A taxonomic revision of the *Formica cinerea* group (Hymenoptera: Formicidae)

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Abstract

A taxomomic revision considering 21 taxa so far attributed to the W Palaearctic *Formica cinerea* group is presented. Five taxa are recognised as *bona species*: *Formica cinerea* Mayr, 1853, *F. fuscocinerea* Forel, 1874, *F. selysi* Bondroit, 1918, *F. georgica* n. sp., and *F. corsica* n. sp. 10 taxa are considered as junior synonyms: *F. cinerea* var. *imitans* Ruzsky, 1902, *F. cinerea* var. *armenica* Ruzsky, 1905, *F. cinerea* var. *subrufoides* Forel, 1913, *F. cinerea* var. *cinereoglebaria* Kulmaticky, 1922, *F. cinerea* var. *iberica* Finzi, 1928, *F. cinerea* var. *italica* Finzi, 1928, *Formica cinerea* var. *novaki* Kratochvil, 1941, and *F. balcanina* Petrov & Collingwood, 1993 as synonyms of *Formica cinerea*, *F. lefrancoisi* Bondroit, 1918 as a synonym of *F. fuscocinerea* and *F. torrentium* Bernard, 1967 as a synonym of *F. selysi*. *F. fusca* var. *cinereorufibarbis* Forel, 1874, does not belong to the *F. cinerea* group but is a synonym of *Formica rufibarbis* Fabricius, 1793. *F. cinerea* workers from the Central Balkans (described as *F. balcanina*) have significantly higher genal setae numbers than their Central European counterparts but a discriminant analysis showed a high frequency of intermediates in the area in between (N Italy and Romania). Hence, *F. balcanina* is more probably a geographical form of *F. cinerea* rather than representing a different species. Because of insufficient original descriptions and failing access to type material, five taxa obviously belonging to the *F. cinerea* group cannot be identified to the species level and are listed under *Incertae Sedis*. A dichotomous key, discriminant functions, comparative tables of morphometric data, and 4 figures to the workers are given.

Zusammenfassung

Eine taxonomische Revision der *Formica-cinerea*-Gruppe (Hymenoptera: Formicidae) – Die Revision behandelt alle 21 Taxa, die bisher der westpaläarktischen *Formica- cinerea*-Gruppe zugeordnet wurden. Fünf Arten werden als *bona species* betrachtet: *Formica cinerea* Mayr, 1853, *F. fuscocinerea* Forel, 1874, *F. selysi* Bondroit, 1918, *F. georgica* n. sp., and *F. corsica* n. sp. 10 Taxa werden als jüngere Synonyme angesehen: *F. cinerea* var. *imitans* Ruzsky, 1902, *F. cinerea* var. *armenica* Ruzsky, 1905, *F. cinerea* var. *subrufoides* Forel, 1913, *F. cinerea* var. *cinereoglebaria* Kulmaticky, 1922, *F. cinerea* var. *iberica* Finzi, 1928, *F. cinerea* var. *italica* Finzi, 1928, *Formica cinerea* var. *novaki* Kratochvil, 1941 und *F. balcanina* Petrov & Collingwood, 1993 als Synonyme von *Formica cinerea*, *F. lefrancoisi* Bondroit, 1918 als Synonym von *F. fuscocinerea* und *F. torrentium* Bernard, 1967 als Synonym von *F. selysi*. *F. fusca* var. *cinereorufibarbis* Forel, 1874 gehört nicht zur *F. cinerea*-Gruppe und ist ein Synonym von *Formica rufibarbis* Fabricius, 1784.

Die *F. cinerea*-Population vom Zentralbalkan (beschrieben als *F. balcanina*) zeigt eine deutlich stärkere Wangenbehaarung als die mitteleuropäische Population. Da aber eine Diskriminanzanalyse eine grosse Häufigkeit intermediärer Phäntotypen im Zwischengebiet (Norditalien und Rumänien) zeigen konnte, ist *F. balcanina* mit grösserer Wahrscheinlichkeit lediglich als geographische Form von *F. cinerea* anzusehen. Wegen unzureichender Originalbeschreibungen und Unzugänglichkeit von Typenmaterial können fünf offenbar zur *F. cinerea*-Gruppe gehörige Taxa nicht bis zum Artniveau identifiziert werden. Sie werden unter *Incertae Sedis* aufgelistet. Ein dichotomer Schlüssel, Diskriminanzfunktionen, vergleichende Tabellen morphometrischer Daten und Zeichnungen der Arbeiter werden präsentiert.

Contents

1.   Introduction

The members of the *Formica cinerea* group form a morphologically and biologically well-defined clade of exclusively W Palaearctic distribution. They are completely unknown from Turkestan, the Pamirs, Tian Shan, and other Central Asian mountain ranges or steppes where the ecological niche of the *F. cinerea* group is occupied by members of the *F. subpilosa* Ruzsky, 1902 group. The most widely distributed species, *Formica cinerea*, reaches its easternmost point in W Siberia at 85.10 E, 52.32 N (DLUSSKY 1967). Five species including *F. corsica* n. sp. and *F. georgica* n. sp. are recognised in the presented revision. Europe is most probably the radiation centre of the group – the Alps and their marginal regions are inhabited by three species.

All members of the group except *F. corsica* n. sp. show a high tendency to build up large polycalic colonies that defend territories against other species – a trait that is rare in

W Palaearctic *Serviformica* species. Similar to wood ants, the *F. cinerea* group species show cooperation during transport of larger prey items. Primary habitats of perhaps all species are xerothermous, sandy or gravelly areas along river valleys with a sparse field layer. The species are well adapted to unstable habitats with frequent shifting of soil material and early stages of plant succession. This strong pioneer performance is enabled by a combination of high dispersal capacity either by flight or as colony fragments, of well-developed potency for independent, single-queen colony foundation, and of rapid shifting to polygyny and polycaly for quickly building up dominant populations on unstable habitat spots. Following river valleys during postglacial immigration, they climbed up to 1800 – 2500 m in the Pyrenees, the Alps, the mountains of the Balkan, and the Caucasus, but left also primary riversides to invade sandy steppe regions, aeolic sand dunes, xerothermous forests on sandy soil, and, finally, several types of anthropogenic habitats. The species of the group need a certain percentage of bare soil surfaces to be superior competitors against other *Serviformica* species. A coverage of herbaceous layer plants of < 40 % is optimal and most of the *F. cinerea* group species will no longer occur if it approaches 90 – 95 %.

Most similar by colony structure and ecology and rather similar in external morphology is the Central Asian *F. subpilosa* group which differs from the *F. cinerea* group mainly by smaller eyes and reduced gular and occipital setae numbers. The status of Nearctic *Formica* taxa such as *F. altipetens* Wheeler, 1913, *F. canadensis* Santschi, 1914, *F. montana* Wheeler, 1910, *F. neocinerea* Wheeler, 1913 and *F. francoeuri* Bolton, 1995, which are believed to be related to the *F. cinerea* group (AGOSTI 1989), is not considered here.

The main aim of this revision is to present an objective, data-based argumentation for heterospecifity or synonymy of the 21 taxa attributed to the *F. cinerea* group, which is only possible if a sufficiently large sample is available in each species. This condition is only given in the worker caste. The rarity or lack of gynes and males in many species does not allow reliable conclusions on the diagnostic value of characters in many species. Hence the scope of this revision is usually restricted to the worker caste.

2. Material, methods, and terminology

The institutions from which material was studied have the following acronyms

NHM Basel	– Naturhistorisches Museum Basel/Switzerland
IRSN Bruxelles	– Institut Royal des Sciences Naturelles de Belgique Bruxelles
MHN Genève	– Muséum d'Histoire Naturelle Genève/Switzerland
SMN Görlitz	– Staatliches Museum für Naturkunde Görlitz/Germany
MCZ Cambridge	– Museum of Comparative Zoology of the Harvard University Cambridge Massachusetts /USA
FMNH Helsinki	– Finnish Museum of Natural History, University of Helsinki/Finland
MZ Lausanne	– Musée de Zoologie Lausanne/Switzerland
MNHN Paris	– Museum National d'Histoire Naturelle Paris
ZMLSU Moskva	– Zoological Museum of the Lomonossov State University Moskva
NHM Wien	– Naturhistorisches Museum Wien

All measurements were made on mounted and dried specimens using a goniometer-type pin-holding device, permitting endless rotations around X, Y, and Z axes. A Wild M10 stereomicroscope equipped with a 1.6x planapochromatic objective was used at magnifications of 50 – 320x. A mean measuring error of ± 1 μm is given for small and well-defined structures such as hair length, but may reach 4 μm for measures > 1700 μm with difficult positioning and high influence of air humidity. To avoid rounding errors, all measurements were recorded in μm even for characters for which a precision of ± 1 μm is impossible. In order to reduce irritating reflections of the cuticular surfaces and to get an improved visualisation of the microsculpture, a plastic diffuser was positioned as close as possible to the specimen.

Setae, also called pilosity or simply 'hairs', are differentiated from pubescence hairs in having a much larger diameter – usually 4 – 8 μm in setae and 1 – 2 μm in pubescence. All seta counts (acronyms beginning with »n«) are restricted to standing setae projecting > 10 μm from cuticular surface as they are seen in a profile view that is specifically defined.

In most of the species groups of *Formica*, body ratios are strongly influenced by allometric growth. In order to make body ratios such as CL/CW, SL/CS, or PEW/CS directly comparable in synoptic tables, hypothetic ratios for the assumption of all individuals having an identical cephalic size of 1400 μm were calculated with the following equations.

CL/CW(1400) = CL/CW – 0.0001179 * (1400-CS)

SL/CS(1400)   = SL/CS   – 0.0001082 * (1400-CS)

EYE(1400)   = EYE   – 0.00006236 * (1400-CS)

The collective parameters of these functions were calculated as arithmetic mean from species-specific data of *Formica candida* Smith, 1878, *F. georgica* n. sp., *F. cinerea* Mayr, 1853, *F. clara* Forel, 1886, *F. clarissima* Emery, 1925, *F. corsica* n. sp., *F. cunicularia* Latreille, 1798, *F. fusca* Linnaeus, 1758, *F. fuscocinerea* Forel, 1874, *F. gagates* Latreille, 1798, *F. gagatoides* Ruzsky, 1904, *F. lemani* Bondroit, 1917, *F. litoralis* Kuznetzov-Ugamsky, 1926, *F. lusatica* Seifert, 1997, *F. kozlovi* Dlussky, 1965, *F. pamirica* Dlussky, 1965, *F. rufibarbis* Fabricius, 1793, *F. selysi* Bondroit, 1918, and *F. subpilosa* Ruzsky, 1902.

