1.959 ± 0.091	1.835 ± 0.066	1.666 ± 0.068	1.746 ± 0.034
HTL	1.028 ± 0.037	0.865 ± 0.054	0.876 ± 0.049	0.982 ± 0.060	0.852 ± 0.049	1.008 ± 0.040	1.050 ± 0.116	0.932 ± 0.068	0.866 ± 0.020
PNW	0.903 ± 0.029	0.750 ± 0.044	0.761 ± 0.043	0.826 ± 0.048	0.757 ± 0.041	0.834 ± 0.050	0.735 ± 0.019	0.710 ± 0.043	0.789 ± 0.025
PL	0.568 ± 0.019	0.483 ± 0.040	0.437 ± 0.028	0.504 ± 0.013	0.500 ± 0.025	0.552 ± 0.031	0.555 ± 0.019	0.467 ± 0.031	0.476 ± 0.014
PW	0.375 ± 0.013	0.310 ± 0.023	0.292 ± 0.019	0.329 ± 0.014	0.311 ± 0.018	0.342 ± 0.019	0.311 ± 0.010	0.282 ± 0.015	0.314 ± 0.014
PH	0.472 ± 0.021	0.373 ± 0.023	0.370 ± 0.025	0.432 ± 0.016	0.360 ± 0.018	0.425 ± 0.026	0.382 ± 0.021	0.355 ± 0.018	0.344 ± 0.041
PPL	0.428 ± 0.023	0.387 ± 0.038	0.350 ± 0.022	0.455 ± 0.008	0.380 ± 0.020	0.437 ± 0.018	0.435 ± 0.013	0.366 ± 0.028	0.419 ± 0.015
PPW	0.561 ± 0.023	0.479 ± 0.034	0.451 ± 0.032	0.496 ± 0.014	0.474 ± 0.022	0.532 ± 0.032	0.464 ± 0.024	0.423 ± 0.028	0.473 ± 0.014
PPH	0.542 ± 0.024	0.475 ± 0.034	0.470 ± 0.028	0.492 ± 0.014	0.456 ± 0.022	0.522 ± 0.025	0.475 ± 0.033	0.437 ± 0.036	0.487 ± 0.016
ESL	0.510 ± 0.033	0.360 ± 0.030	0.359 ± 0.027	0.469 ± 0.019	0.404 ± 0.029	0.284 ± 0.036	0.387 ± 0.036	0.315 ± 0.025	0.420 ± 0.010
ESD	0.589 ± 0.047	0.491 ± 0.057	0.473 ± 0.033	0.530 ± 0.022	0.519 ± 0.042	0.430 ± 0.041	0.418 ± 0.013	0.410 ± 0.031	0.446 ± 0.031
FI = sFW	0.166 ± 0.015	0.233 ± 0.016	0.260 ± 0.009	0.242 ± 0.006	0.295 ± 0.013	0.308 ± 0.010	0.311 ± 0.012	0.294 ± 0.012	0.353 ± 0.006
sFLW	0.379 ± 0.015	0.385 ± 0.019	0.390 ± 0.008	0.415 ± 0.017	0.381 ± 0.013	0.433 ± 0.012	0.486 ± 0.012	0.471 ± 0.012	0.425 ± 0.008
ESLI=sESL	0.410 ± 0.016	0.334 ± 0.021	0.336 ± 0.019	0.401 ± 0.024	0.376 ± 0.020	0.242 ± 0.025	0.378 ± 0.031	0.313 ± 0.018	0.387 ± 0.009
FLI	2.299 ± 0.182	1.657 ± 0.036	1.447 ± 0.054	1.714 ± 0.043	1.291 ± 0.036	1.406 ± 0.034	1.563 ± 0.075	1.598 ± 0.052	1.202 ± 0.020

Table 2. Mean values (in mm) ± SD of morphometrics of QUEENS of the *schencki*-group species, number measured in parenthesis. The standardised values (i.e., divided by HW) and traditional indices most useful in discriminating between these species are also given (see methods).

