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A taxonomic revision of the Palaearctic members of the *Formica cinerea*, *F. subpilosa* and *F. rufibarbis* species groups (Hymenoptera: Formicidae)

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Abstract

A taxonomic revision of the Palaearctic members of the *Formica cinerea*, *F. subpilosa* and *F. rufibarbis* species groups is provided under application of Numeric Morphology-Based Alpha-Taxonomy. Twentyfour numerically described phenotypic characters were investigated in 1,486 nest samples with 5,242 worker ants. The recorded characters included one size indicator, eleven shape variables, ten seta characters and two pigmentation characters – resulting in about 105,000 primary data. The three species groups were delimited on the basis of eight shape and one seta character. Species hypotheses were formed by exploratory data analyses which were then tested by linear discriminant analyses. The revision considered 57 Palaearctic taxa and recognized 31 valid species, 1 subspecies, 17 synonyms and 8 *incertae sedis*. Six species were described as new: *Formica iranica* n.sp., *F. kirgisica* n.sp. and *F. superpilosa* n.sp. as members of the *F. subpilosa* group and *F. himalayensis* n.sp. and *F. gebaueri* n.sp. as members of the *F. rufibarbi*s group. The newly described *Formica lhasaensis* n.sp. from Tibet and *F. rufolucida* Collingwood 1962 cannot be allocated to one of the focal species groups and belong to other clades. *Formica torrentium* Bernard 1967, *F. tombeuri* Bondroit 1917, *F. sinae* Emery 1925 and *F. lusatica* Seifert 1997 were raised to species rank. *Formica decipiens* Bondroit 1918 is shown as junior synonym of *F. tombeuri* Bondroit 1917, *F. cinerea italica* Finzi 1928 as junior synonym of *F. fuscocinerea* Forel 1874 and *Formica glauca* Ruzsky 1896 as junior synonym of *Formica clara* Forel 1886. Subclusters indicated by exploratory data analyses within the main clusters of *Formica cunicularia* Latreille 1798 and *F. subpilosa* Ruzky 1902 were considered as intraspecific polymorphism. A determination key for the whole Palaearctic range is provided. Z-stack images in standard viewing positions are given for all newly described species. Interspecific hybridization is shown between *Formica cinerea* Mayr 1853 and *F. selysi* Bondroit 1918 locally in the Alps and between *F. cinerea* and *F. balcanina* Petrov & Collingwood 1993 in a hybrid zone in Romania.

Keywords *Serviformica* | cryptic species | numeric morphology-based alpha-taxonomy | hybridization | geographic variability | intraspecific polymorphism | subspecies

Content

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1 Introduction

The members of the *Formica cinerea* Mayr 1853 group and of the *Formica subpilosa* Ruzsky 1902 group form morphologically and ecologically well-defined clades of mainly West and Central Palaearctic distribution. All species are preferentialy found in open habitats completely without or only with patches of shrub or trees. They prefer places with incomplete cover of the herb layer and are typical for river banks and other sandy or gravelly alluvial habitats as well as coastal or inland sand dunes. In both the *F. cinerea* and *F. subpilosa* groups there are species with adaptation to flooding. There is also a high adaptation to unstable habitats with frequent shifting of soil material and early stages of plant succession. Thus, in particular *Formica cinerea* group species are among the earliest colonizers of anthropogenous habitats such as open-cast mining sites, heaps, river and road embankments or construction zones. Some species of the *F. cinerea* and *subpilosa* groups show a high tendency to build up large polycalic colonies that defend territories against other species - a trait rare in Palaearctic *Serviformica* species. Supercolonial species of the *F. cinerea* group received big attention in public media due to their huge numbers and very aggressive behavior against humans which led to closure of playgrounds for children in the cities of Munich, Tübingen and Dresden in Germany.

Formica cinerea group species are completely unknown from Turkestan, the Pamirs, Tian Shan, and other Central Asian mountain ranges or steppes where they are ecologically replaced by members of the *F. subpilosa* group. In fact, we found no site where members of both groups occurred syntopically. This is explained by the widely distant radiation centres and the most similar ecological niches which prevented that sympatry could secondarily develop. The most widely distributed species considered in this paper, *Formica cinerea*, reaches its easternmost point in W Siberia at 85.10 E, 52.32 N (Dlussky 1967) but Europe is undoubtedly the radiation centre of the *F. cinerea* group. Following river valleys during postglacial immigration, *F. cinerea* group species climbed up to 2500 m in mountains of Europe and the Caucasus and those of the *F. subpilosa* group up to 3100 m in the Central Asian mountains or to 3900 m in East Tibet.