The process to discriminate most similar species included (a) the reduction of variance in primary data (SEIFERT 2002), (b) the removal of allometric variance by species-specific functions valid for species pairs (SEIFERT 2002), (c) the calculation of nest sample means and (d) a canonical discriminant analysis provided by the SPSS 10.0 statistical package.

Definition of descriptive terms and numeric characters

CL   –maximum cephalic length in median line; the head must be carefully tilted to the position with the true maximum. Excavations of occiput and/or clypeus reduce CL.

CL(1400) = CL/CW – 0.0001179 * (1400-CS); the allometrically corrected ratio of CL/CW predicted for the assumption of CS = 1400 μm

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

CW   –maximum cephalic width; this is either across, behind, or before 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)

EYE(1400) = EYE – 0.00006236 * (1400-CS)

Full face view — the dorsal aspect of head with both maximum CL and maximum CW in visual plane

Genae — the lateral part of head delimited by anterior margin of eye and anterolateral corner of head capsule

GHL — length of longest seta on dorsal plane of first gaster tergite

nGEN — bilateral sum of setae protruding more than 10 μm from genal margin with head in full face view

nGU — bilateral sum of setae protruding more than 10 μm from cuticular surface of gula as visible in lateral view

nHFEX — sum of setae protruding more than 10 μm from cuticular surface of the extensor profiles of both hind femora

nHFFL — sum of setae protruding more than 10 μm from cuticular surface of the flexor profile of both hind femora

nHT — bilateral sum of setae protruding more than 10 μm from cuticular surface of the extensor profile of hind tibia

nOcc — with maximum head length and width in visual plane, bilateral sum of setae protruding more than 10 μm from occipital margin and the head sides anterior to level of anterior eye margin

nPE — bilateral sum of setae on protruding more than 10 μm from margin of petiole scale dorsal of spiracle in caudal or frontal viewing position

nPN — bilateral sum of setae protruding more than 10 μm from cuticular surface on pronotum

nPR — bilateral sum of setae protruding more than 10 μm from cuticular surface on propodeum and lateral metapleuron (excluding setae fringing the metapleural gland orifice and those on ventrolateral edge of metapleuron).

PEW — maximum width of petiole

PDG — pubescence distance on dorsum of first gaster tergite. The number of pubescence hairs **n** crossing a transverse measuring line of length **L** is counted, hairs just touching the line are counted as 0.5. The pubescence distance PDG is then given by **L/n**. Exact counting is promoted by clean surfaces and flat, reflexion-reduced illumination directed slightly skew to the axis of pubescence hairs. The counting was performed at magnifications of 320 x.

SL — maximum straight line scape length excluding the articular condyle.

SL(1400) = SL/CS – 0.0001082 * (1400-CS); the allometrically corrected ratio SL/CS predicted for the assumption of CS = 1400 μm

3.   Taxonomic significance of characters

Setae numbers on different body surfaces are the leading discriminative characters in this species group. Nest sample means of primary (crude) setae data are frequently sufficient for species separation. In discrimination of most similar species, removal of allometric variance and calculation of multiple discriminants as described by SEIFERT (2002) may be necessary.

Surface characters such as pubescence or microsculpture, as a rule, do not substantially contribute to species separation. The three dimensional structure of microsculpture, however, may serve as accessory discriminator in few cases such as *F. fuscocinerea* vs. *F. cinerea* or *F. fuscocinerea* vs. *F. corsica* n. sp.

Insignificant interspecific differentiation is also visible in shape of mesosoma or petiole. *Formica selysi*, the only species with notable deviation in these characters, is much better recognised by its extreme setae characters.

The use of colour pattern as a taxonomic character of the *F. cinerea* group has a long tradition that is unfortunately maintained (last use e.g. in PETROV & COLLINGWOOD 1993 or CZECHOWSKI et al. 2002). There is no indication that proportions of reddish and dark pigmentation have any taxonomic value. Concolourous blackish colour morphs and such with increased portion of reddish-brown pigmentation in particular on mesosoma and genae may occur within the same local population of the same species as it was observed in *F. cinerea*, *F. fuscocinerea*, *F. selysi*, and *F. georgica*. The syntopic occurrence of colour polymorphism suggests it more likely to have a simple genetic basis rather than representing an environmentally induced modification. Geographic zonality in colour morph frequency (e.g. dark morphs dominating in the northern and reddish morphs in the southern and south-eastern parts of the geographic range of *F. cinerea*) is much better explained by differential selection of genotypes instead of indicating different taxa.

The basic shape and numeric ratios of head such as CL/CW or SL/CS are almost equal in any species of the *F. cinerea* group which contrasts the situation in the *F. fusca* or *F. rufibarbis* group in which notable interspecific differentiation can be found.

4.   Diagnosis of the *Formica cinerea* group

Within the Palaearctic members of the subgenus *Serviformica*, the *F. cinerea* group can be distinguished from any other species complex by a combination of large eyes and most developed occipital and gular pilosity. The extreme values of nest sample means range 0.301 – 0.327 in EYE (1400), 6.0 – 81.3 in nOcc, and 1.3 – 46.3 in nGu.

By morphology, the next related species complex is apparently the *F. subpilosa* group, being also similar in colony structure and habitat selection and taking over in Central Asia just the ecological niche occupied by the *F. cinerea* group in the W Palaearctic. The taxonomic separation of both groups might be questioned in view of the fact that *Formica pamirica* Dlussky, 1965, the most hairy species of the *F. subpilosa* group and a typical river bank species, shows partial overlap with the least hairy species of the *F. cinerea* group in occipital and gular setae numbers. However, a clear separation of both groups and a monophyly of at least the *cinerea* group is supported by eye size differences (Tab. 1) which are significant for p < 0.0001 in any of the 24 possible between-group

comparisons. Four taxa of the *F. subpilosa* group can be distinguished by discriminant functions as different entities (SEIFERT, unpublished results).

Tab. 1 Allometrically corrected eye size index EYE(1400) of 5 species of the *F. cinerea* and 4 species of the *F. subpilosa* group given as arithmetic mean ± standard deviation [lower extreme, upper extreme] and number of specimens

Formica cinerea group:

F. cinerea Mayr, 1853	0.311 ± 0.006 [0.301, 0.323] n = 22
F. fuscocinerea Forel, 1874	0.318 ± 0.005 [0.305, 0.327] n = 39
F. selysi Bondroit, 1918	0.305 ± 0.004 [0.301, 0.314] n = 10
F. corsica n. sp.	0.311 ± 0.007 [0.301, 0.323] n = 15
F. georgica n. sp.	0.307 ± 0.004 [0.301, 0.314] n = 12

Formica subpilosa group:

F. subpilosa Ruzsky, 1902	0.283 ± 0.007 [0.276, 0.297] n = 10
F. litoralis Kuznetzov-Ugamsky, 1926	0.284 ± 0.006 [0.277, 0.297] n = 10
F. clarissima Emery, 1925	0.288 ± 0.009 [0.278, 0.301] n = 14
F. pamirica Dlussky, 1965	0.282 ± 0.006 [0.271, 0.290] n = 15

5. Treatment by species

5.1 *Formica cinerea* Mayr, 1853

Formica cinerea Mayr, 1853; Italy: Tyrol: Bolzano [type investigated]

Formica cinerea var. *imitans* Ruzsky, 1902; Orenburg/W Siberia [synonymy by distribution and by redescription of DLUSSKY 1967]

Formica cinerea var. *armenica* Ruzsky, 1905; Armenia [synonymy by type investigation]

Formica cinerea var. *subrufoides* Forel, 1913; Italy: Tyrol: Bolzano [synonymy by type investigation]

Formica cinerea var. *cinereoglebaria* Kulmaticky, 1922; Poland: Nizina Wielkopolsko-Kujawska [synonymy by distribution; Nomen Nudum; no caste given]

Formica cinerea var. *iberica* Finzi, 1928a; Spain: Pyrenees [synonymy by type investigation]

Formica cinerea var. *italica* Finzi, 1928a; Calabria: Mte Martinello [synonymy by type investigation]

Formica cinerea var. *novaki* Kratochvil, in Novak & Sadil, 1941; Czechia [synonymy by distribution]

Formica balcanina Petrov & Collingwood, 1993; Holotype locality: Serbia: Deliblato Sands [original description, paratype material]

Formica cinerea fuscocinerea Forel, sensu CZECHOWSKI et al. (2002) [misidentification]

Investigated type material:

F. cinerea: 1 type worker, labelled »Tirol G. Mayr \ zu G. Mayr Bd. III. p. 101, 277 \ Type \ *Form. cinerea* det.G. Mayr«, NHM Wien.

F. armenica: 1 lectotype det. Dlussky, labelled by Ruzsky »*F. cinerea* var. *armenica*. M. Arar.«; 1 paralectotype queen det. Dlussky, labelled by Ruzsky »*Form. cinerea* var. *armenica* Ruzsky M. Ararat Satunin«, both in ZMLSU Moskva.

F. subrufoides: 2 worker types labelled by Forel himself as »*F. cinerea* Mayr v. *subrufoides*, type Forel, Bozen (Tirol) 20. Juli (Forel)« and 1 worker type labelled »*F. cinerea* Mayr v. *subrufoides*, type, Bozen (Tyrol)«, both MHN Genève.

F. iberica: 1 worker type labelled »Pyren. coll. G. Mayr \ *F. cinerea* det G. Mayr \ Tipo \ *F. cinerea* var. *iberica* Finzi 28 \ M.C.Z. CoType 28815«, MCZ Cambridge.

F. italica: Two worker syntypes labelled »Mte. Martinello Stauder 5.6.13 \ Tipo \ *F. cinerea* var. *italica* Finzi 28 \ M.C.Z. CoType 28814«, MCZ Cambridge.

