Myrmica constricta Karavajev, 1934 – a cryptic sister species of *Myrmica hellenica* Finzi, 1926 (Hymenoptera: Formicidae)

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Abstract

Multiple evidence is presented that *Myrmica constricta* Karavajev, 1934 represents a cryptic sister species (= sibling species) of *Myrmica hellenica* Finzi, 1926: (a) males differ significantly in length of appendage pilosity, relative scape length and absolute body size; (b) a discriminant analysis (DA) and a leave-one-out-cross-validation discriminant analysis (LOOCV-DA) using 14 morphometric characters separated 90 worker nest samples of both species with a predicted error rate of 1.1 %; (c) as unsupervised method, a principal component analysis of the same data set fully confirmed this clustering; (d) Mantel tests showed a significant effect of the hypothesised con- vs. heterospecificity on the morphological distance (OMD) as well as on the Bray-Curtis similarity index (BCSI) of worker nest samples, also when controlling for geographical distance (OMD: partial correlation r = 0.3480, p < 0.01; BCSI: r = –0.3254, p < 0.01) and hence provide a further independent argument for heterospecificity. A DA and a LOOCV-DA clearly allocated the types of *M. hellenica* (with p = 1.000 and p = 0.981, respectively), *M. rugulosoides* var. *striata* Finzi, 1926 (in both analyses with p = 1.000) and *M. rugulosa* var. *rugulososcabrinodis* Karavajev, 1929 (both with p = 1.000) to the *M. hellenica* cluster and the types of *M. constricta* (both with p = 1.000) to the *M. constricta* cluster. Hence, *M. striata* and *M. rugulososcabrinodis* are demonstrated as junior synonyms of *M. hellenica*. *Myrmica constricta* is a more western and northern species and goes north to 60°N while the Ponto-Caucasian *M. hellenica* does not pass 46°N. The species are sympatric in Italy and the Balkans and there are no clear suggestions for hybridisation in this area. A distribution map, comparative morphometric tables and drawings of both species are presented as well as data on colony structure, habitat selection and behaviour of *M. constricta*.

Keywords: sibling species, cryptic diversity, numeric morphology-based alpha-taxonomy, discriminant functions

1. Introduction

Some species complexes of West to Central Palaearctic *Myrmica* Latreille, 1804 ants represent a major challenge for ant taxonomy. One of these critical groups encompasses the nomenclatural entities *Myrmica hellenica* Finzi, 1926, *Myrmica rugulososcabrinodis* Karavajev, 1929, *M. rugulosoides* var. *striata* Finzi, 1926, *Myrmica rugulosa* var. *constricta* Karavajev, 1934, *M. specioides* Bondroit, 1918, *Myrmica sancta* Karavajev, 1926, *M. scabrinodis ahngeri* Karavajev, 1926, *Myrmica turcica* Santschi, 1931 and *Myrmica georgica* Seifert, 1987. The first four entities, called here the *M. hellenica* complex, are characterised in the workers by the absence of any lamellar outgrowth at the scape base, only small divergence of frontal lobes, weak sculpture, small to moderate body size, a narrow and rather low petiole without a truncated, sharply angular or step-like dorsal profile. The last five entities, called here the *M. specioides* complex, share these petiole and sculpture characteristics but gradually to considerably increase the frontal lobe divergence, the surface area of the basal scape lobes and the body size.

The naming history of the *M. hellenica* complex has been a nomenclatural odyssey, among other things because of insufficient investigation methods, problems in accessing types and unwarranted faith in published information. In more detail, the developments after 1970 were:

The entity distributed in Asia Minor, in low to moderate altitudes of the Caucasian region, along the northern and eastern Black Sea coast and on the Balkans had been named *M. sancta sancta* by Arnoldi (1970). Seifert (1988), relying on Arnoldi's morphometric and zoogeographic statements and matching these with own observations (but having no access to type material of *M. sancta*) adopted this naming and raised *M. sancta* to species rank. Radchenko & Elmes (2004), having access to the types of both *M. sancta* and *M. rugulososcabrinodis*, noted that the name *M. sancta* cannot refer to this ant and proposed the name *M. rugulososcabrinodis* instead. The other entity which is distributed from the Balkans across Central Europe north to S Finland had been treated as *M. hellenica* by Seifert (1988, 1996, 2007). Radchenko et al. (1997) and Czechowski et al. (2002) accepted this conception. Agosti & Collingwood (1987), following a personal communication by Seifert, were the first to publish a '*Myrmica hellenica* Forel' under species rank in their key on Balkan ants but it was not clear which ant this name really referred to – the drawing of the head obviously depicts *M. rugulosa* Nylander, 1846 while the verbal description effectively applies to more than one species.

The investigation of the types of each of the nine aforementioned taxa and the application of advanced methods of numeric morphology-based alpha-taxonomy (NUMOBAT) allowed a much better interpretation of the complicated situation in the *M. hellenica* and *M. specioides* species complexes. Contours of the taxonomic structure of the *M. specioides* complex are already visible but their credible confirmation needs an extension of sample size in the south-eastern taxa. In the *M. hellenica* complex, however, sufficient sample numbers were available and allow a presentation of conclusions in this paper. We use morphological and zoogeographic arguments to prove our view.

2. Methods

Measurements were made on mounted and dried specimens using a goniometer-type pin-holding stage, permitting full rotations around X, Y, and Z axes. A Zeiss Jena Technival 2 stereomicroscope (2.0x accessory front lens, numeric aperture 0.12, magnification up to 250x), equipped with a Halogen spot light illumination was used until the year 1992. A Leica M10 stereomicroscope (1.6x planapochromatic front lens, numeric aperture 0.25, magnification up to 320x) was used after 1992 with the following illumination: A Schott KL 1500 cold-light source equipped with two flexible, focally mounted light cables, providing 30°-inclined light from variable directions, allowed sufficient illumination over the full magnification range and a clear visualisation of silhouette lines. A Schott KL 2500 LCD cold-light source in combination with a Leica coaxial polarised-light illuminator provided optimum resolution of tiny structures and micro-sculpture at highest magnifications. Simultaneous or alternative use of the cold-light sources depending upon the required illumination regime was quickly provided by regulating the voltage up and down. The improvement of microscopic equipment, increased standardisation and better knowledge of measuring errors after 1992 reduced the measuring error from 3 μm to 1 μm for smaller structures such as FR and from 5 μm to 2 μm for larger structures such as cephalic length, as compared to Seifert (1988). The 'lower-quality data' taken before 1993 could not always be replaced by reinvestigation with the new system providing 'higher-quality data'. To avoid rounding errors, all measurements were recorded in μm even for characters for which a precision of ± 1 μm is impossible.

Definition of numeric characters and descriptive terms:

CL – Maximum cephalic length in median line (Fig. 5); the head must be carefully tilted to the position with the true maximum. Excavations of occiput and/or clypeus reduce CL. Longitudinal carinae or rugae on anterior clypeus are included into the measurement – if exactly median, in their full height and, if of doubtful position, in their half height.

CS – Cephalic size; the arithmetic mean of CL and CW, used as a less variable indicator of body size.

CW – Maximum cephalic width; in *Myrmica* this is always across the eyes.

EYE – Eye-size index: the arithmetic mean of the large (EL) and small diameter (EW) of the elliptic compound eye is divided by CS, i.e. EYE = (EL+EW)/(CL+CW).

FL – Maximum anterior divergence of frontal carinae (= maximum frontal lobe width, Fig. 5). In specimens with frontal carinae parallel or converging frontad FL is not defined, then FL = FR.

FR – Minimum distance between frontal carinae. In specimens with parallel frontal carinae or ones converging frontad FR is not defined; FR then is measured at the level of the centre of frontal triangle.

FUHL – Length of longest hair on second funiculus segment.

F2 – Median length of second funiculus segment in SVP *d*.

F3 – Median length of third funiculus segment in SVP *d*.