morph	tavasinii (3)	schencki (20)	caucasicola (1)	siciliana (5)	lacustris (4)	koreana (9)	onoyamai (8)
HL	1.423 ± 0.035	1.317 ± 0.053	1.414	1.312 ± 0.018	1.360 ± 0.032	1.112 ± 0.041	1.298 ± 0.025
HW	1.393 ± 0.032	1.226 ± 0.056	1.288	1.244 ± 0.050	1.278 ± 0.005	1.024 ± 0.023	1.186 ± 0.023
FW	0.237 ± 0.023	0.294 ± 0.021	0.420	0.374 ± 0.018	0.404 ± 0.019	0.310 ± 0.045	0.444 ± 0.013
FLW	0.490 ± 0.010	0.454 ± 0.027	0.574	0.460 ± 0.012	0.518 ± 0.032	0.476 ± 0.033	0.511 ± 0.013
SL	1.107 ± 0.050	0.968 ± 0.023	1.092	0.960 ± 0.020	1.030 ± 0.058	0.891 ± 0.036	1.008 ± 0.017
AL	2.320 ± 0.100	2.076 ± 0.100	2.352	2.112 ± 0.052	2.240 ± 0.059	1.851 ± 0.061	2.160 ± 0.067
HTL	1.127 ± 0.012	0.988 ± 0.025	1.120	0.976 ± 0.009	1.040 ± 0.035	0.907 ± 0.055	0.995 ± 0.021
PL	0.653 ± 0.006	0.569 ± 0.020	0.686	0.576 ± 0.032	0.673 ± 0.095	0.538 ± 0.030	0.619 ± 0.011
PW	0.453 ± 0.012	0.373 ± 0.018	0.406	0.376 ± 0.009	0.387 ± 0.021	0.307 ± 0.020	0.406 ± 0.012
PH	0.597 ± 0.006	0.462 ± 0.019	0.532	0.460 ± 0.007	0.515 ± 0.018	0.396 ± 0.030	0.460 ± 0.017
PPL	0.493 ± 0.015	0.458 ± 0.018	0.686	0.416 ± 0.055	0.440 ± 0.056	0.423 ± 0.014	0.510 ± 0.013
PPW	0.727 ± 0.038	0.588 ± 0.021	0.504	0.604 ± 0.009	0.623 ± 0.042	0.476 ± 0.041	0.628 ± 0.014
PPH	0.697 ± 0.025	0.578 ± 0.017	0.616	0.600 ± 0.026	0.623 ± 0.046	0.469 ± 0.037	0.647 ± 0.018
ESL	0.540 ± 0.010	0.333 ± 0.023	0.322	0.414 ± 0.034	0.317 ± 0.049	0.299 ± 0.018	0.416 ± 0.009
ESD	0.690 ± 0.010	0.521 ± 0.042	0.490	0.558 ± 0.023	0.510 ± 0.053	0.421 ± 0.031	0.621 ± 0.040
SCW	1.120 ± 0.035	1.026 ± 0.049	1.092	1.000 ± 0.020	1.050 ± 0.060	0.875 ± 0.034	1.063 ± 0.013
SCL	1.547 ± 0.023	1.420 ± 0.045	1.610	1.476 ± 0.017	1.560 ± 0.016	1.242 ± 0.056	1.463 ± 0.027
AH	1.333 ± 0.099	1.227 ± 0.054	1.330	1.220 ± 0.026	1.290 ± 0.023	1.102 ± 0.032	1.245 ± 0.033
FI = sFW	0.170 ± 0.015	0.240 ± 0.011	0.326	0.301 ± 0.021	0.315 ± 0.019	0.302 ± 0.033	0.375 ± 0.006
sFLW	0.352 ± 0.010	0.370 ± 0.013	0.446	0.370 ± 0.018	0.400 ± 0.029	0.464 ± 0.017	0.430 ± 0.007
ESLI = sESL	0.388 ± 0.010	0.271 ± 0.016	0.250	0.333 ± 0.023	0.248 ± 0.038	0.292 ± 0.011	0.351 ± 0.009
FLI	2.083 ± 0.180	1.545 ± 0.053	1.370	1.232 ± 0.015	1.280 ± 0.042	1.549 ± 0.119	1.151 ± 0.014

Table 3. Mean values (in mm) ± SD of morphometrics of MALES of the *schencki*-group species, number measured in parenthesis. The standardised values (i.e., divided by HW) and traditional indices most useful in discriminating between these species are also given (see methods).