F. balcanina: Three paratype workers from N Greece, labelled by Collingwood »DROSOPYGI I.IX.84« stored in SMN Görlitz.

Morphometrically investigated material

– **typical *F. cinerea*** (53 samples with 137 individuals): ARMENIA: Mount Ararat, leg. Satunin, 1900, lectotype *F. armenica*; AUSTRIA: Kärnten: Arnoldstein, 1994.05.22; CZECHIA: Brno, Morava river, 1940; FINLAND: Hanko, Kolaviken-E, ca. 1960; Koverhar, ca. 1960; Uimaharju 10 km NE, 1996.07.13; FRANCE: Grande Chartreuse, ca. 1910, paratype *F. lefrancoisi*; GERMANY: Bayern: Lenggries 3 km N, 1994.07.02 201; Bayern: Lenggries 9 km S, 1994.08.02; Bayern: Linderhof 1 km WSW, 1995.06.17; Bayern: Mittenwald-S, Isar, 1993.06; Bayern: Vorderriss 2 km E, 1994.07.08 g18 (samples No. g6, g9, g18); Bayern: Wallgau, Isar, 1993.06.08; Brandenburg: Lauchhammer-West,1982; Lauchhammer-West, 1986.08.07; Sachsen: Halbendorf/Spree, 1964.05.29; Sachsen: Lömischau, 1959.06.10; Lömischau, 1962.04.25; Lömischau, 1962.05.30; Lömischau, 1963.05.18; Lömischau, 1965.07.09; Sachsen: Neudorf/Spree, 1965.09.05; Sachsen: Wartha 1 km E, Olba/Halde, 1963.07.06; Sachsen-Anhalt: Klein Schmölen, 1993.08.11; Sachsen-Anhalt: Mücheln 1 km N, 1996.05.12 (sample No, 12,20); ITALY: Bologna, Biano, coll. G. Mayr, before 1900; Bologna, coll. G. Mayr, before 1900; Bolzano, before 1913, type *F. subrufoides*; Mte. Martinello, 1913, type *F. italica*; Tyrol: Bolzano, before 1854, type *F. cinerea*; Tyrol: Ura 6 km SW, 2002; POLAND: Breslau: Raudten 1919.09.30; Novy Targ: Lopuzsna, 1989.09.13; Pieniny Mts.: Kroscienka 1989.09.15; RUSSIA: Central Caucasus: Itkol, 1980.07.08; N Caucasus: Mineralniye Vody-1980.07.06; SLOVAKIA: east of Kosice: Michalovce 3 km N; 1983.08.29; east of Kosice: Vinne 1 km W, 1983.08.29; SPAIN: Huesca: Castiello de … (illegible), 1966.06; Pyrenees: before 1900, type *F. iberica*; SWEDEN: Öland: Byrums Sandvik, 1992.06.14 (samples No 1, 20); SWITZERLAND: Binn, 1942.08.30; Valais: Fully, 1994.05.16 (samples No 6, 31, 101, g77); Il Castro, 2000.04.09; Lugano, before 1900 (Forel); Valais: Pfynwald, 1996.05.18 (samples No P19, P20); Val Bavona, 1936.08.02.

– **intermediates between the nominal populations of *F. balcanina* and *F. cinerea*** (6 samples with 22 individual workers): BULGARIA: Velingrad vic., Svetka Petka,1983.07.14; ITALY: Trentino: Latsch: St.Martin, 1999.07.25; Trentino: Lana 2.3 km ESE, 2002 samples

No. 1; ROMANIA: Delta of Danube: Letea Forest, 1985.08; Medias-Birthelm, 1987.07.22; Siebenbürgen: Seidlitz, (coll. G. Mayr, before 1900).

– **nominal population of *F. balcanina*** (11 samples with 28 individual workers): BULGARIA: Melnik, 1982.08.28; Melnik, 1989.08.21; Melnik vic., Karlanovo, 1983.07.07; Melnik vic., Rozen, 1982.08.27; Rhodopy: Batchkovo vic., 1982.08.13; Slatni Pjasazi, 1970.07.17; GREECE: Drosopyghi, 1984.09.01; ITALY: Trentino: Lana 2.3 km ESE, 2002 (samples No. 2); ROMANIA: Retezat: Cimpusel, 1988.07.03; SERBIA: Osijec, 1984.09.16; UKRAINE: Kiev: southern city wall, 1988.09.28.

Description

– **typical worker population from outside the Balkans** (Fig. 1, Tabs. 2, 3): Medium-sized, mean CS 1363. Head moderately elongated, CL/CW(1400) 1.123. Scape of average length, SL/CS(1400) 1.050. Clypeus finely microreticulate and with a median keel. Frontal triangle finely transversally microcarinulate and with about 35 – 70 short pubescence hairs. Eyes with few scattered microsetae of 4 – 7 µm length. Dorsal plane of scape without, genae without or only occasionally with few setae. Setae numbers on remaining head, pronotum, mesonotum, petiole and gaster high; setae numbers on propodeum lower. Nest sample means of setae numbers: genae 0 – 3, occipital margin in dorsal aspect 24 – 62, gula 7 – 23; propodeum and lateral metapleuron 2 – 27, extensor profile of both hind femora 0 – 2.5, flexor profile of both hind femora 14 – 34; extensor profile of hind tibae 0 – 1. In anterior view, number of setae surpassing petiolar scale margin above spiracular level 9 – 27; within all these fringe setae, setae projecting dorsad about as numerous as those projecting laterad, the latter almost always present. Lateral mesonotum anterior of metathoracic spiracle densely microcarinulate, with an mean carinular crest distance of 4 – 5 µm; mean width of carinulae equal or slightly smaller than width of smooth interspaces (Fig. 1.). Transition between dorsal and caudal profiles of propodeum in larger workers broadly convex, in smaller workers more angular and under an angle of 140°. Dorsal crest of petiole in frontal view usually convex, in larger specimens frequently forming a blunt angle of 140°. Petiole scale in lateral aspect rather thick, wedge-shaped, with convex anterior and rather straight posterior profile. Head, mesosoma, petiole, and gaster covered by a dense silvery pubescence, PDG 6.3 – 7.5. Colour polymorphism. Dark morph: head, mesosoma, petiole and gaster blackish, scape, mandibles, and legs to a varying degree reddish brown. Reddish morph: whole body reddish brown, vertex and gaster with a blackish colour component. For morphometric data of 134 workers see Tab. 2.

– **worker population from the Balkans:** Differs from workers of the nominal population by the following characters. Slightly shorter scape, SL/CS(1400) 1.024. Nest sample means of setae numbers larger: nGEN 8 – 22, nOCC 55 – 81, nGU 27-46, nHFFL 29 – 47, nPE 19 – 28. For morphometric data of 28 workers see Tab. 2.

Comments

Formica cinerea is the only species of the group with a very extended distributional range stretching from N Spain to W Siberia (Tjumen, 65.28 E, 57.09 N; Barnaul, 83.45 E, 53.20 N; Bijsk 85.10 E, 52.32 N; DLUSSKY 1967) and from S Greece north to Finland at 65 °N.

Within this huge range, only weak geographic variation exists – with the exception of a steeply positive gradient of genal pilosity from Central Europe to the Central Balkans. In the Pyrenees, the Alps and the Caucasus the overall abundance of *F. cinerea* is clearly decreased by the competitive pressure of *F. selysi*, *F. fuscocinerea*, or *F. georgica* n. sp. No observations of *F. cinerea* are known so far from the British Isles. *F. cinerea* is apparently the only species of the group occurring in Czechia, Poland, and the steppes of S Russia, making the synonymy of the following taxa, from which no type material could be investigated, sufficiently probable: *F. imitans* Ruzsky, 1902, *F. cinereoglebaria* Kulmaticky, 1922, and *F. novaki* Kratochvil, 1941.

Without giving an explanation, Czechowski et al. (2002) have named the *F. cinerea* population in the mountain areas of S Poland as *F. cinerea* subsp. *fuscocinerea* Forel. I could investigate two worker samples from this region which were lighter morphs, structurally indistinguishable from *F. cinerea* and comfortably placed within the *F. cinerea* cluster by a canonical discriminant vector: $+0.56$ ($p = 0.021$) in the sample Nowy Targ: Lopuzsna, 1989.09.13 and $+1.02$ ($p = 0.002$) in the sample Pieniny Mts.: Kroscienka, 1989.09.15 (see following section). Furthermore, on ground of zoogeographical arguments, *F. fuscocinerea* is not expected to occur in S Poland.

F. cinerea var. *imitans* Ruzsky, 1902 has been considered by DLUSSKY (1967) as a subspecies of *F. cinerea* which replaces the nominal subspecies in the steppes of the Ukraine and S Russia. Dlussky, who fixed a »lectoergatotype« in a worker specimen from near Orenburg/W Siberia, could only propose colour characters as a difference between *F. imitans* and *F. cinerea*. The fact that sympatric colour polymorphism is known within any species of the group except *F. corsica* n. sp., invalidates Dlussky's colour argument. According to my own observations, *Formica cinerea* var. *imitans* is most probably a reddish ecomorph of *F. cinerea* that became absolutely dominant in the continental steppe zone. Such reddish ecomorphs locally emerge within the Central European range of *F. cinerea* and do then occur syntopically with the dark morph under apparently equal environmental conditions, which suggests a genetic basis of the colour polymorphism. The three sites with syntopic occurrence of reddish and dark morphs (Pfynwald/Valais, Lauchhammer/Brandenburg, Merseburg/Sachsen-Anhalt) are 1200 to 1600 km away from the next *F. imitans* site in Dlussky's map and also transitionary colour forms have been found in Sachsen. If we accept Dlussky's hypothesis of referring »*F. imitans*« to the population in the steppe zone eastwards from 28° E and »*F. cinerea*« to the population W, NW and SW of this area, a comparison of 65 nest samples of »*F. cinerea*« and of 5 nest samples of »*F. imitans*« gives the following situation (arrangement of data: »*F. cinerea*« / »*F. imitans*«): CS 1346 ± 139 / 1474 ± 71, CL/CW 1.123 ± 0.018 / 1.124 ± 0.006, SL/CS 1.045 ± 0.025 / 1.045 ± 0.006, nGEN 3.7 ± 6.6 / 4.2 ± 2.7, nOCC 44.7 ± 11.8 / 51.9 ± 9.6, nGU 18.7 ± 7.5 / 23.4 ± 10.7, nPR 11.0 ± 5.2 / 11.4 ± 8.7, nPE 17.6 ± 4.6 / 20.3 ± 5.2, nHFEX 0.1 ± 0.4 / 0.1 ± 0.1, nHFFL 25.8 ± 7.5 / 24.8 ± 6.5, nHT 0.2 ± 0.4 / 0.4 ± 0.5. The few weak differences are insignificant when compared to the differences usual between related species of the *F. cinerea* group. The larger head size data of the »*F. imitans*« samples may be accidental or a result of differing environmental conditions (e.g. higher seasonal temperatures in the soils of continental steppes). Attempts to separate western »*F. cinerea*« and eastern »*F. imitans*« by a canonical discriminant function using allometrically corrected data of 10 characters completely failed.