IF2 – Ratio of the median length of second funiculus segment divided by its maximum diameter in SVP *d*.
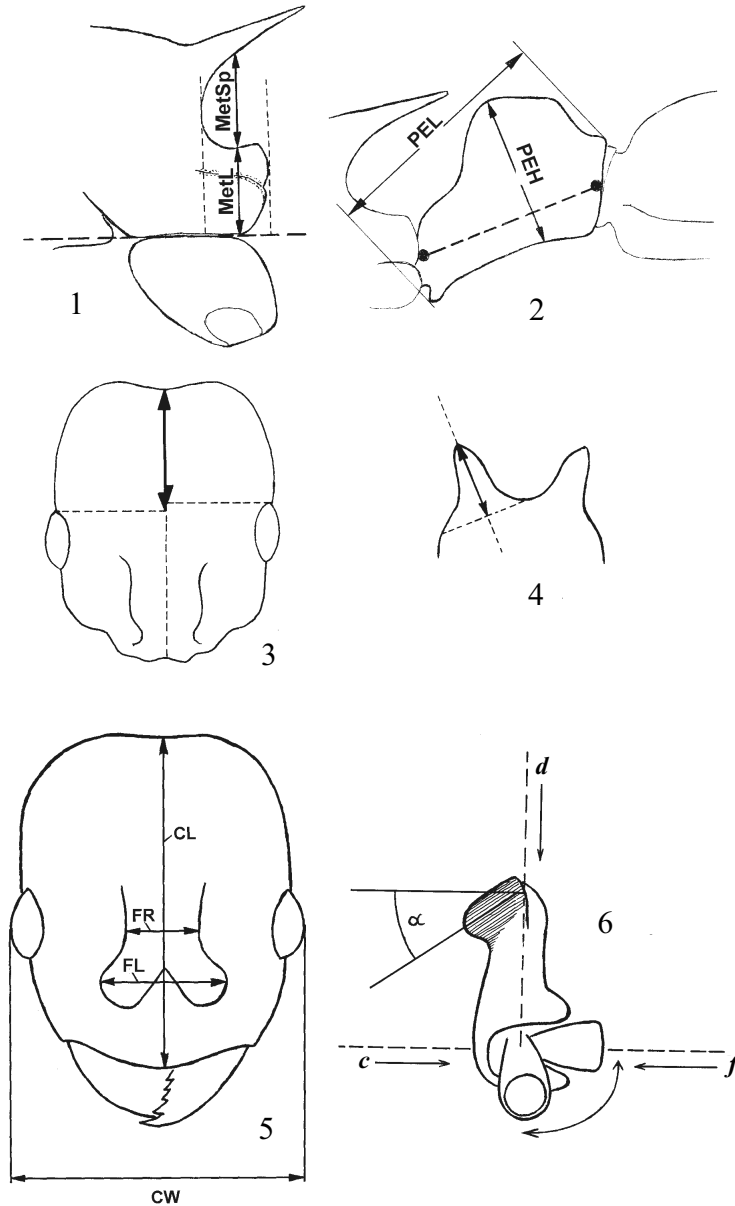
Figs 1–6   Fig. 1: Mode of measuring MetSp and MetL. Fig. 2: Mode of measuring petiolar height and length. Fig. 3: Mode of measuring the postocular distance PoOc. Fig. 4: Mode of measuring spine length in dorsofrontal view. Fig. 5: Mode of measuring cephalic length, cephalic width, minimum frons width, and maximum frontal lobe width. Fig. 6: Standard viewing positions *c*, *d*, and *f* of scape relative to the plane of movement of the hinge joint formed by distal scape and pedicellus. The angle *α* describes the caudal slope of scape lobe.

MeHL – Length of longest hair on mesonotum.

MetFlHL – Length of longest hair on flexor profile of hind metatarsus.

MetL – The height of metapleuron including the propodeal lobe measured in lateral view perpendicular to the straight section of metapleuro-coxal border (heavy dashed line in Fig.1). The lower endpoint of measuring line is the metapleuro-coxal border and the upper one the upper margin of propodeal lobe. The level of the measuring line is positioned in the middle between the frontalmost point of subspinal excavation and the caudalmost point of propodeal lobe (fine dashed lines in Fig. 1).

MetSp – The height of subspinal excavation from upper margin of propodeal lobe to lower spine margin measured along the dorsal continuation of the measuring line for MetL (Fig.1).

ML – Mesosoma length in alates; measured in lateral view from the caudalmost portion of propodeum to the frontalmost point of the anterior pronotal slope (i.e. not to the frontalmost point of the whole pronotum that is often concealed by the posterior head!).

PEH – Maximum petiole height measured perpendicular to a reference line defined as follows: the frontal endpoint of the reference line is marked by the centre of the petiole-propodeal junction and the caudal endpoint by the centre of petiole-postpetiolar junction (dark spots in Fig. 2).

PEL – Maximum measurable diagonal petiole length from the tip of subpetiolar process to the dorsocaudal corner of the caudal cylinder (Do not confuse this with the corner of the movable inner sclerite, Fig. 2).

PEW – Maximum width of petiole.

PoOc – Postocular distance. Use a cross-scaled ocular micrometer and adjust the head to the measuring position of CL. Caudal measuring point: median occipital margin; frontal measuring point: median head at the level of the posterior eye margin. Note that many heads are asymmetric and average the left and right postocular distance (Fig. 3).

PPHL – Length of longest hair on dorsal postpetiole.

PPW – Maximum width of postpetiole.

ScLH – Scape lobe height measured perpendicular to a reference line at SVP *f* or *c*. Maximum height at which cuticular projections such as lobes or carinae protrude above the upper profile of scape base. The reference line is the cord of the curved dorsal scape profile stretching from midpoint of scape length to the point just before the projections at scape bent begin to raise.

SL – Maximum straight line scape length. Distal measuring point: the most distal point of the dorsal lamella of the hinge joint capsula. Proximal measuring point: the most proximal point of scape shaft near the neck of articular condyle. Note that the border region between shaft and condylar neck is usually asymmetric. To measure the real maximum avoid caudal viewing positions and use frontal to dorsal views! In species with basal scape lobes or dents (e.g. *schencki*, *scabrinodis* or *lobicornis* groups) the lobes are excluded from measurement!

SP – Maximum length of propodeal spines as bilateral arithmetic mean. Measured in dorsofrontal view from spine tip to a point at the bottom of the interspinal meniscus (Fig. 4). With the spines' dorsal edge in measuring plane, the spine tip must be focussed at a magnification with low depth of focus. Then, while keeping this focussing, the sharpest point at the bottom of interspinal meniscus is the basal measuring point. This mode of measuring is less ambiguous than other methods but results in some spine length in species with reduced spines.

SVP – Standard viewing position of scape defined by position relative to the moving plane of the hinge joint between scape and first funiculus segment (Fig. 6). Dorsal view **d** is directed perpendicular to this moving plane (in this position the anterior margins of upper and lower lobe of the distal scape end are congruent and the basal curvature of scape is not or only weakly visible). Frontal view **f** and caudal view **c** are within the moving plane and perpendicular to the longitudinal scape axis – i.e. when the scape is imagined to be directed strictly laterad from head, viewing position **f** is the frontal and viewing position **c** the caudal aspect of scape. SVPs such as **cd** and **df** describe intermediate viewing positions.

Removal of allometric variance

In order to make body ratios such as CL/CW, SL/CS or SP/CS directly comparable in synoptic tables, a removal of allometric variance (RAV) was performed with the procedure described by Seifert (2008). RAV was calculated for the assumption of all individuals having an identical cephalic size of 1.0 mm. We applied specific RAV functions the parameters of which were calculated as the arithmetic mean of the species-specific functions of *M. constricta* and *M. hellenica*.

$$CL/CW_{1.0} = CL/CW / (-0.0711*CS+1.1278)*1.0567$$
$$SL/CS_{1.0} = SL/CS / (-0.0908*CS +0.9101)*0.8193$$
$$EYE/CS_{1.0} = EYE/CS / (0.0257*CS +0.1811)*0.2067$$
$$FL/CS_{1.0} = FL/CS / (-0.0034*CS+0.4481)*0.4447$$
$$FR/CS_{1.0} = FR/CS / (-0.0261*CS+0.4078)*0.3817$$
$$PEW/CS_{1.0} = PEW/CS / (-0.0470*CS+0.2899)*0.2429$$
$$PPW/CS_{1.0} = PPW/CS / (-0.0537*CS+0.4358)*0.3821$$
$$PEH/CS_{1.0} = PEH/CS / (-0.0501*CS+0.3722)*0.3220$$
$$PEL/CS_{1.0} = PEL/CS / (-0.0588*CS+0.5273)*0.4685$$
$$PPHL/CS_{1.0} = PPHL/CS / (-0.0775*CS+0.2542)*0.1767$$
$$SP/CS_{1.0} = SP/CS / (0.1363*CS+0.1986)*0.3349$$
$$MetL/CS_{1.0} = MetL/CS / (-0.0164*CS+0.2504)*0.2339$$
$$MetSp/CS_{1.0} = FR/CS / (-0.0137*CS+0.1697)*0.1560$$
$$PoOc/CL_{1.0} = PoOc/CL / (-0.0076*CS+0.4261)*0.4184$$
$$SW/SL_{1.0} = SW/SL / (-0.0128*CS+0.1287)*0.1159$$

Discriminant analysis and error estimation

A canonical discriminant analysis (DA) was performed using the SPSS 10.0 statistical package based on sample means. All characters passed the tolerance test in a DA to the level of 0.01 as implemented by SPSS both when calculated as primary (crude) or as indexed data. The performance and reliability of a DA was assessed by the degree of coincidence of *a-priori* and *a-posteriori*-hypotheses (error rate) and by a statistics of *a-posteriori*-probabilities. A parallel run of an ordinary DA and of a 'Leave-One-Out Cross-Validation' DA (LOOCV-DA, Lachenbruch & Mickey 1968, Lesaffre et al. 1989) was performed to realistically estimate the error rate. The data presented by Seifert & Schultz (2008) show that the

arithmetic mean of the pessimistic error indication by the LOOCV-DA and the optimistic error indication by the ordinary DA is close to the true error rate. This is of particular importance when sample size is smaller than triple the character number – a situation in which an ordinary DA is biased to confirm the taxonomist's prejudice. As a further analysis avoiding the prejudice problem we also ran a principal component analysis using SPSS.