morph.	ravasinii (3)	schencki (20)	caucasicola (1)	siciliana (5)	lacustris (4)	koreana (9)	onoyamai (8)
HL	0.994 ± 0.039	0.893 ± 0.037	1.078	0.818 ± 0.034	0.872 ± 0.036	0.806 ± 0.070	0.850
HW	0.985 ± 0.042	0.858 ± 0.031	1.022	0.779 ± 0.032	0.860 ± 0.029	0.770 ± 0.065	0.800
SL	0.391 ± 0.022	0.387 ± 0.023	0.448	0.346 ± 0.021	0.292 ± 0.022	0.306 ± 0.036	0.315
AL	2.363 ± 0.114	1.998 ± 0.101	2.296	1.812 ± 0.086	2.124 ± 0.114	1.875 ± 0.179	1.980
HTL	1.303 ± 0.062	1.100 ± 0.071	1.288	1.004 ± 0.052	1.230 ± 0.026	0.985 ± 0.089	1.100
PL	0.604 ± 0.030	0.520 ± 0.029	0.658	0.512 ± 0.028	0.592 ± 0.062	0.505 ± 0.029	0.550
PW	0.365 ± 0.018	0.321 ± 0.026	0.378	0.292 ± 0.012	0.301 ± 0.024	0.275 ± 0.042	0.290
PH	0.448 ± 0.031	0.352 ± 0.019	0.462	0.315 ± 0.011	0.358 ± 0.038	0.343 ± 0.050	0.350
PPL	0.424 ± 0.011	0.392 ± 0.031	0.490	0.331 ± 0.013	0.356 ± 0.032	0.351 ± 0.031	0.430
PPW	0.536 ± 0.027	0.476 ± 0.026	0.532	0.433 ± 0.012	0.482 ± 0.032	0.413 ± 0.058	0.400
PPH	0.529 ± 0.020	0.461 ± 0.036	0.560	0.420 ± 0.017	0.430 ± 0.027	0.418 ± 0.042	0.490
SCW	1.150 ± 0.051	1.056 ± 0.064	1.190	0.970 ± 0.040	1.100 ± 0.042	0.980 ± 0.126	1.120
SCL	1.633 ± 0.091	1.400 ± 0.092	1.610	1.307 ± 0.059	1.544 ± 0.093	1.305 ± 0.138	1.420
AH	1.420 ± 0.094	1.248 ± 0.082	1.540	1.152 ± 0.065	1.360 ± 0.089	1.153 ± 0.100	1.280
SI_2 = sSL	0.397 ± 0.023	0.431 ± 0.024	0.438	0.445 ± 0.027	0.339 ± 0.014	0.397 ± 0.015	0.394
PI_2 = sPL	0.613 ± 0.015	0.606 ± 0.023	0.644	0.657 ± 0.031	0.687 ± 0.052	0.657 ± 0.031	0.688
sPH	0.454 ± 0.028	0.411 ± 0.023	0.452	0.405 ± 0.014	0.416 ± 0.036	0.444 ± 0.028	0.438
PI_1 = PL/PH	1.351 ± 0.030	1.479 ± 0.071	1.425	1.626 ± 0.082	1.655 ± 0.063	1.488 ± 0.132	1.571