F. cinerea var. *armenica*: The lectotype worker represents a lighter-coloured form of *F. cinerea*. The specimen has the anterior head and pronotum lighter (yellowish brown) and is according to its morphometric data a member of the eastern *F. cinerea* (»*F. imitans*«) population: CS 1538, CL/CW(1400) 1.123, SL/CS(1400) 1.037, nGEN 2, nOCC 52, nGU 23, nPR 4, nPE 22, nHFEX 0, nHFFL 34, nHT 0.

F. cinerea var. *subrufoides*: The sample means of morphometric data of three syntype specimens are fully consistent with the *F. cinerea* conception except for the subaverage absolute size: CS 1142.2, CL/CW(1400) 1.131, SL/CS(1400) 1.056, nGEN 0.3, nOCC 42.7, nGU 14.7, nPR 10.7, nPE 15.7, nHFEX 0.0, nHFFL 21.7, nHT 0.0.

F. cinerea var. *iberica*: The type specimen shows a strong reddish colour component. Except for the longer setae on gastral tergites, it matches in any character the conception of F. cinerea: CS 1540, CL/CW(1400) 1.115, SL/CS(1400) 1.021, nGEN 0, nOCC 39, nGU 18 (13 setae still attached to the gula, 5 setae disrupted but conserved within the glue patch on the card board), nPN 50(left half 25, right half damaged by pinning), nMN 23, nPR 5, nPE 14, nHFEX 0, nHFFL 17, nHT 0, GHL 135.

F. cinerea var. *italica*: The two type specimens are of large size but are in any other character within the usual range of *F. cinerea*. Their sample means are: CS 1674.7, CL/CW(1400) 1.112, SL/CS 1.058, nGEN 0.0, nOCC 29.5, nGU 11.0, nPR 5.0, nPE 16.5, nHFEX 0.0, nHFFL 26.5; nHT 0.0.

F. balcanina: It is obvious that the population from the Central Balkans (= *balcanina*) differs from the nominal population of *F. cinerea* by much more abundant genal setae. On the other hand, there are many intermediate samples in N Italy and Romania which occur sympatrically with typical *F. cinerea* and *F. balcanina* and even specimens from S Bulgaria and the north central Caucasus are phenotypically intermediate. Any attempt to define an interspecific border between *Formica balcanina* and *Formica cinerea* using discriminant functions testing the existence of only two, but variably composed, preestablished groups failed. The most realistic solution, a canonical discriminant D(11) computing CS and allometrically corrected data of CL/CS, SL/CS, nGEN, nOCC, nGU, nPR, nPE, nHFEX, nHFFL and nHT supported the hypothesis that intermediate phenotypes are frequent (Tab 2). This suggests easy and fertile hybridisation of *F. cinerea* and *F. balcanina* in wide overlap areas in N Italy, the Balkans and possibly also N Caucasus. As a consequence both taxa should not be considered as heterospecific. This case clearly differs from the situation in certain parapatric species in which differential characters remain stable also in close proximity to the interspecific border line defined by the centre of a very narrow contact zone (SEIFERT 1995). A canonical discriminant function considering two instead of three groups (by incorporating the 7 intermediate samples into the *F. cinerea* cluster) predicted that *F. cinerea* and *F. balcanina* simultaneously occurred within the same polycalic colony system, which is a further argument against heterospecificity.

Tab. 2 Nest sample means of morphometric data of different groups of *Formica cinerea* to test the species conceptions of *Formica cinerea* and *F. balcanina* equivocally proposed by PETROV & COLLINGWOOD (1993) and SEIFERT (1996). Established groups: samples belonging to the *cinerea* conception (mainly from outside the Balkans), samples belonging to the *F. balcanina* conception (mainly from the Balkans) and samples not fitting either conception (intermediate samples from mainly N Balkans and N Italy). n = number of nest samples, i = number of measured individuals; arrangement of data: arithmetic mean ± standard deviation [lower extreme, upper extreme]. p = significancy level in a modified *t* test with corrected degrees of freedom according to WELCH (1947). D(11) = canonical discriminant computing CS and allometrically corrected data of CL/CS, SL/CS, nGEN, nOCC, nGU, nPR, nPE, nHFEX, nHFFL and nHT

	»*F. cinerea*« (n = 52, i = 134)	p	»*F. cinerea* x *balcanina*« (n = 7, i = 22)	p	»*F. balcanina*« (n = 11, i = 28)
D(11)	−1.78 ± 0.97 [−3.25, 0.86]	0.0001	2.16 ± 0.97 [0.80, 3.57]	0.0001	9.57 ± 1.39 [7.72, 11.32]
CS	1354 ± 144 [1003, 1675]	n.s.	1356 ± 172 [1099, 1648]	n.s.	1365 ± 101 [1160, 1518]
CL/CW (1400)	1.122 ± 0.020 [1.071, 1.165]	n.s.	1.119 ± 0.010 [1.105, 1.135]	0.05	1.130 ± 0.008 [1.120, 1.143]
SL/CS (1400)	1.050 ± 0.022 [0.985, 1.098]	n.s.	1.042 ± 0.017 [1.009, 1.058]	0.1	1.024 ± 0.025 [0.989, 1.059]
nGEN	0.66 ± 0.76 [0.0, 2.5]	0.001	6.00 ± 2.32 [3.0, 8.5]	0.001	17.01 ± 5.01 [8.0, 22.0]
nOCC	40.4 ± 8.2 [24.3, 62.0]	0.002	51.6 ± 5.9 [41.0, 57.5]	0.002	64.1 ± 7.4 [55.3, 81.3]
nGU	15.7 ± 3.7 [2.0, 23.0]	0.01	21.6 ± 4.0 [17.5, 28.5]	0.001	33.4 ± 6.6 [26.7, 46.0]
nPR	10.6 ± 5.4 [2.0, 27.0]	n.s.	13.3 ± 5.9 [6.0, 20.6]	n.s.	11.7 ± 5.4 [7.0, 21.0]
nPE	16.4 ± 4.0 [9.3, 26.8]	n.s.	19.6 ± 5.1 [12.5, 26.0]	n.s.	23.0 ± 3.2 [18.7, 28.0]
nHFEX	0.07 ± 0.36 [0.0, 2.5]	n.s.	0.11 ± 0.20 [0.0, 0.5]	n.s.	0.25 ± 0.38 [0.0, 1.0]
nHFFL	22.8 ± 4.6 [14.3, 34.0]	0.001	29.2 ± 3.0 [24.7, 33.6]	0.001	38.2 ± 6.0 [28.7, 47.3]
nHT	0.18 ± 0.34 [0.0, 1.3]	n.s.	0.41 ± 0.38 [0.0, 1.0]	n.s.	0.69 ± 0.77 [0.0, 2.3]

5.2 *Formica fuscocinerea* Forel, 1874

Formica fusca var. *fuscocinerea* Forel, 1874; Switzerland: Einsiedeln near Zürich and Zürich [types investigated]

Formica lefrancoisi Bondroit, 1918; Switzerland: Zürich [synonymy by investigation of

type material; lectotype by present designation]

Formica lefrancoisi Bondroit, 1918, sensu KUTTER (1977)

Formica lefrancoisi Bondroit, 1918, sensu SEIFERT (1996)

Investigated type material:

Formica fuscocinerea: 1 lectotype worker (with CW = 1143 µm, designated by B. Seifert 1999) and paralectotype worker together with a gyne on the same pin, labelled by Forel »*Formica cinerea* Mayr var. *fusco-cinerea* Forel, ♀ type Zürich, ♀ type Einsiedeln«; 1 paralectotype worker and 2 paralectotype gynes on another pin labelled by Forel »*cinerea* ♀, Zürich; *F. fusco-cinerea* Forel«; all material stored in MHN Genève.

Formica lefrancoisi: 1 worker lectotype, designated by Seifert in 1994, and labelled »Zürich Forel«; 2 worker paralectotypes with locality label »Grande Chartreuse«, all material stored in IRSN Bruxelles.