Geographic analysis of within- and between-species morphological distance

The morphological distance was analysed on the basis of sample means of the eight characters $CL/CW_{1.0}$, $SL/CS_{1.0}$, $FL/CS_{1.0}$, $FR/CS_{1.0}$, $PEW/CS_{1.0}$, $PPW/CS_{1.0}$, $PPHL/CS_{1.0}$ and $SP/CS_{1.0}$. Combining the lower- and higher- quality data sets allowed evaluating 56 *M. constricta* and 59 *M. hellenica* samples. For each possible putatively con- and heterospecific pair of samples, i.e., a total of 6555 data pairs, the morphological and geographic distance were calculated. Morphological distance for a character was calculated as the linear distance divided by the arithmetic mean of the character-specific standard deviations of *M. hellenica* and *M. constricta*. The overall morphological distance (OMD) was calculated as arithmetic mean of the eight character-specific distances. As a complementary analysis we calculated the Bray-Curtis similarity index (BCSI, Bray & Curtis 1957), based on the same data. Geographical analyses of OMD and BCSI were then performed to indirectly indicate gene flow, within and between the putative species. Assessing these relationships by simply evaluating the correlation coefficient between morphological and geographical data and testing its statistical significance is problematic because data in such matrix distance analyses are not independent of each other: changing the position of one data point would change the distance from that data point to n-1 others. Hence, to check the significance of correlations, we applied the Mantel test (Mantel 1967, Sokal & Rohlf 1995) which is more appropriate than alternatives to overcome the problem of dependence in matrices. Using IBDWS 3.15 (San Diego State University; http://ibdws.sdsu.edu/~ibdws/), we ran 100 bootstrap randomisations.

Determination of standardised air temperatures (TAS)

Standardised summer air temperature (TAS) of a collecting site was defined by Seifert & Pannier (2007) as the 30-year average of the mean air temperature at 2 metres height of the period 1 May to 31 August. We used data of 385 meteorological stations from within or near the geographical range of the two *Myrmica* species, including 58 Turkish stations. The data were from different sources – national meteorological services or internet websites – and the reference period was largely 1971–2000. However, for some countries the reference period was not explicitly stated. It is possible that some of these referred to the period 1961–1990 – the expected error due to global warming is then about –0.43 °C (Schönwiese et al. 2004, 2005). This deviation is only 2.6 % of the total TAS-range found in the two species and should not strongly affect the results. The TAS-value of a given collecting site was predicted by averaging the data of the three next meteorological stations inversely weighted to their distance and corrected for altitude differences with a gradient of –0.66 °C for 100 m growing altitude (Seifert & Pannier 2007).

3. Materials

The sample data are given here as follows: locality, date, geographic coordinates in decimal format [in square brackets, number of decimals corresponding to the accuracy of the estimate]. In samples without exact dates available, names of collectors are given to allow an approximate estimation of the collecting period.

Myrmica hellenica Finzi, 1926

59 samples with 164 workers were subject to a numeric character analysis.

Armenia: Khosrovsky Zapovednik, 9.vi.1985 [40.023°N, 44.916°E]; Goktscha/Sevan, pre 1945 (Arnoldi No.3997) [40.4°N, 45.3°E]; no locality given, 1.ix.1930 [40.250°N, 45.040°E, coordinates assumed]. **Azerbaijdzhan:** Shusha/Gov. Elisavetpol viii.1906, lectotype *rugulososcabrinodis* (Karavajev No 3985) [40.6°N, 47.1°E]. **Bulgaria:** Betova viii.1985 [42°N, 25°E]; Burgas vii.1985 [42.509°N, 27.470°E]; Maritza river, near Turkish border, vii.1985 [41.776°N, 26.206°E]; Melnik, 13.–17.vi.1984 [41.521°N, 23.379°E]; Obsor, 1.vii.1980 [41.817°N, 27.833°E]; Sandanski, 8.–12.vi.1984 [41.560°N, 23.289°E]. **Croatia:** Mrkviste. 27.vi.1910 [44.5°N, 16.0°E]; Momiano, iv.1922 [45.439°N, 13.711°E]. **Georgia**: above Borisacho, 1500 m, 11.viii.1985 (No5) [44.933°N, 42.533°E]; Betscho, Mt. Tschusbi, 23.vii.1909 (Karavajev No 3981) [43.1°N, 42.4°E]; Passanauri, 1600 m, 18.ix.1975 [42.350°N, 44.708°E]; Passanauri, 1600 m, 29.vii.1984 [42.350°N, 44.708°E]; Pizunda, 8.viii.1984 [43.156°N, 40.350°E]; Sotschi, vii.1980 [43.571°N, 39.743°E]; Tbilissi, 400 m, 20.viii.1985 [41.722°N, 44.782°E]. **Greece:** Kassandra, Polichronon, iii.1989 [40.017°N, 23.533°E]; Korinthos-45 km W, 5.vi.1994 [38.000°N, 22.436°E]; Nestos-Delta, 2004 (No 1.3) [40.850°N, 24.800°E]; Patras (Forel-1913), type *M. hellenica* [38.239°N, 21.743°E]. **Italy:** Bologna (Minozzi) [44.500°N, 11.340°E]; Bologna iii.1919 [44.500°N, 11.340°E]; Gabrovizza; v.1927 [45.726°N, 13.729°E]; Gambarie, 16.v.1994 [38.167°N, 15.833°E]; Opcina, 18.viii.1920, type *M. striata* [45.687°N, 13.786°E]; Repen Tabor, iv.1922 [45.718°N, 13.812°E]; Grado, 3.vii.1921 [45.679°N, 13.387°E]. **Russia:** Kabardinka/Black Sea coast [44.646°N, 37.945°E]; Maikop [44.602°N, 40.104°E]. **Slovenia:** Krsko-Brezice, Vrbina, vi.2001 [45.928°N, 15.440°E]. **Turkey:** Damar, 3.ix.1995 [41.250°N, 41.567°E]; Borcka Civan-3 km S, 29.vi.1993 (No 1184) [41.300°N, 41.700°E]; Camlidere/Isik valley, 23.vi.1947 [40.500°N, 32.479°E]; Cayurbici, vi.1985 [40.8°N, 39.3°E]; Cildir to Camlicatak, 24.–26.vi.1993 [41.120°N, 42.940°E]; Ikizdere-5 km S, 13.viii.2000 (samples TR98, TR172) [40.739°N, 40.575°E]; Karabuk, 2000 m, [41.2°N, 32.6°E]; Kastamonu, 5.vii.1989 (No 3220) [41.4°N, 33.8°E]; Kure, v.1985 [41.800°N, 33.710°E]; N of Uzungol village 18.viii.2000 (No TR165) [40.622°N, 40.287°E]; Ordu-50 km S, (A. Schulz samples 3186, 3192) [40.5°N, 37.9°E]; Ovitdagi Gecidi-30.vi.1993 (No 1195) [40.80°N, 40.90°E]; near Kastamonu, 5.vii.1989 (No 98) [41.4°N, 33.8°E]; Sarigöl-20 km NW, 28.vi.1993 (No 1177) [40.90°N, 41.25°E]; Scuruca Gecidi-2 km E, 29.vi.1993 [41.400°N, 41.500°E]; Ucburgu, 250 m vi.1985 [41.317°N, 32.100°E]; near Posof, 25.vi.1993 (samples No 1142, 1145) [41.511°N, 42.729°E]. **Ukraine:** Crimea (Karavajev) [45.2°N, 34.2°E]; Kertsch 24.iv.1923 [45.351°N, 36.442°E]; Stary Krym-6 km W, 12.vi.2003 [45.020°N, 34.994°E]; Simferopol, 18.ix.1919 [44.960°N, 34.093°E]; Simferopol, 1919 (No 5151) [44.960°N, 34.093°E]; **Serbia-Montenegro:** Mokra Njiva, 26.vi.1911 [42.802°N, 18.935°E].

Myrmica constricta Karavajev, 1934

56 samples with 145 workers were subject to a numeric character analysis.

Material from four additional Polish sites, credibly reported by Czechowski et al. (2002), was not seen. These sites are given in italics and were considered in distribution maps and climatic analysis.