Morphometrically investigated material (37 samples with 119 individuals):

AUSTRIA: Innsbruck: Arzl, 1994.04.03; Kirchberg (16.00 E,47.36 N), 1901; Matzleinsdorf, 2002.07.31; Rattenberg 3 km ENE, 1994.07.05; St. Pölten-Spratzern, 1994.05.13 (samples No. 012, 092); St. Pölten-Wagram, 1994.05.13 (sample No. 033, 060); Vorarlberg: Feldkirch, 1940; GERMANY: Bayern: Augsburg-S, 1994.07.01 (samples No. 013, 074, 097); Frauenwinkel/Salzach, 1995.06.22; Bad-Tölz-S, 1992.04.05; Lenggries 3 km N, 1994.07.02 (samples No. 073, 207, 208); Lenggries-N, 1995.08.06; Lenggries-N, 1995.09.05; Linderhof 1 km W, 1995.06.16 (samples No. 8, 9); Pfaffenhofen, 2002.07.29 (samples No. 647, 651 – 653); Vorderriss 2 km E, 1994.07.08 (samples No. 6, g14, g15, g86); Weilheim 5 km W, 1995.07.12; ITALY: Bologna, coll. G. Mayr, before 1900; SWITZERLAND: Luzern, 1963.06; Zürich: Einsiedeln, before 1875; Zürich, before 1875 (lectotype *F. lefrancoisi*); Zürich, before 1875, lectotype *F. fuscocinerea*.
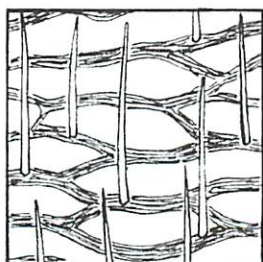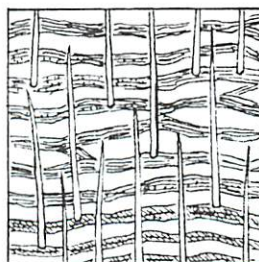

Fig. 1   Fig. 2

Fig. 1 *Formica cinerea*, microsculpture and pubescence on lateral mesonotum anterior of metathoracic spiracle. Scale bar: 20 µm

Fig. 2 *Formica fuscocinerea*, microsculpture and pubescence on lateral mesonotum anterior of metathoracic spiracle. Scale bar: 20 µm

Description of worker (Fig. 2, Tab. 3):

Size slightly below the *F. cinerea* group average, mean CS 1301. Head moderately elongated, CL/CW(1400) 1.129. Scape of average length, SL/CS(1400) 1.040. Clypeus with a median keel, finely microreticulate, its anteriormost portion finely longitudinally microcarinulate. Frontal triangle finely transversally microcarinulate and with 40 – 50 short pubescence hairs. Eyes with few scattered microsetae of 4 – 7 µm length. Dorsal plane of scape and genae without setae. Setae numbers on remaining head, pronotum, mesonotum, and propodeum lower, those on gula and petiole much lower than in *F. cinerea*. Nest sample means of setae numbers: genae 0 – 0.7, occipital margin in dorsal aspect 6.3 – 45.8, gula 3.7 – 12.3; propodeum 0 – 6.5, extensor profile of both hind femora 0 – 0.3, flexor profile of both hind femora 4.0 – 21.7; extensor profile of hind tibiae 0 – 1.0. In anterior view, number of setae surpassing petiolar scale margin above spiracular level 0.7 – 10.7; within all these fringe setae, setae projecting dorsad clearly more numerous than those projecting laterad, the latter frequently entirely absent. Overall impression of mesosomal surface intermediate between the conditions in *F. fusca* and *F. cinerea*. Microsculpture of lateral mesonotum anterior of metathoracic spiracle in the form of a fine network of much elongated, ellipsoid or acutely rhomboid meshes. The inner surface of the meshes is flat and shining; the ripples of the net are not thicker than 2 µm thick while the average small diameter of a mesh is about 8 µm – i.e. the ratio of sculptured surface against shining surface is 1 : 4 or smaller (Fig. 2). Transition between dorsal and caudal profiles of propodeum broadly convex or angulate convex. Petiole scale in upper third much wider than basally, its dorsal crest in frontal view convex or forming an angle of 140°; in lateral aspect rather thick, wedge-shaped, with convex anterior and rather straight posterior profile. Head, mesosoma, petiole, and gaster covered by an appressed silvery pubescence, PDG 6.8. Colour polymorphism. Morphs with a yellowish-red colour component on mesosoma and anterior head more frequent than in Central European population of *F. cinerea*; entirely dark, intermediate, or patchily coloured morphs can occur syntopically. For morphometric data of 119 workers see Tab. 3.

Comments

The known range of *Formica fuscocinerea* includes the Alps and their foothills from 8.30 E to 16.49 E and the N Apennine. Most probably its postglacial spreading started from a Balkan and/or Italian refuge centre. *F. fuscocinerea* seems to be rare or absent in the western Alps and no records from more than 150 km north or east of the Alps are known so far which is most probably caused by competitive pressure of *F. cinerea* and/or *F. selysi*. In Switzerland, Germany and Austria the 55 known sites are situated in altitudes between 200 and 1050 m a.s.l. and concentrate to river valleys where sandy river banks are obviously its primary natural habitat. However, any kind of open anthropogenic habitat with a high percentage of bare soil surface may be inhabited, including artificial structures made with stones or concrete along rivers, streets or railway lines. *F. fuscocinerea* also occurs as a dominant pavement ant in the stone deserts of big city centres (e.g. Zürich, Innsbruck, Linz, Wien) where it feeds on dead insects at the margins of car roads.

F. fuscocinerea is definitely no synonym of *F. cinerea* or *F. fusca*. As a diagnostic difference to *F. cinerea*, the three syntype workers of *F. fuscocinerea* from Zürich show a setae reduction on ventral head (nGU 6, 8, 4), have only few setae on dorsal margin of scale (nPE 4, 9, 0), none on lateral scale margin, and show the typical microsculpture on lateral mesonotum anterior of metathoracic spiracle (Fig. 2). These specimens belong to the species that has been called *Formica lefrancoisi* Bondroit, 1918 from KUTTER (1977) to SEIFERT (1996).

The type series of *F. lefrancoisi* includes two species. The lectotype worker from Zürich (a gift of Forel to Bondroit) is in all characters including mesosomal microsculpture coincident with the types of *F. fuscocinerea*. The two paralectotype workers from Grande Chartreuse/France are weakly haired *F. cinerea*.

The heterogenous W Palaearctic nest samples of *F. cinerea* could be convincingly separated from those of *F. fuscocinerea* by a canonical discriminant D(10) using CS and allometrically corrected data of CL/CS, SL/CS, nGEN, nOCC, nGU, nPR, nPE, nHFEX and nHFFL :

F. fuscocinerea   −2.487 ± 0.996 [−4.16, −0.01] (n = 37)
F. cinerea   +1.841 ± 0.993 [−0.09, +3.89] (n = 70).

99.1 % of all subjective determinations are confirmed by the function. Only one sample of *F. fuscocinerea* from Germany: Pfaffenhofen 2002.07.29 (No 647) is misidentified. The type samples are clearly allocated to either cluster and have the following D(10):

−3.17 lectotype of *F. lefrancoisi* from Zürich (p < 0.001),

−2.95 paralectotype of *F. fuscocinerea* from Zürich (p < 0.001),

−2.36 lectotype and paralectotype of *F. fuscocinerea* from Einsiedeln (p < 0.001),

+0.56 two paralectotypes of *F. lefrancoisi* from Grande Chartreuse (p = 0.020),

+0.84 holotype of *F. iberica* from the Pyrenees (p = 0.007),

+1.30 two syntypes of *F. italica* from Mte. Martinello (p = 0.001),

+1.36 holotype of *F. cinerea* from Tyrol (p < 0.001),

+1.91 three paratypes of *F. balcanina* from Drosopygi (p < 0.001),

+2.16 four syntypes of *F. subrufoides* from Bolzano (p < 0.001) and

+3.74 type of *F. armenica* from Armenia (p < 0.001).

A less complex discriminant function correctly identifying each sample within and near to the geographic range of *F. fuscocinerea* is given in section 8.

5.3 *Formica selysi* Bondroit, 1918

Formica cinerea var. *selysi* Bondroit, 1918; France: Alpes Maritimes: Saint Etienne de Tinée [types investigated]

Formica torrentium Bernard, 1967; France: Hautes-Pyrénées: Barèges [synonymy by investigation of types]

Investigated type material:

F. selysi: 8 worker syntypes labelled »St. Etienne de Tinée Alp. mar. \ 1150 m \ *Formica v. selysi* type Bondr.«, IRSN Bruxelles.

F. torrentium: 2 gynes on the same pin, labelled »Bareges 4.7. 7.46 \ types ♀ de torrentium \ No. 169 *Formica torrentium*«, MNHN Paris. The top specimen with CW = 1955 μm and PEW = 1034 μm is fixed by present designation as lectotype while the lower paralectotype shows CW = 2010 μm and PEW = 1115 μm.

Morphometrically investigated worker material (34 samples with 78 individuals): AUSTRIA: Forchach 1.5 km S, 1994.05.01; Prutz 3 km N, 1994.05.15; Starkenbach 1 km SW, 1994.05.15; FRANCE: Bedarrides (44.02 N, 4.53 E), before 1960; Brout-Vernet (46.11 N, 3.16 E); before 1960; Cannes, coll. Bondr., before 1920; Capbreton (43.49 N, 1.26 W), coll. Bondr, before 1920; Cluses/Arve, 1990.07.18; Crorenz, 1985.07.10; Gedre (42.47 N, 0.01 E), coll. Bondroit, before 1920; Haute Savoie: Morzine; Jausiers (44.25 N, 6.44 E), coll. Bernard; La Bourboule (45.35 N, 2.43 E); La Teste (44.47 N, 1.06 W), coll. Bondr.; Salanches coll. Collingwood, before 1970; Alpes Maritimes: St. Etienne de Tinée, before 1920; GERMANY: Baden-Württemberg: Burkheim, 1993.05.01; Baden-Württemberg: Kaiserstuhl: Oberbergen 2 km N, 1990.07 (samples BA1, BB5, BB6); Bayern: Wallgau/Isar, 1993.08.21; Bayern: Lenggries 3 km N, 1994.07.02; Bayern: Linderhof 1 km W, 1995.06.16; Bayern: Linderhof 4 km WSW, 1995.06.17; Bayern: Mittenwald 1 km S, 1995.06.20; Bayern: Mittenwald: Krün, 1995.06.20; Bayern: Vorderriss 2 km E, 1994.07.08; ITALY: Bologna, coll. G. Mayr, before 1900; SWITZERLAND: Genève, coll. Bondroit, before 1920; Il Fuorn, 1998.07.26 (samples No 198, 202); La Punt 2.0 km NE, 1998.07.29; Valais: Pfynwald, 1990.07.14 (samples No. 11, 49).

Description of worker (Tab. 3):

Medium-sized, mean CS 1368. Head moderately elongated, CL/CW(1400) 1.127. Scape of average length, SL/CS(1400) 1.052. Clypeus with a median keel, finely microreticulate, its anteriormost portion finely longitudinally microcarinulate. Frontal triangle finely transversally microcarinulate and with 40 – 50 short pubescence hairs. Eyes with few scattered microsetae of 4-7 μm length. Dorsal plane of scape without setae. Most hairy species of the group. All surfaces of head, mesosoma, petiole, gaster, coxae and legs strongly setose. In contrast to all other species, extensor side of femora with semierect setae. Nest sample means of setae numbers: genae 2.5 – 26.3, occipital margin in dorsal aspect 27.5 – 67.0, gula 18.0 – 59.3, propodeum 17.8 – 54.5, extensor profile of both hind femora 7.0 – 44.0, flexor profile of both hind femora 28.0 – 60.0; extensor profile of hind tibiae 5.5 – 18.5. In anterior view, number of setae surpassing petiolar scale margin above spiracular level 15.5 – 51.3. Transition between dorsal and caudal profiles of propodeum broadly convex. Petiole scale narrower than in other species, its dorsal crest in frontal view convex; petiole scale in lateral aspect thicker than in other species, with convex anterior and rather straight or slightly convex posterior profile and a rather blunt apex. Head, mesosoma, petiole, and gaster covered by a dense, appressed, silvery pubescence, PDG 7.0. The pubescence hairs on gaster tergites thicker than usual, having 3 – 4 μm diameter, which produces at lower magnifications a silvery surface impression. Colour of

cuticula more superimposed by the silvery pubescence than in other species and less varying than in *F. cinerea*. A frequent colouration is: vertex, mesosoma, petiole and gaster dark brown, coxae, appendages, lateral and anterior head medium or lighter brown. Lighter morphs with increased reddish colour component locally occurring (France: Massive Central, Switzerland: Wallis). For morphometric data of 78 workers see Tab. 3.

Comments

Formica selysi cannot be confused because of its extreme pilosity. In the worker, nest sample means of nHFEX range 7.0 – 44.0 while the upper extreme known in 125 samples of other species is 2.5. Similar is the situation in nHT (Tab. 2). Gynes are as easily identified: individual values of nHFEX range 11 – 47 and those of nHT 5 – 22. Among 29 investigated gynes of other species (7 of *F. fuscocinerea*, 1 of *F. balcanina*, 1 of *F. georgica* n. sp., and 20 of *F. cinerea*) only one gyne of *F. cinerea* showed one small hair in the nHFEX position and most probably no species will approach the data of *F. selysi* if many more specimens would have been investigated.

The lectotype and paralectotype gynes of *F. torrentium* from the Pyrenees diagnostically show nHFEX 30 and 28 and nHT 17 and 11. They are in any morphometric character tested consistent with 12 gynes from other regions – sequence of data: lectotype *F. torrentium*, paralectotype *F. torrentium* (range of variation from outside the locus typicus): CS 1947, 1998 (1912 – 2023); CL/CW 0.991, 0.988 (0.961 – 1.004); SL/CS 0.829, 0.847 (0.819 – 0.888); ML/CS 1.859, 1.823, (1.762 – 1.938); PEW/CS 0.531, 0.558 (0.519 – 0.576); nOCC 64, 54 (49 – 67); nGEN 16, 16 (8 – 24); nGU 35, 30 (22 – 45); nPR 59, 42 (27 – 58); nPE 30, 28 (24 – 38); nHFEX 25, 20 (11 – 47); nHFFL 48, 34 (32 – 60); nHT 17, 11 (5 – 22).

The known geographic range of *Formica selysi* stretches from the Pyrenees (1.26 W) across S France to the Alps (11.51 E) and from the N Apennine (44.20 N) to the Vosges (48.14 N). According to Petrov & Collingwood (1993), the easternmost site known is Gorizia (45.57 N, 13.37 E). *F. selysi* is abundant in the southern half of France and the western Alps. Most probably the postglacial spreading of *F. selysi* started from an Iberian and/or Italian refuge centre. Primary habitats are undoubtedly river banks. Artificial habitats such as stone or concrete constructions on river dams or along roads are also inhabited as well as pavements and walls in the centre of cities (Brixen/ N Italy, Hellrigl pers. comm.).

Concluded from observations in the Alps and northern Prealps, *F. selysi* is obviously better adapted to river sites with a higher velocity of flow and more frequent inundation than the competing *F. cinerea* and *F. fuscocinerea* (F. Bernard's name *F. torrentium* suggests the same adaptation also in the Pyrenees). As result, *F. selysi* is more frequent on river banks with coarser material and it is often the eudominant ant species on isolated gravel islands within the river. In the Alps, *F. selysi* goes higher than *F. fuscocinerea* and *F. cinerea*, following the river banks up to 1780 m. Lude et al. (1996) and Lude et al. (1999) described adaptations of *F. selysi* to inundation and shifting of river bank material: 72 % of the nests survived inundations lasting for 9 – 43 hours and the ants could dig out through 10 – 20 cm of sand or gravel deposited on the nest entrances. If nest entrances were damaged, floating worker clusters with gynes and broods in the centre could be formed. After landing, the workers used their antennae and forelegs to save detached larvae or eggs from the water surface.

5.4 *Formica georgica* n. sp.

Type material

Holotype and two paratype workers, labelled »Caucasus: Georgia: Passanauri 1600 m, 42.21 N, 44.41 E, leg. Wesenigk 1984.07.24«; 5 paratype workers labelled »Caucasus: Georgia: 42.21 N, 44.41 E, 1000 m leg. Wesenigk 1984.07.30«; 3 paratype workers labelled »Caucasus: Georgia: 42.40 N, 45.10 E, 1400 m verdichtete Wiese am Fluss leg. Seifert 1985.08.13«; 3 paratype workers labelled »Caucasus: Georgia: Mzcheta 41.51 N, 44.46 E, 600 m Sandbank am Fluss Kura leg. Seifert 1985.07.23 659u«; 3 paratype workers labelled »Caucasus: Georgia: 1800 m 42.41 N, 44.37 E, Kazbegi Gänseweide am Terek-Fluss leg. Seifert 1985.08.10 – 1194«; all series in SMN Görlitz.

Morphometrically investigated material (11 samples with 34 individual workers): GEORGIA: Passanauri, 1600 m, 42.21 N, 44.41 E, 1984.07.24; 42.16 N, 44.40 E, 1000 m, 1984.07.30; Omaló, 45.37 E, 42.32 N, 1600 m, 1985.07.31; Shenako, 45.42 E, 42.23 N, 1800 m, 1985.08.01; Shatili, 42.40 N, 45.10 E, 1400 m, 1985.08.13; Mzcheta, 41.51 N, 44.46 E, 600 m, 1985.07.23; Kazbegi, 42.41 N, 44.37 E, 1850 m, 1985.08.08; Kazbegi, 42.41 N, 44.37 E, 1800 m, 1985.08.10 (samples No. 641u, 640o, 1194); above Borisakho, 44.56 E, 42.32 N, 1500 m, 1985.08.12; all series in SMN Görlitz.

Description of worker (Fig. 4, Tab. 3):

Largest species of the group, mean CS 1403. Head moderately elongated, CL/CW(1400) 1.127. Scape of average length, SL/CS(1400) 1.047. Clypeus with a median keel, finely microreticulate, its anteriormost portion finely longitudinally microcarinulate. Frontal triangle finely transversally microcarinulate and with 40 short pubescence hairs. Eyes with few scattered microsetae of 4 – 7 µm length. Dorsal plane of scape without setae. Hairy species: All surfaces of head except genae, mesosoma, petiole, gaster, coxae, flexor margin of all femora with many setae. Nest sample means of setae numbers: genae 0 – 2.4, occipital margin in dorsal aspect 28.3 – 60.8, gula 10.3 – 20.8, propodeum 29.3 – 47.3, extensor profile of both hind femora 0 – 0.4, flexor profile of both hind femora 20.3 – 46.0; extensor profile of hind tibiae 0.0 – 1.3. In anterior view, number of setae surpassing petiolar scale margin above spiracular level 17.7 – 32.0; within these fringe setae, those directed dorsad equally numerous than those directed laterad. Transition between dorsal and caudal profiles of propodeum broadly convex or angulate-convex. Lateral mesonotum anterior of metathoracic spiracle densely microcarinulate, with an mean carinular crest distance of 4 – 5 µm; mean width of carinulae equal or slightly smaller than width of smooth interspaces. Dorsal margin of petiole in frontal view convex or (preferentially in larger specimens) forming an angle of 140°; in lateral aspect with convex anterior and slightly convex posterior profile and a rather acute apex. Head, mesosoma, petiole, and gaster covered by appressed, silvery pubescence comparable to situation in *F. cinerea*, PDG 8.0. Colour variable. Reddish morph: Vertex dark brown, gaster blackish brown, all remaining body parts light reddish brown. Dark morph: Whole head except the mandibular corners, whole mesosoma except the ventrolateral pronotum, and whole gaster blackish brown; remaining body parts more or less reddish brown. Intermediate colour forms with patchily coloured mesosoma occur. For morphometric data of 34 workers see Tab. 3.
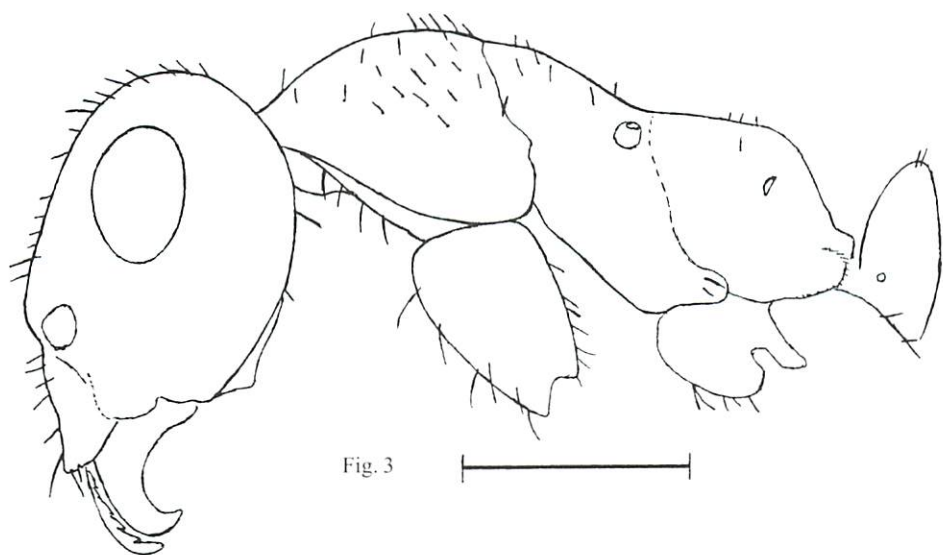
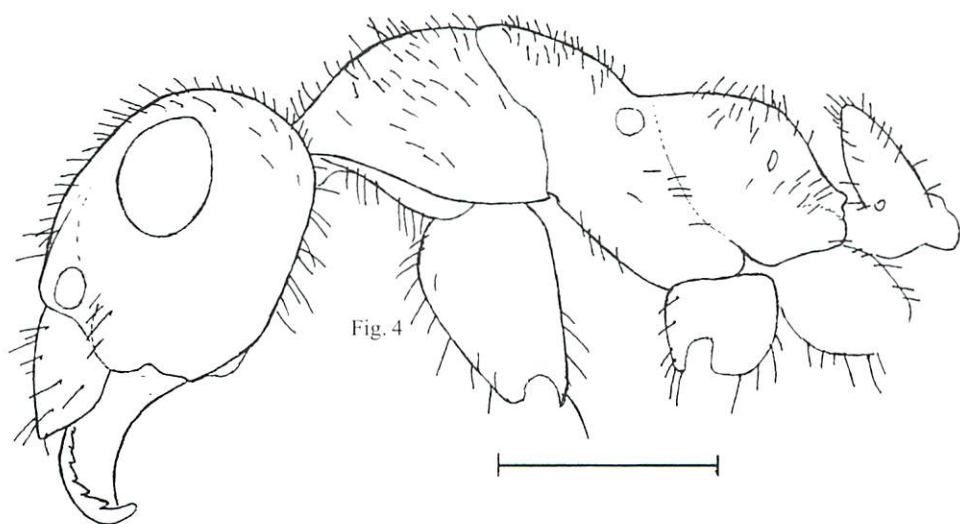Fig. 3   *Formica corsica* n. sp., holotype, lateral aspect of head, mesosoma, and petiole. Scale bar: 661 μm