Austria: Musau/Lech, 850m, 1.v.1994 (sample K27 and sample without number) [47.546°N, 10.680°E]; Prutz, 15.v.1994 (No g22) [47.076°N, 10.661°E]; Rückersdorf, 31.vii.1991 [46.560°N, 14.559°E]; St. Pölten, 13.v.1994 (No 060) [48.219°N, 15.650°E]; Starkenbach, 15.v.1994 (No g27) [47.189°N, 10.627°E]. **Bulgaria:** Melnik, 30.vii.1982 [41.521°N, 23.379°E]. **Croatia:** Albona (= Labin), v.1922 [45.095°N, 14.120°E]. **Finland:** Tvärminne, 11.vii.2003 (No 79-03) [59.844°N, 23.230°E]; Hanko (Hangö), Kolaviken 21.vii.1988 [59.817°N, 23.000°E]. **Germany:** Casel v.1992 [51.683°N, 14.132°E]; Dauban 16.viii.2002 [51.283°N, 14.634°E]; Halbendorf, 16.v.1992 (sample No 035 and without No) [51.300°N, 14.549°E]; Halbendorf, 29.v.1964 [51.299°N, 14.556°E]; Kaltwasser, Inselsee, 16.vii.2007 [51.279°N, 14.941°E]; Kleinsaubernitz 23.vii.1991 (No 42) [51.267°N, 14.607°E]; Kostebrau, Wischgrund, 1981 [51.529°N, 13.804°E]; Kostebrau, Wischgrund 7.viii.1986 (sample No 1) [51.529°N, 13.804°E]; Kostebrau, Wischgrund 8.viii.1986 (samples No 2, 3, 5) [51.529°N, 13.804°E]; Lauchhammer, Kippe 1008, 1987 (samples RE and WA) [51.503°N, 13.798°E]; Lauchhammer, Revier 55, 1982 [51.503°N, 13.798°E]; Lenggries-4 km S, 13.viii.1994 (samples 3L11, 3L6) [47.642°N, 11.579°E]; Litschen-Friedersdorf, 13.viii.1982 (samples No 1, 2) [51.372°N, 14.402°E]; Litschen-Friedersdorf, 10.viii.1986 (samples No 1, 2, 3) [51.372°N, 14.402°E]; Lömischau, 9.v.1964 [51.284°N, 14.566°E]; Pechhütte, 29.vi.1988 [51.593°N, 13.731°E]; Schipkau, 1989 [51.519°N, 13.881°E]; Usedom, 2.vii.2001 (samples No 0, 108, 230) [54.098°N, 13.876°E]; Vorderriß, 8.vii.1994 [47.567°N, 11.458°E]; Vorderriß 26.viii.1994 [47.567°N, 11.458°E]; Wallgau 28.vi.1994 [47.527°N, 11.300°E]. **Italy:** Aspromonte NP, 16.v.1994 [38.300°N, 15.800°E]; Venezia Giulia, S.Canziano, pre 1926 [45.798°N, 13.466°E]; Venezia Giulia, Valbruna, pre 1926 [46.490°N, 13.494°E]. **Poland:** Pieniny: Sromowe Wyżne, 29.vi.1996 [49.403°N, 20.335°E]; *Beskidy: Miedzygrodzie near Sanok [49.597°N, 22.193°E]; Gdańsk: Sobieszowo Island [54.359,18.815°E]; Island Wolin [53.995°N, 14.645°E]; Siedlce [52.165°N, 22.267°E]*. **Romania:** Medias 22.vii.1987 [46.133°N, 24.517°E]. **Switzerland:** Cazis, 15.vii.1938 [46.717°N, 9.433°E]; Cazis, 6.xi.1938 [46.717°N, 9.433°E]; Rothenbrunnen, 1939 [46.767°N, 9.417°E]; Zizers, 6.x.1939 [46.933°N, 9.567°E]; Fully, 16.v.1994 (two samples) [46.139°N, 7.110°E]; Mont Rosel, v.1987 [46.133°N, 7.070°E]; Sion, (No 3708, Forel, coll. Mayr) [46.231°N, 7.362°E]; Zürich (leg. Forel, coll. Mayr) [47.374°N, 8.541°E]. **Ukraine:** UKR: Kiev, Nikloskaya Slobodka, 1.viii.1919, type *M. constricta* (Karavajev No 2770) [50.434°N, 30.532°E]. **Serbia-Montenegro:** Cernica 31.viii.1986 [42.426°N, 21.429°E].

4. Results

Multiple evidence for heterospecificity of *Myrmica hellenica* and *M. constricta*

In all, we have gathered fourfold evidence of heterospecificity of *M. hellenica* and *M. constricta*, through (i) discriminant analysis, (ii) principal component analysis, and (iii) geographic analysis of worker morphometric data, as well as through (iv) male morphology.

(i) Even when including lower-quality data sets of the eight characters $CL/CW_{1.0}$, $SL/CS_{1.0}$, $FL/CS_{1.0}$, $FR/CS_{1.0}$, $PEW/CS_{1.0}$, $PPW/CS_{1.0}$, $PPHL/CS_{1.0}$ and $SP/CS_{1.0}$, both the DA and LOOCV-DA indicate the existence of two morphological entities. The error rate for 115 samples was 3.9 % in the DA and 4.3 % in the LOOCV-DA and all type samples are unambiguously allocated to either cluster (Fig. 7): the *M. constricta* types with p = 0.998 (DA) and p = 0.997 (LOOCV-DA) to the *M. constricta* cluster and those of *M. rugulososcabrinodis* (p = 0.992 DA, p = 0.989 LOOCV-DA), *M. striata* (p = 1.000 DA, p = 0.998 LOOCV-DA) and *M. hellenica* (p = 1.000 DA, p = 0.981 LOOCV-DA) to the *M. hellenica* cluster. The performance of the system is improved when only the higher-quality data set is evaluated and when character number is extended to 14 by adding $EYE/CS_{1.0}$, $PEH/CS_{1.0}$, $PEL/CS_{1.0}$, $MetL/CS_{1.0}$, $MetSp/CS_{1.0}$, $PoOc/CL_{1.0}$ and $SW/SL_{1.0}$ (Fig. 8). The predicted error rate falls to 1.1 % in these 90 samples, 0 % in the DA and 2.2 % in the LOOCV-DA, and the types of *M. constricta* are unambiguously allocated to the *M. constricta* cluster (p = 1.000 both in DA and LOOCV-DA) and those of *M. rugulososcabrinodis* to the *M. hellenica* cluster (p = 1.000 both in DA and LOOCV-DA). These error analyses are clear arguments in favour of a considerable robustness of the system and against a subjective identification bias.
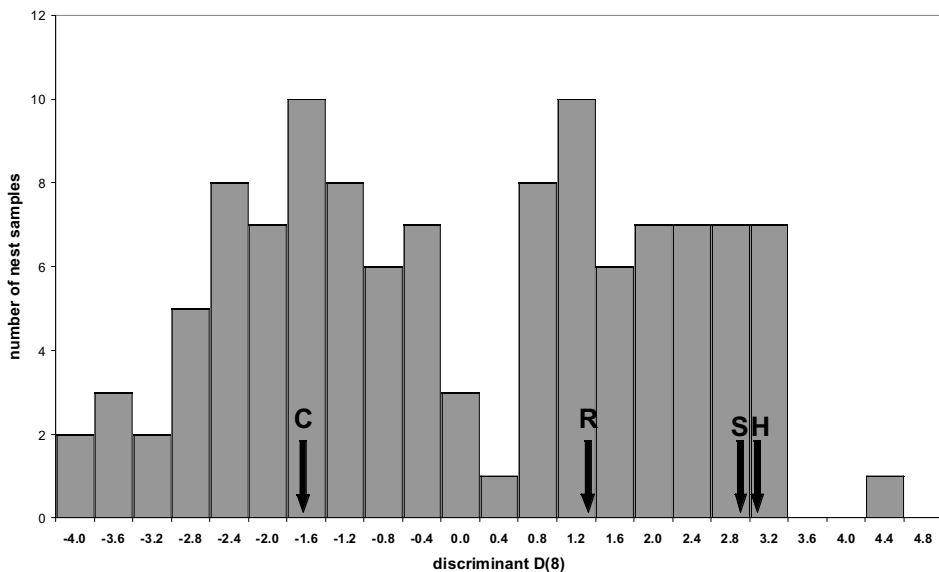

Fig. 7   Discriminant analysis using 8 characters and combining lower- and higher-quality data. The positions of the type samples are marked with arrows (*a-posteriori* probabilities in brackets): C = syntype sample of *M. constricta* Karavajev, 1934 (p = 0.997), R = lectotype sample of *M. rugulososcabrinodis* Karavajev, 1929 (p = 0.989), S = syntype sample of *M. striata* Finzi, 1926 (p = 1.000), H = syntype sample of *M. hellenica* Finzi, 1926 (p = 1.000).
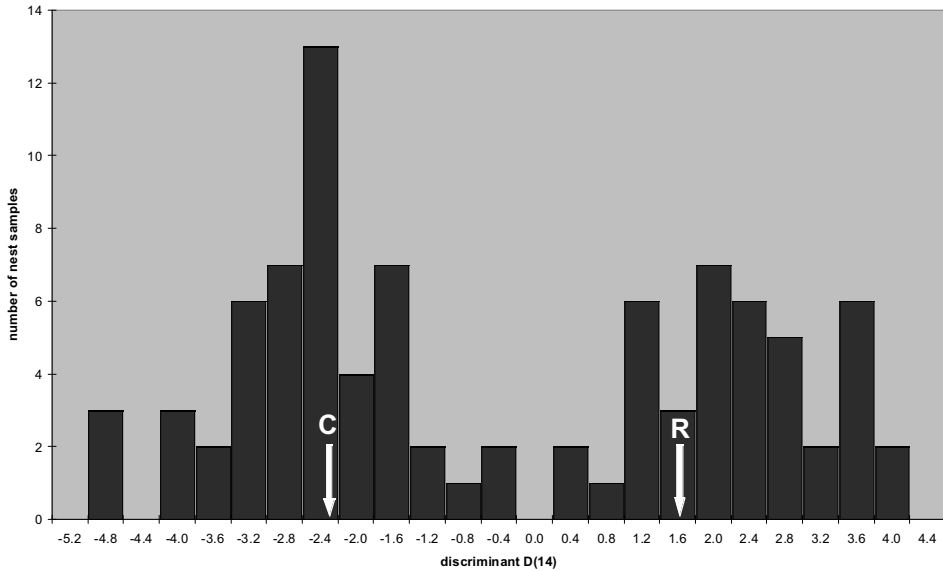
Fig. 8   Discriminant analysis considering 14 characters, only new higher-quality data were used. The position of the type samples are marked with arrows (*a-posteriori*-probabilities in brackets): C = syntypes of *M. constricta* Karavajev, 1934 (p = 1.000), R = lectotype sample of *M. rugulososcabrinodis* Karavajev, 1929 (p = 1.000).