Fig. 4   *Formica georgica* n. sp., holotype, lateral aspect of head, mesosoma, and petiole. Scale bar: 834 μm

Comments:

Formica georgica n. sp. is abundant throughout Georgia from 600 to 1900 m and follows there the course of rivers where it occurs on sand and gravel banks or poor pastures near the river side and at traffic roads. However, in contrast to *F. cinerea*, there is some tendency to penetrate also mesophilic meadows with more developed field layer where it competes with species of the *F. rufibarbis* and *F. fusca* group.

Formica georgica differs from *F. cinerea* by much higher nPR and significantly higher setae numbers on the flexor side of metatibiae and petiole scale (Tab. 3). Based upon nest samples means, *F. georgica* is convincingly separable from *F. cinerea* throughout its range by a canonical discriminant D (11) using CS and allometrically corrected data of CL/CS, SL/CS, nGEN, nOCC, nGU, nPR, nPE, nHFEX, nHFFL and nHT:

F. georgica	$+3.251 \pm 1.189$ [+0.66, +4.73]	(n = 11)
F. cinerea	-2.906 ± 0.974 [−4.88, −0.62]	(n = 70).

100 % of all subjective determinations are confirmed by the function. The involved type samples are clearly allocated to either cluster and have the following D(11):

−4.58 type of *F. armenica* from Armenia ($p < 0.001$),

−3.77 two syntypes of *F. italica* from Mte. Martinello ($p < 0.001$),

−3.60 holotype of *F. iberica* from the Pyrenees ($p < 0.001$),

−3.08 three paratypes of *F. balcanina* from Drosopygi ($p < 0.001$),

−2.91 two paralectotypes of *F. lefrancoisi* from Grande Chartreuse ($p < 0.001$),

−2.49 four syntypes of *F. subrufoides* from Bolzano ($p < 0.001$),

−1.47 holotype of *F. cinerea* from Tyrol ($p < 0.001$) and

+3.69 holotype sample of *F. georgica* from Passanauri ($p < 0.001$).

The three Caucasian samples of *F. cinerea* do not approach to *F. georgica*, instead they seem to increase their distance with D(11) amounting minus 4.87, minus 4.58 and minus 1.42. The lectotype of *F. armenica* is also fully outside the range of variation of all measured *F. georgica* individuals. A less complex discriminant function with comparable performance is explicitly given in section 8.

5.5 *Formica corsica* n. sp.

Type material

1st series, labelled »CORSICA: Asco, 2000 m leg. A. Delestrade 1991.06.19 No 1514«: holotype and 2 paratypes in SMN Görlitz, 3 paratypes MNHN Paris.

2nd series, labelled »CORSICA: Niolo, 2000 m Mte Albanu leg. A. Delestrade 1992.09.13 No 1659«: 4 paratypes MNHN Paris, 3 paratypes SMN Görlitz.

3rd series, labelled »CORSICA: Bavela, 1900 m leg. A. Delestrade 1991.09.21 No 1518«: 6 paratypes MNHN Paris, 3 paratypes SMN Görlitz. 4th series, labelled »CORSE MONTE-ROTONDO 2400 m 7-VII-1974 J-P. HEBRARD REC.«: 13 paratypes MNHN Paris, 3 paratypes SMN Görlitz.

Morphometrically investigated material (11 samples with 29 individual workers from the following sites in Corsica):

Ajaccio, »Tarunato« (or »Tanunato«, badly written), without date, coll. F. Bernard; Corsica, without date, coll. F. Bernard; Timozzo, sheep farm, 1600 m, 1974.07.05; Timozzo, sheep farm, 1500 m, 1974.07.07; Montee, before Lac de l'Oriente, 1800 – 2000 m, 1974.07.06; Lac de l'Oriente, margin of the lake, 2061 m, 1974.07.06; Monte Rotondo, 2400 m, 1974.07.07; Asco, 2000, 1991.06.19 (No 1514); Bavela, 1900 m, 1991.09.21 (No 1518); Niolo, Mte Albanu, 2000 m, 1992.09.13 (No 1659).

Description of worker (Fig. 3, Tab. 3)

Smallest species within the *F. cinerea* group, CS 1200 ± 48. Head slightly more elongated than in *F. fuscocinerea*, CL/CW(1400) 1.139. Scape of average length, SL/CS(1400) 1.048. Clypeus in the anterior half and lateral corners densely longitudinally carinulate and with a median keel. Frontal triangle finely transversely microcarinulate and with about 25 short pubescence hairs. Eyes with few scattered microsetae of 3 – 4 µm length and large, EYE/CS in the holotype 0.310. Dorsal plane of scape and genae without setae. Least developed pilosity within the *F. cinerea* group: in the sample mean, occipital margin in dorsal aspect with only 6.0 – 15.0 setae and gula with only 1.3 – 3.3 setae; extensor profile of both hind femora without, their flexor profile with 8 – 13.3 setae; extensor profile of hind tibiae without or occasionally with one small seta. In holotype, craniad surface of both procoxae with 19, pronotum with 37, mesonotum with 10, propodeum with 4, and petiole scale in anterior view with 4 setae. Lateral mesonotum anterior of metathoracic spiracle densely microcarinulate, with a mean carinular crest distance of 6 µm; mean strength of carinulae about 4 µm while the mean width of smooth interspaces only 2 µm – i.e. the ratio of sculptured surface against shining surface is about 2 : 1 and similar to the situation in *F. cinerea* (Fig. 1). Dorsal and caudal profiles of propodeum forming a bluntly rounded angle of 150°. Petiole scale in frontal view rather narrow and with a rounded dorsal crest, in lateral aspect rather thick, wedge-shaped, and with convex anterior and posterior profiles. Head, mesosoma, petiole, and gaster blackish brown and covered by a dense silvery pubescence (PDF 10.0 and PDG 7.1 in the holotype).

Comments

F. corsica n. sp. has the weakest gular and occipital pilosity and the smallest body size of any species in the group and deviates strikingly from *F. cinerea* in most of the setae characters. A conspecificity or close relatedness with *Formica lemani*, a species of the *F. fusca* group with a habitat selection most similar to *F. corsica*, can be fully excluded since *F. lemani* shows nest sample means of nOcc and nPE of only 0.0 – 1.0, a shorter and denser gastral pubescence with much thinner hairs, a significantly shorter scape, much smaller eyes, and a much wider petiole scale with a sharper dorsal crest. *F. corsica* differs from the next similar species *F. fuscocinerea* by nest samples means of nGU ranging in the interval [1.0, 3.3] (in *F. fuscocinerea* [3.7, 12.3]) and by a densely microcarinulate lateral mesonotum with an mean crest distance of 6 µm. The mean strength of carinulae is about 4 µm while the mean width of the smooth interspaces is only 2 µm – i.e. the ratio of sculptured surface to shining surface is about 2 : 1. In *F. fuscocinerea* this ratio is 1 : 4 or

smaller and the microsculpture shows the form of a reticulum with elongated meshes. The occipital and propodeal pilosity of *F. corsica* is significantly weaker than in *F. fuscocinerea* but there is some overlap of sample means. Based upon (nest) sample means, *F. corsica* can be separated from *F. fuscocinerea* by a discriminant D(10) using CS and allometrically corrected data of CL/CS, SL/CS, nGEN, nOCC, nGU, nPR, nPE, nHFEX and nHFFL:

F. corsica -1.290 ± 0.358 [-2.01, -0.49] (n = 11)

F. fuscocinerea $+2.621 \pm 1.296$ [$+0.56$, $+5.22$] (n = 37).

A simplified discriminant function is explicitly given in section 8.