(ii) Being an unsupervised method, the principal component analysis of the higher-quality data set confirms the conclusion of heterospecificity as a result most likely independent of an observer's bias. The first two factors of the PCA, describing 39.1 % of total variance, separated the two species' clusters without overlap (Fig. 9).

(iii) Mantel tests based on the morphological distance (OMD) as well as based on the Bray-Curtis similarity index (BCSI) showed a significant association for pairwise values between worker morphology and the type of pairing, i.e., whether the data points paired were (putatively) con- or heterospecific (OMD: $r = 0.4109$, $p < 0.01$; BCSI: $r = -0.4370$, $p < 0.01$). This statistical result is expected, should the hypothesis of heterospecificity indeed apply, but a potential influence of geographical distance, through genetic isolation by distance which then is reflected in worker morphology, could still underpin the effect. However, also Mantel tests controlling for geographical distance still showed a significant effect of (putative) con- vs. heterospecificity (OMD: partial correlation $r = 0.3480$, $p < 0.01$; BCSI: $r = -0.3254$, $p < 0.01$) and this is a strong, independent argument in favour of the heterospecificity hypothesis.

(iv) The results of our male morphology analyses are in line with heterospecificity, pending confirmation by analysis of a larger sample than available presently, though. Figs. 10 and 11 suggest strong differences in hind metatarsal pilosity. The flexor margin of hind metatarsus shows long erect to suberect setae in *M. hellenica* but only short, fine and subdecumbent hairs (better termed as pubescence) in *M. constricta*. The longest hair on flexor margin of hind metatarsus was 61–97 µm long in 19 *M. constricta* males but 128–158 µm long in the five examined *M. hellenica* specimens. Tab. 1 suggests the *M. hellenica* male to generally have longer setae, a longer scape, wider petiole and larger size.
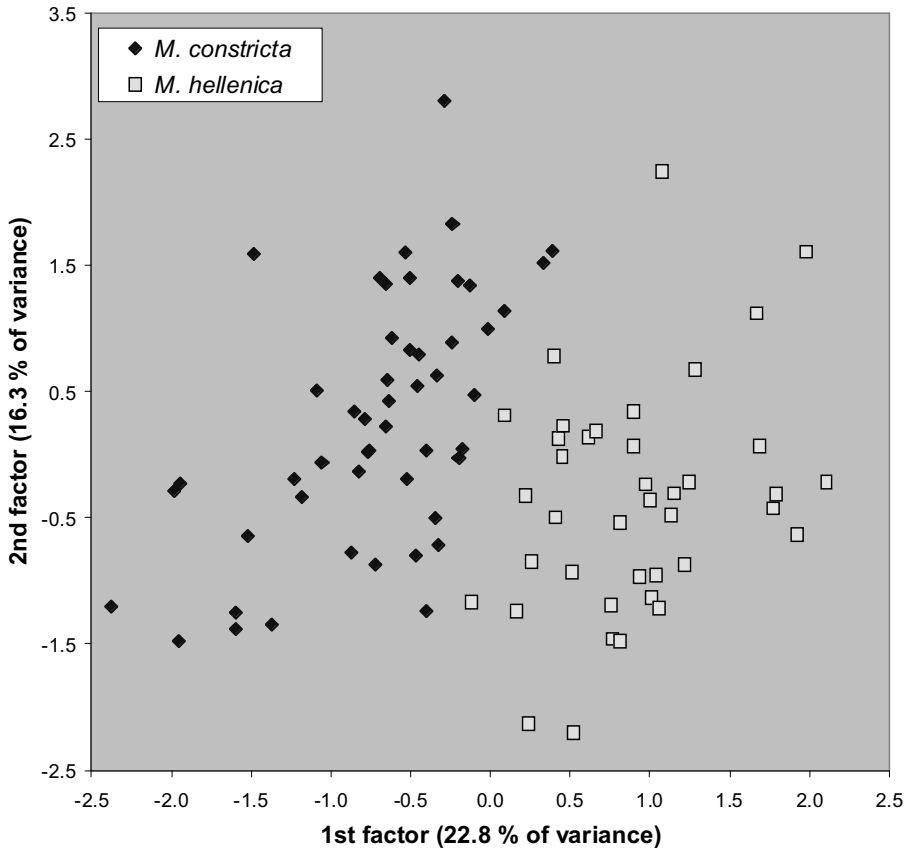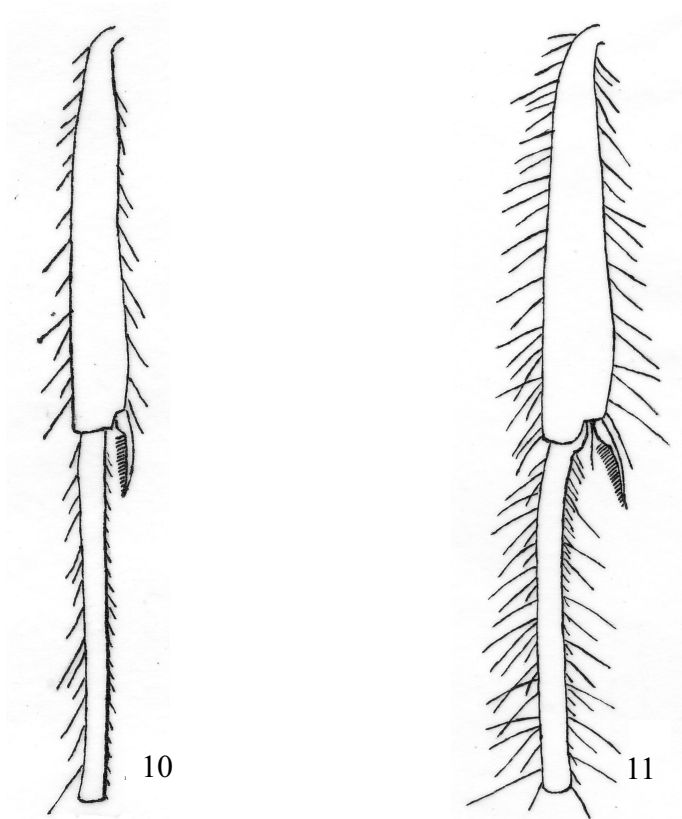

Fig. 9   Principal component analysis of RAV-corrected worker nest sample means of 14 characters – only higher-quality data were used. *M. constricta* (dark rhombs, n = 50); *M. hellenica* (light squares, n = 40).

Figs 10, 11   Hind tibia and metatarsal segment of *M. constricta* (10) and *M. hellenica* (11) males.

Following presentation of (i)–(iv) it also has to be pointed out that 31 worker-associated gynes of *M. constricta* but only 14 of *M. hellenica* were available for this study and that the number of characters thoroughly investigated in each of these specimens was only ten. This did not allow to develop a convincing method to separate the species in this caste – the predicted error rate is 4.5 % (2.2 % by DA and 6.7 % by LOOCV-DA). *M. constricta* gynes are on the average smaller and shorter-spined but in other characters most similar to *M. hellenica* (Tab. 2).

Finally, we wish to point out that there also is one problematic sample from the Maritza river in S Bulgaria collected by C. A. Collingwood in July 1985. The two workers are clearly allocated to *M. hellenica* by DA and LOOCV-DA, and the single male appears as a weakly haired *M. hellenica*, but the single gyne is classified as *M. constricta* by both DA and LOOCV-DA, with her small body size being the most probable reason for these putative misclassifications. If indeed representing a single colony, this sample could indicate occasional hybridisation of *M. hellenica* and *M. constricta*.

Tab. 1 Morphometric data of *M. constricta* and *M. hellenica* males. Asterisks correspond to significance levels p of the modified *t*-test of Welch (1947): * 0.05, ** 0.02, *** 0.01, **** 0.001, ***** 0.0001; i = number of individuals.

	M. constricta i = 18	p	*M. hellenica* i = 5
CL [μm]	760 ± 22 [717,800]	***	843 ± 36 [792,881]
CL/CW	0.888 ± 0.014 [0.861,0.912]		0.895 ± 0.026 [0.871,0.936]
SL/CL	0.394 ± 0.035 [0.306,0.436]	**	0.467 ± 0.038 [0.415,0.521]
SL/SW	3.206 ± 0.341 [2.47,3.72]		3.420 ± 0.245 [3.01,3.66]
F2/CL	0.153 ± 0.008 [0.142,0.168]	*	0.164 ± 0.010 [0.154,0.179]
IF2	1.885 ± 0.116 [1.702,2.043]		1.818 ± 0.100 [1.718,1.985]
F3/CL	0.105 ± 0.004 [0.099,0.114]		0.109 ± 0.011 [0.101,0.127]
ML/CL	2.131 ± 0.039 [2.051,2.211]		2.131 ± 0.090 [2.006,2.252]
PEW/CL	0.311 ± 0.012 [0.288,0.332]	***	0.347 ± 0.025 [0.311,0.382]
PPW/CL	0.481 ± 0.019 [0.457,0.514]		0.501 ± 0.038 [0.441,0.542]
FuHL/CL	0.110 ± 0.015 [0.066,0.126]	****	0.152 ± 0.014 [0.142,0.177]
OccHL/CL	0.153 ± 0.025 [0.110,0.198]		0.194 ± 0.039 [0.159,0.254]
MeHL/CL	0.196 ± 0.020 [0.158,0.220]		0.215 ± 0.025 [0.193,0.253]
PPHL/CL	0.187 ± 0.028 [0.137,0.238]	****	0.237 ± 0.010 [0.230,0.253]
MetFlHL/CL	0.103 ± 0.012 [0.082,0.124]	*****	0.166 ± 0.010 [0.156,0.183]
MetFlHL [μm]	78 ± 10 [61,97]	*****	140 ± 12 [128,158]

Tab. 2   Morphometric data of *M. constricta* and *M. hellenica* gynes. Asterisks correspond to significance levels p of the modified *t*-test of Welch (1947): * 0.05, ** 0.02, *** 0.01, **** 0.001, ***** 0.0001; i = number of individuals.

	M. constricta i = 31	p	*M. hellenica* i = 14
code	cons		hell
CS	1112 ± 34 [1049,1192]	*****	1202 ± 39 [1086,1247]
CL/CW	1.020 ± 0.015 [0.969,1.041]		1.011 ± 0.015 [0.993,1.042]
SL/CS	0.765 ± 0.019 [0.733,0.799]		0.766 ± 0.016 [0.781,0.852]
FL/CS	0.449 ± 0.010 [0.434,0.474]		0.448 ± 0.011 [0.430,0.469]
FR/CS	0.402 ± 0.009 [0.380,0.420]	*	0.391 ± 0.015 [0.373,0.426]
PEW/CS	0.266 ± 0.012 [0.247,0.306]	**	0.276 ± 0.012 [0.256,0.293]
PPW/CS	0.426 ± 0.014 [0.398,0.469]	***	0.441 ± 0.016 [0.405,0.463]
SP/CS	0.294 ± 0.023 [0.248,0.353]	*****	0.347 ± 0.028 [0.306,0.400]
MW/CS	0.770 ± 0.016 [0.736,0.818]	*****	0.798 ± 0.018 [0.774,0.833]
ML/CS	1.524 ± 0.024 [1.480,1.576]		1.532 ± 0.015 [1.506,1.559]

Towards simpler means of identifying workers

As non-taxonomist practitioners would usually flinch from applying the complex identification methods presented above, we have tried to find simpler procedures. Zoogeography will help in a number of cases: *M. hellenica* is only known from sites south of 46°N and *M. constricta* is not known so far from Asia Minor and the Caucasian region. Unfortunately, there is no single key character enabling a reasonably safe separation in the Italo-Balkanian and S Ukrainian region of sympatric occurrence. We simplified as much as possible by using absolute measurements, omitting allometric corrections and reducing the number of characters. With all measurements given in mm, a discriminant

D(8) = 99.631 PEW +0.975 PPW +8.6 SP –30.075 FR –43.979 CL +11.751 FL +26.238 SL +54.450 PoOc –20.678

separates the 90 nest samples means of the higher-quality data set with a predicted error rate of 1.1 % (DA 0 %, LOOCV-DA 2.2 %):

M. constricta   –1.918 ± 0.946 [–3.81, –0.25] n = 40

M. hellenica   2.396 ± 1.064 [0.27, 4.61] n = 50.

This is not truly simple – the more so, as reproducibly measuring these characters needs some training, good equipment and careful consideration of the character definitions. When the given discriminant function is not applied to nest samples but to 194 individual workers, the range of confused determination is within D(8) [–0.95, 1.59]. We recommend to start with a single specimen per nest and only to investigate one or two further specimens when D(8) is within this range of uncertainty.

Formal taxonomic treatment, synonymies, zoogeography and biology

After the above line of arguments in favour of heterospecificity of the entities under consideration, we treat the formal taxonomic aspects and comment on biology and present distribution.

Myrmica hellenica Finzi, 1926

Myrmica rugulosa var. *hellenica* Finzi, 1926, p. 93 [First available use of *Myrmica scabrinodis* r. *rugulosa* var. *hellenica* Forel, 1913]; Greece: Patras [name allocation by type investigation]

Myrmica rugulosoides var. *striata* Finzi, 1926, p. 96; Italy: Opcina near Trieste [name allocation by type investigation]

Myrmica rugulosa var. *rugulososcabrinodis* Karavajev, 1929; Caucasus and Armenia [name allocation by type investigation]

Myrmica rugulosa caucasica Arnoldi, 1934; unnecessary replacement name for *Myrmica rugulosa* var. *rugulososcabrinodis* Karavajev, 1929

Myrmica sancta sancta Karavajev, sensu Arnoldi 1970 [misidentification]

Myrmica sancta Karavajev, sensu Seifert 1988 [misidentification]

Type material investigated

M. hellenica: three syntype workers from Greece: Patras, leg. U. Sahlberg; MHN Geneve.

M. rugulososcabrinodis: Lectotype and paralectotypes (by present designation): three workers on the same pin labelled: 'Shusha, Elisavetp. g. VIII. 1906. Zaizev', '3985.Coll.Karavievi', 'Lectotype (top specimen) *Myrmica rugulososcabrinodis* Karavajev 1929, desig. B. Seifert 2005' [red printed label] and 'Syntypus *Myrmica rugulosa* v. *rugulososo-scabrinodis* Kar.' [red, handwritten label of A. Radchenko]. The lectotype is the largest specimen with CW = 1038 μm. ZMU Kiev.

M. striata: one type worker labelled 'Opcina 15.8.20 Auencia', 'Tipo, *Myrmica* var. *striata* Finzi, 1926'. Absolute measurements of this specimen in mm according to lower-quality measuring: CW 1.025, FL 0.479, FR 0.371, PEW 0.275, PPW 0.432; MCZ Harvard.

Tab. 3   Morphometric data of *M. constricta* and *M. hellenica* workers. Only higher-quality data considered. Asterisks correspond to significance levels p of the modified *t*-test of Welch (1947): * 0.05, ** 0.02, *** 0.01, **** 0.001, ***** 0.0001; i = number of individuals, n = number of nest samples.

|	Primary data of individuals				RAV-corrected nest sample means		
	M. constricta i = 96	p	*M. hellenica* i = 102		*M. constricta* n = 50	p	*M. hellenica* n = 40
CS	963 ± 44 [832,1056]	*****	1047 ± 55 [899,1191]	CS	965 ± 35 [886,1041]	*****	1041 ± 49 [904,1158]
CL/CW	1.060 ± 0.017 [1.028,1.109]		1.056 ± 0.018 [0.989,1.099]	CL/CW$_{1.0}$	1.056 ± 0.015 [1.025,1.102]		1.058 ± 0.019 [0.986,1.089]
SL/CS	0.815 ± 0.015 [0.784,0.854]	****	0.823 ± 0.018 [0.774,0.861]	SL/CS$_{1.0}$	0.811 ± 0.012 [0.785,0.834]	*****	0.827 ± 0.016 [0.793,0.865]
SW/SL	0.113 ± 0.006 [0.100,0.127]	*****	0.117 ± 0.008 [0.100,0.140]	SW/SL$_{1.0}$	0.112 ± 0.005 [0.099,0.124]	*****	0.118 ± 0.007 [0.104,0.133]
PoOc/CL	0.414 ± 0.008 [0.395,0.436]	*****	0.422 ± 0.009 [0.400,0.442]	PoOc/CL$_{1.0}$	0.413 ± 0.007 [0.397,0.430]	*****	0.422 ± 0.008 [0.408,0.438]
EYE	0.208 ± 0.006 [0.197,0.227]	**	0.206 ± 0.006 [0.192,0.223]	EYE$_{1.0}$	0.209 ± 0.006 [0.200,0.226]	****	0.205 ± 0.005 [0.197,0.217]
FL/CS	0.443 ± 0.010 [0.420,0.465]		0.446 ± 0.012 [0.419,0.483]	FL/CS$_{1.0}$	0.443 ± 0.008 [0.425,0.458]		0.446 ± 0.011 [0.424,0.477]
FR/CS	0.384 ± 0.010 [0.365,0.405]		0.382 ± 0.013 [0.353,0.413]	FR/CS$_{1.0}$	0.384 ± 0.009 [0.365,0.400]		0.384 ± 0.012 [0.358,0.404]
PEW/CS	0.236 ± 0.010 [0.211,0.257]	*****	0.249 ± 0.009 [0.231,0.276]	PEW/CS$_{1.0}$	0.234 ± 0.008 [0.213,0.249]	*****	0.252 ± 0.007 [0.238,0.268]
PPW/CS	0.373 ± 0.013 [0.339,0.412]	*****	0.389 ± 0.014 [0.354,0.426]	PPW/CS$_{1.0}$	0.371 ± 0.010 [0.350,0.392]	*****	0.393 ± 0.011 [0.375,0.423]
PEH/CS	0.320 ± 0.011 [0.298,0.346]	**	0.324 ± 0.011 [0.301,0.352]	PEH/CS$_{1.0}$	0.318 ± 0.009 [0.298,0.336]	*****	0.327 ± 0.009 [0.314,0.346]
PEL/CS	0.473 ± 0.015 [0.435,0.508]	****	0.466 ± 0.012 [0.434,0.498]	PEL/CS$_{1.0}$	0.471 ± 0.014 [0.440,0.502]		0.468 ± 0.012 [0.432,0.500]
PPHL/CS	0.177 ± 0.012 [0.146,0.214]		0.179 ± 0.011 [0.156,0.210]	PPHL/CS$_{1.0}$	0.174 ± 0.008 [0.152,0.195]	*****	0.183 ± 0.009 [0.159,0.204]
SP/CS	0.321 ± 0.018 [0.263,0.354]	*****	0.355 ± 0.021 [0.297,0.411]	SP/CS$_{1.0}$	0.323 ± 0.015 [0.288,0.348]	*****	0.348 ± 0.015 [0.320,0.371]
MetL/CS	0.238 ± 0.009 [0.212,0.263]	*****	0.232 ± 0.011 [0.206,0.259]	MetL/CS$_{1.0}$	0.237 ± 0.007 [0.223,0.253]	*	0.233 ± 0.009 [0.212,0.254]
MetSP/CS	0.154 ± 0.013 [0.133,0.198]	****	0.160 ± 0.013 [0.131,0.199]	MetSP/CS$_{1.0}$	0.154 ± 0.011 [0.136,0.184]	***	0.161 ± 0.011 [0.137,0.188]