The habitat selection of *F. corsica* deviates from that of related species. One should expect a member of the *F. cinerea* group to prefer xerothermous sand or gravel banks of rivers or lakes with sparsely developed field layer plants. However, according to Casevitz-Weulersse (pers. comm. 8 June 2001) and the labels of investigated samples, the main habitats of *F. corsica* are subalpine or mountain meadows between 1500 and 2400 m, including also moist grasslands at margins of glacier lakes. Casevitz-Weulersse emphasised that these ants have to live under conditions of hard and rather long winters, of extreme annual temperature amplitudes, rich precipitations of rain and snow, and violent winds. The activity period is restricted from June to September and the nests were found under stones or under bark. The unusual small size of the workers is possibly an expression of bad growth conditions or the increased need to use preformed microspaces for nesting. The specimens in the collection of F. Bernard, labelled »*Ajaccio, Tarunato*«, would indicate a site at altitudes below 1000 m. This site, however, should be confirmed by future investigations since the published and unpublished statements of Bernard are known to be full of mistakes.

6.   Taxa erroneously attributed to the *Formica cinerea* group

Formica fusca var. *cinereorufibarbis* Forel, 1874; Type locality: Zürich: hospital (1874).

Two worker syntypes and one gyne syntype labelled by Forel himself »Z.hôpital« \ »*F. cinereo-rufibarbis*« \ »Type«, stored in MHN Genève are by no means members of the *F. cinerea* group but definitely belong to *Formica rufibarbis*. This synonymy had already been stated by COLLINGWOOD (1978) but fell into oblivion.

7.   *Formica Incertae Sedis* within the *Formica cinerea* group

Reliable conclusions on the species identity of the following taxa are not possible because of failing access to type material and insufficient original descriptions. Future revisors are recommended not to list them up in speculative synonymic lists but instead to keep these taxa under *Incertae Sedis* until genuine type material is reliably identified and investigated.

Formica fusca var. ***fuscorufibarbis*** Forel 1874; Switzerland: Valais

According to the description and type localities this taxon is most probably a synonym of either *F. fuscocinerea* or *F. cinerea* but no synonym of *F. selysi*. Types could not be discovered during a search in the collections of Genève, Basel, and Lausanne.

Formica cinerea cinereoimitans Ruzsky, 1905

This name was mentioned by Ruzsky within the section treating *Formica cinerea* var. *imitans* on page 405. Full text in translation from the Russian: »Transitional forms (*cinereoimitans* m.) with dark legs, dark brown patches on head and thorax or with the whole thorax darkened«. A future identification of type material seems impossible as neither the type locality nor a figure are given.

Formica cinerea var. *brevisetosa* Karavajev, 1927; Ukraine [unresolved junior primary homonym of *Formica rufa brevisetosa* Ruzsky, 1926]

Formica cinerea var. *sabulosa* Karawajew, 1931; Ukraine: Cherson

Formica cinerea var. *ochracea* Karawajew, 1937; Ukraine: Kinburn

All three taxa of Karavajev should be members of the *F. cinerea* group but a decision on their species identity is not possible at present.

8.   Key, discriminant functions, and comparative tables to the workers.

Investigation of small-sized nest samples provides the most reliable determination though the majority of individual ants is diagnosable. Any numeric data provided in this simplified key refer to nest sample means of $>= 2$ individuals. Setae numbers refer to the bilateral sum of the considered body part/s. In difficult cases, use the discriminant functions presented after this dichotomous key.

1a Extensor profile of hind femora with many short, semierect setae: nHFFL > 5. Pyrenees, S France, western and Central Alps, N Italy .... *F. selysi*

1b Extensor profile of hind femora without or very very few short, semierect setae: nHFFL < 5 2

2a Whole propodeum including lateral metapleuron with many erect setae: nPR > 28 (excluding setae fringing metapleural gland orifice and those on ventrolateral edge of metapleuron). E Caucasus. .... *F. georgica*

2b Whole propodeum including lateral metapleuron with fewer erect setae: nPR < 28 (excluding setae fringing metapleural gland orifice and those on ventrolateral edge of metapleuron) 3

3a Number of standing setae on underside of head < 3.5. Only Corsica .... *F. corsica*

3b Number of standing setae on underside of head > 3.5. Outside Corsica 4

4a Number of setae protruding more than 10 μm from margin of petiole scale dorsal of spiracle in caudal or frontal view smaller: nPE $0.7 – 10.7$; setae projecting dorsad more numerous than those projecting laterad, the latter frequently entirely absent. Microsculpture of lateral mesonotum anterior of metathoracic spiracle in the form of a fine network of much elongated, elipsoid or acutely rhomboid meshes. Inner surface of meshes flat and shining; the ripples of the net are not thicker than 2 μm while the average small diameter of a mesh is about 8 μm – i.e. the ratio of sculptured surface against shining surface is 1 : 4 or smaller (Fig. 2). Eastern and Central Alps, N Apennine. Use discriminant functions .... *F. fuscocinerea*

4b Number of setae protruding more than 10 μm from margin of petiole scale dorsal of spiracle in caudal or frontal view larger: nPE 9.3 – 26.8; setae projecting dorsad as numerous as those projecting laterad; the latter always present. Lateral mesonotum anterior of metathoracic spiracle densely microcarinulate, with a mean carinular crest distance of 4 – 5 μm; mean width of carinulae equal or slightly smaller than width of smooth interspaces (Fig. 1). Palaearctic region from Iberia to 85° E .... *F. cinerea*

Discriminant functions

F. fuscocinerea vs. *F. cinerea*:

D(fu/ci) =

+0.9 nOCC	/ (0.021579 * CS + 8.3)
+1.9 nGU	/ (0.010300 * CS – 0.4)
–0.3 nPR	/ (0.009945 * CS – 6.6)
+2.3 nPE	/ (0.013978 * CS – 6.8)
+1.5 nHFFL	/ (0.014122 * CS + 1.3)
–5.8	

D(fu/ci) < 0: *F. fuscocinerea*, > 0: *F. cinerea*.

F. georgica vs. *F. cinerea*:

D(ge/ci) =

+0.25 nGEN	/ (0.020625 * CS – 0.7)
–0.40 nOCC	/ (0.024535 * CS + 12.8)
–1.07 nGU	/ (0.013622 * CS – 1.1)
+5.80 nPR	/ (0.030706 * CS – 17.7)
–1.85 nPE	/ (0.020449 * CS – 7.6)
+0.25 nHFFL	/ (0.022056 * CS – 2.1)
–3.0	

D(ge/ci) < 0: *F. cinerea*, > 0: in *F. georgica*.

F. corsica vs. *F. fuscocinerea*:

D(co/fu) = 2 nGu + 0.1 nOcc + 0.5 nPR
D(co/fu) < 9.4 in *F. corsica* and > 9.4 in *F. fuscocinerea*.

Tab. 3   Nest sample means of morphometric data of workers of the *Formica cinerea* group. Arrangement of taxa from the left to the right with growing hairiness. Strings of asterisks are a visual help to find most discriminative characters in comparisons between neighbouring species; n = number of nest samples, i = number of measured individuals; arrangement of data: arithmetic mean ± standard deviation [lower extreme, upper extreme]

	F. corsica n.sp. (n = 11, i = 32)		*F. fuscocinerea* (n = 37, i = 119)		*F. cinerea* (n = 70, i = 184)		*F. georgica* n. sp. (n = 11, i = 34)		*F. selysi* (n = 34, i = 78)
CS	1199 ± 49 [1110, 1296]	**	1305 ± 104 [1072, 1494]		1355 ± 139 [1003, 1675]		1403 ± 68 [1326, 1493]		1368 ± 82 [1222, 1527]
CL/CW (1400)	1.140 ± 0.016 [1.111, 1.170]		1.129 ± 0.017 [1.080, 1.151]		1.123 ± 0.018 [1.071, 1.165]		1.127 ± 0.011 [1.111, 1.147]		1.137 ± 0.014 [1.097, 1.156]
SL/CS (1400)	1.049 ± 0.019 [1.014, 1.082]		1.039 ± 0.019 [0.974, 1.066]		1.045 ± 0.024 [0.985, 1.098]		1.047 ± 0.016 [1.023, 1.074]		1.052 ± 0.014 [1.017, 1.074]
nGEN	0.00 ± 0.00 [0,0]		0.10 ± 0.21 [0, 0.7]		3.76 ± 6.34 [0.0, 22.0]	**	0.50 ± 0.69 [0.0, 2.4]	***	16.02 ± 5.90 [2.5, 26.3]
nOcc	11.3 ± 2.8 [6.0, 15.0]	**	26.7 ± 10.1 [6.3, 45.8]	**	45.3 ± 11.8 [24.3, 81.3]		47.0 ± 8.2 [28.3, 60.8]		52.6 ± 8.5 [27.5, 67.0]
nGU	2.2 ± 0.6 [1.3, 3.3]	***	7.5 ± 2.4 [3.7, 12.3]	***	19.1 ± 7.8 [2.0, 46.0]		16.6 ± 3.3 [10.3, 20.8]	**	37.0 ± 8.8 [18.0, 59.3]
nPR	0.8 ± 1.1 [0.0, 3.0]		2.3 ± 1.7 [0.0, 6.8]	**	11.1 ± 5.4 [2.0, 27.0]	****	38.8 ± 6.8 [29.3, 47.3]		36.3 ± 10.0 [17.8, 54.5]
nPE	5.3 ± 1.8 [2.0, 8.3]		5.8 ± 2.7 [0.7, 12.3]	***	17.8 ± 4.7 [9.3, 28.0]		23.9 ± 4.2 [17.7, 32.0]	*	30.8 ± 7.9 [15.5, 51.3]
nHFEX	0.00 ± 0.00 [0.0, 0.0]		0.01 ± 0.05 [0.0, 0.3]		0.10 ± 0.35 [0.0, 2.5]		0.06 ± 0.14 [0.0, 0.4]	***	26.1 ± 9.2 [7.0, 44.0]
nHFFL	10.9 ± 1.9 [8.0, 13.3]		14.2 ± 3.2 [4.0, 21.7]	**	25.9 ± 7.3 [14.7, 47.3]		31.6 ± 7.1 [20.3, 46.0]	*	45.4 ± 8.5 [28.0, 60.0]
nHT	0.20 ± 0.30 [0.0, 0.7]		0.14 ± 0.32 [0.0, 1.0]		0.28 ± 0.47 [0.0, 2.3]		0.35 ± 0.56 [0.0, 1.3]	***	10.68 ± 3.61 [5.5, 18.5]

9. Acknowledgements

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