Description

— worker (Tab. 3; Figs 12–15, *M. hellenica* type; Figs 16–18; eastern population): Size rather small (mean CS 1.047 mm). Head moderately elongated, (CL/CW 1.056), in frontodorsal view without central clypeal excavation. Postocular distance rather large (PoOc/Cl 0.422) and eye moderately-sized (EYE/CS 0.206). Scape rather long (SL/CS 0.823). Scape base in caudal view angularly curved, without any lamellar outgrowth, in the western population only showing suggested dorsal and caudal carinae which become stronger in the Caucaso-Anatolian region (Figs 16–18). Frontal carinae weakly diverging towards the frontal lobes (FL/FR 1.173), their minimum distance relatively large (FR/CS 0.382).
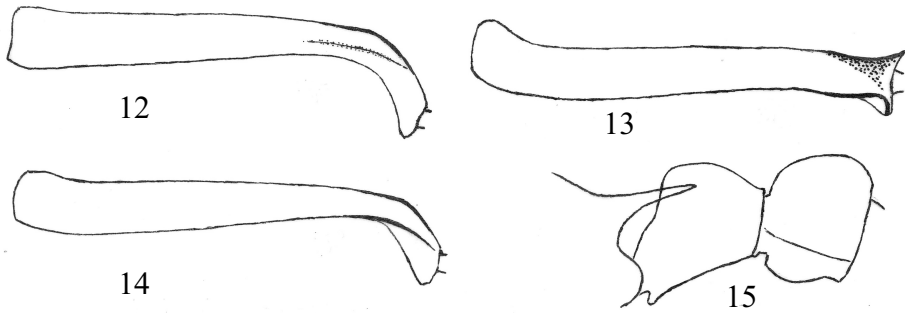
Figs 12–15   Scape (Figs 12–14) in different standard viewing positions (Fig 12: SVP *c*,
                    Fig 13: SVP *d*, Fig 14: SVP *cd*), Fig 15: propodeum and waist segments of a
                    M. hellenica syntype worker (S-Balkan population).

Petiole rather narrow (PEW/CS 0.249) and low (PEH/CS 0.324), with subparallel but usually weakly convex sides, its frontal and dorsal profiles forming an angle > 90° and meeting in a rounded corner, its dorsocaudal profile moderately sloping down, without pronounced angularity or steps. Postpetiole higher than long and of moderate width (PPW/CS 0.389). Propodeal spines of medium length (SP/CS 0.355), only weakly erected. Central height of propodeal lobe clearly larger than equal-level height of subspinal excavation (MetL 0.232, MetSp 0.160). Sculpture on whole body comparable to that of European *M. specioides*, in the Caucaso-Anatolian population frequently a little stronger. Whole body uniformly light to medium reddish brown.
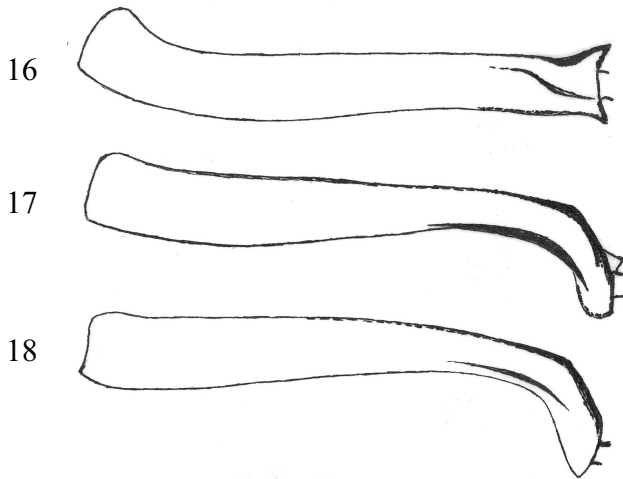
Figs 16–18   Scape of a *M. hellenica* worker of the Caucasian population in different viewing
                    positions (Fig 16: SVP *d*,Fig 17: SVP *cd*, Fig 18: SVP *c*).

Biology and distribution

M. hellenica is a Ponto-Caucasian to East Mediterranean species; its northern range does not extend beyond 46°N (Fig. 22). It is in abundance and apparently also in competitive power the absolutely dominating *Myrmica* species at the Caucasian coast of the Black Sea at altitudes below 600 m a.s.l. but climbs up to 1600 m along the south-facing river valleys of the Great Caucasus. In more southern regions it is frequently found higher than 1600 m. The highest known site from Anatolia, Ovitdagi Gecidi, at 2300 m a.s.l., is situated in the transition zone between the mild Black Sea climate (Trabzon, 30 m, January +6.8 °C) and the very cold NE-Anatolian climate (Erzurum, 1840 m, January –10.0 °C). Interpolation between these two stations and considering a winter temperature decline of 0.5 °C per 100 m increasing altitude predicts the January temperature of this site to be –5 °C and other Anatolian sites between 1600 and 2000 m are only little warmer. The predicted mean air temperature TAS of the *M. hellenica* sites from 1 May to 31 August, shows an enormous amplitude with 17.73 ± 4.02 [7.45,23.83] °C (n = 55). This suggests low winter and summer temperatures not to be among the primary factors limiting the northward expansion of *M. hellenica.* In comparison, the mean summer temperatures of the *M. constricta* sites are only slightly lower but show much less variation with TAS 16.29 ± 1.76 [13.74,22.71] °C (n = 46). Ecological plasticity of *M. hellenica* is also indicated by the high diversity of occupied habitats: sand and gravel banks of rivers, marshy places, open pastures and meadows, open pine wood, deciduous woodland, street margins, gardens and city parks.

Myrmica constricta Karavajev, 1934

Myrmica rugulosa var. *constricta* Karavajev 1934 (27 September); expressely introduced as replacement name for *Myrmica rugulosa* var. *minuta* Karavajev, 1929 [junior primary homonym of *minuta* Ruzsky 1905]; Ukraine: Kiev: Nikloskaya Slobodka.

Myrmica rugulosa v. *slobodensis* Arnoldi, 1934 (10 October); Ukraine: Kiev: Nikloskaya Slobodka [description].

Type material investigated

M. constricta: 9 syntype workers, 3 syntype males and 1 syntype gyne labelled '2770.Coll. Karavaievi' [on each pin, according to Karavajev (1934) from the same nest], 'Kiev Sosnovy les za Niklosk. slobodkoy, Karavajev' [only on one pin] and 'Syntypus *Myrmica scabrinodis constricta* Kar. [red, handwritten label of A. Radchenko] or 'Syntypus *Myrmica rugulosa constricta* Kar.' [red, handwritten label of A. Radchenko].
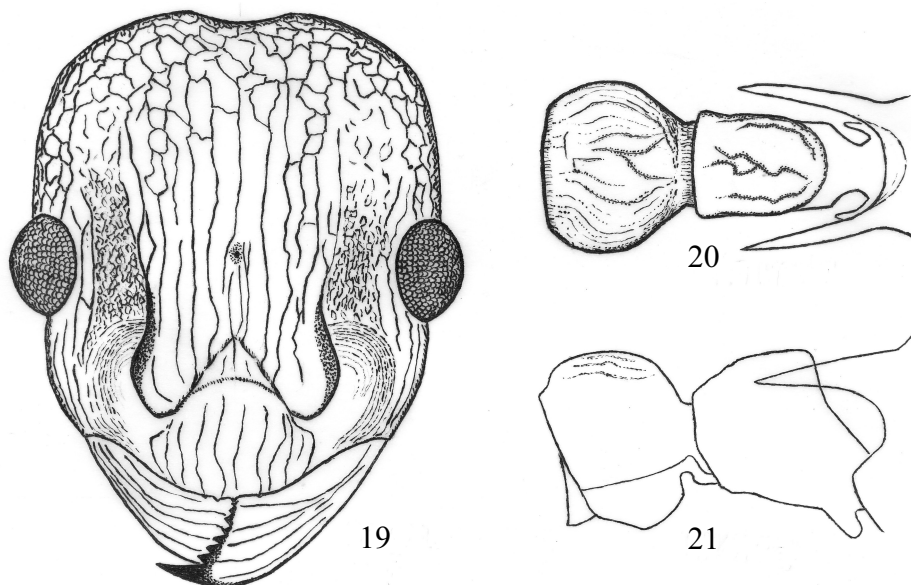
Figs 19–21   *Myrmica constricta* worker; dorsal aspect of head (19) and waist segments in dorsal (20) and lateral (21) view.

Description

— worker (Tab. 3; Figs 19–21): Size very small (mean CS 0.963 mm). Head rather elongated (CL/CW 1.060), in frontodorsal view without central clypeal excavation. Postocular distance smaller than in *M. hellenica* (PoOc/CL 0.414), eye moderately-sized (EYE/CS 0.208). Scape rather long, but shorter than in *M. hellenica* (SL/CS 0.815). Scape base in caudal view angularly curved, without any lamellar outgrowth, only showing suggested dorsal and caudal carinae, comparable to western population of *M. hellenica* (Figs

12–14). Frontal carinae weakly diverging towards the frontal lobes (FL/FR 1.152), their minimum distance rather large (FR/CS 0.384). Petiole narrow (PEW/CS 0.236) and low (PEH/CS 0.320), with subparallel, almost linear sides, its frontal and dorsal profiles forming an angle > 90° and meeting in a rounded corner, its dorsocaudal profile moderately sloping down, without pronounced angularity or steps. Postpetiole higher than long, but rather narrow (PPW/CS 0.373). Propodeal spines significantly shorter than in *M. hellenica* (SP/CS 0.321), only weakly erected. Central height of propodeal lobe clearly larger than equal-level height of subspinal excavation (MetL 0.238, MetSp 0.154). Sculpture on whole body on average weaker than in *M. hellenica*, reticulate structures on posterior vertex in the northern population of *M. constricta* often more pronounced. Whole body uniformly light to medium reddish brown.

Comments

Heading the description of a *Myrmica* sample which is probably conspecific with *M. constricta*, Arnoldi (1934) wrote the caption '*Myrmica rugulosa rugulosa slobodensis* Karavajev 1932 (*M. rugulosa* var. *minuta* Karav. 1929, praeoc.)'. Alternatively, in a morphometric table on page 156, he used the term '*rugulosa* v. *slobodensis*' without giving a genus name. This could suggest that he also intended a ternary naming. Arnoldi's type sample of *M. slobodensis*, a gift of Karavajev, according to Arnoldi collected 'in the environs of Kiev', is most probably a part of the ants that Karavajev collected from the type nest of *M. constricta.* Everything is in favour of this interpretation: all the features Arnoldi mentioned fully match those of Karavajev's type series: very small, pale workers with FL/FR = 1.166, with sculpture differing from *M. rugulosa*, associated by small, short-scaped males with very low petiole. Additionally Arnoldi's naming '**slobod**ensis' gives a clear suggestion to Nikloskaya **Slobod**ka – the locus typicus of *M. constricta*. There are also nomenclatural aspects to be considered. Firstly, Arnoldi's caption is a wrong citation – we cannot find a reference to this name in Karavajev (1932). Secondly, supposing that this material indeed refers to *M. constricta* and accepting a ternary naming, *M. rugulosa* v. *slobodensis* Arnoldi (10 October 1934) is a junior synonym of *M. rugulosa* var. *constricta* Karavajev (27 September 1934) – in Bolton (1995) we find a wrong publication date and hence a wrong synonymy *M. constricta*: '*Myrmica rugulosa* var. *slobodensis* Arnoldi, 1934 ... senior synonym of *constricta*: Karavajev 19**36**:274'. Thirdly, if considering the caption as name giving combination of words, Arnoldi's name would not be available because it is infrasubspecific. Whatever is judged in this complicated case – there is no constellation in which *M. slobodensis* would have priority over *M. constricta*. We have decided in favour of availability and senior synonymy.

Biology and distribution

The actual distribution (Fig. 22) suggests that the postglacial expansion of *M. constricta* started from an Appenino-Balkanian glacial refuge. In the northern parts of its range (north of 52°N) it is apparently only locally found and surely a rare ant, though probably being somewhat under-recorded by misidentification. *M. constricta* almost always is found on sun-exposed, sandy or gravelly soils with significant parts of bare surfaces along margin zones of rivers and lakes. The desiccation of topsoil may be sometimes extreme in these habitats but in deeper soil layers humidity is kept at a sufficient level by ground water influence or tight

substrata. *M. constricta* vanishes after complete closure of the field layer. The primary habitat, and main corridor for postglacial expansion, apparently consists of river banks and sand dunes along glacial stream valleys. This habitat selection should have enabled a very soon and rapid spreading to the north already in the Alleröd. Vegetation development after 9000 B.P. and later anthropogenous destruction of natural river habitats must have led to a strong loss of habitats and should have generated the actual population fragmentation in the northern range. Secondary, anthropogenous habitats are early succession stages at sandy margins of residual lakes and on sandy heaps in brown-coal stripmining regions as it is observed in eastern Saxony. Five records are from coastal sand dunes or sand banks of the Baltic Sea from NE-Germany up to S-Finland. *M. constricta* does not reach high mountain ranges – in S-Italy it goes up to 1000 m. Nests are frequently constructed in the root layer of grass tussocks or under moss crusts and more rarely in bare soil. They can be polygynous, contain up to 1600 workers, may have several entrance holes but show weaker sand ejections compared to syntopic *M. rugulosa* nests. The average nest density in 9 Central European sites was 5.7 nests / 100 m², with a maximum of 20.4 nests / 100 m². Alates occur in the nests from end of July to early October. There is one observation of swarming in late afternoon on a sandy river bank near Melnik, Bulgaria, 30 August 1982. *M. constricta* is apparently largely zoophagous and aggressive to other *Myrmica* species and *Tetramorium* and tries to kill them when these ants approach the nest entrances. On the other hand, there is no interference with the frequently closely associated *Manica rubida*.
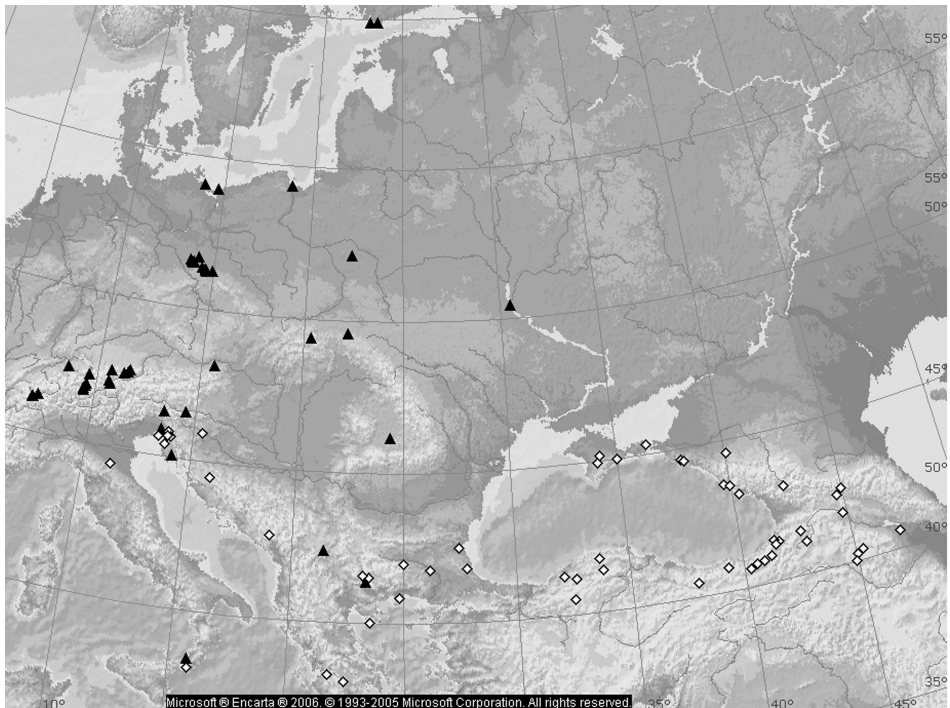

Fig. 22   Distribution map of *Myrmica constricta* (black triangles) and *M. hellenica* (light rhombs).

5. Acknowledgements

6. References

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