The members of the *Formica rufibarbis* group have a Transpalaearctic distribution and occur in diverse open, moderately to strongly xerothermous habitats which include open woodland, xerothermous grassland, pastures, meadows as well as semiurban or urban habitats. They have low densities in habitats dominated by *F. cinerea* or *F. subpilosa* group species. Despite of moderate polygyny in some species, supercolonial structures have never been observed in members of the *Formica rufibarbis* group.

Our basic working philosopy or methodology is Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT, Seifert 2009) in connection with background information provided by zoogeography and nest sample composition. The last taxonomic revisions of the *Formica cinerea* group (Seifert 2002), the *F. subpilosa* group (Seifert & Schultz 2009a) and the *F. rufibarbis* group (Seifert & Schultz 2009b) already used NUMOBAT approaches but knowledge since then has improved due to introduction Nest-Centroid clustering (NC clustering, Seifert et al. 2013), introduction of new differential characters and extension of the sample size. NC clustering is an exploratory data analysis which is extremely useful for formation of initial taxonomic hypotheses but shows a weakness in that it may disguise hybridization scenarios (Seifert 2021, 2024, 2025) while in cases of intraspecific polymorphism it may produce clusters that can be misinterpreted as species-level entities (Seifert 2016). Within the ants considered here, hybridization may occur locally in the Alps between *Formica cinerea* and *selysi* (Purcell et al. 2016 and this paper) but also in a hybrid zone in Romania between *Formica balcanina* Petrov & Collingwood 1993 and *F. cinerea* (see below). Hybridization and within-species geographic variation, in particular in *F. cinerea*, cause conflicts in finding taxonomic decisions. This complicated structure led us to return in one case to a subspecific classification. Weyna et al. (2022) showed that hybridization is more frequent in ants than in other insect groups such as beetles and flies. A recent synopsis showed hybridization to occur in 19% of the 180 ant species autochthonous for Central and North Europe (Seifert 2023 and references cited therein). These belonged to the genera *Myrmica, Tetramorium, Temnothorax*, *Lasius*, *Camponotus*, the subgenus *Coptoformica* and the *Formica rufa* group. There is no indication for hybridization between species of the *Formica subpilosa* group in our data. This should be due to the absence of detailed local investigations in contact zones rather than reflecting a real situation. In the *Formica rufibarbis* group, direct evidence for hybridization is also lacking but several samples with intermediate morphology between *F. clara*, *F. lusatica* and *F. cunicularia* are suspicuous to represent hybrids. We consider here the status of 53 Palaearctic taxa attributed to the *Formica cinerea*, *F. subpilosa* and *F. rufibarbis* groups plus 2 taxa outside of these focal groups. Nearctic taxa such as *Formica altipetens* Wheeler 1913, *F. canadensis* Santschi 1914, *F. montana* Wheeler 1910, *F. neocinerea* Wheeler 1913 and *F. francoeuri* Bolton 1995, supposed to be related to the *F. cinerea* group (Agosti 1989), are not considered here.

The presented paper is the result of an extensive morphological study of Palaearctic *Serviformica* ants running over three decades. By 17 October 2025, 2,468 nest samples with 8,250 worker individuals were studied in up to 25 characters resulting in 175,200 numeric data. This allowed the development and testing of taxonomic hypotheses. We present here the first results of the new investigation system for three species groups, which represent 50% of the whole data, and hope to publish revisions of the remaining species groups within the next two years.

2 Material

NUMOBAT data of the species groups considered in this paper comprise 1,486 worker samples with 5,242 individuals and about 105,000 primary data. The material is from the whole Palaearctic with some gaps in West Siberia. With the exception of type specimens and other samples of special relevance, data of this material are not presented in detail in the main text of this paper, but listed up in the electronic supplementary information SI1 (worker individuals), SI2 (nest sample means of workers).

The abbreviations of type depositories are as follows:

IRSN Bruxelles - Institut Royal des Sciences Naturelles de Belgique Bruxelles, Belgium
MCZ Cambridge – Museum of Comparative Zoology of the Harvard University, Cambridge, USA
MHN Genève – Muséum d'histoire naturelle de Genève, Genève, Switzerland
MNHN Paris - Museum National d'Histoire Naturelle Paris, France
MZ Lausanne - Musée de Zoologie Lausanne, Switzerland
NHM Wien – Naturhistorisches Museum Wien, Austria
NRM Stockholm – Naturhistoriska Riksmuseet Stockholm, Sweden
SMN Görlitz – Senckenberg Museum für Naturkunde Görlitz, Germany
ZM Amsterdam - Zoological Museum Amsterdam, Netherlands
ZMLSU Moskva - Zoological Museum of the Lomonossov State University Moskva, Russia
ZMU Kiev - Zoological Museum of the University of Kiev, Ukraine

3 Methods

The applied species concept

The GAGE species concept (Seifert 2020) is used here. It states that species are separable clusters defined alone by nuclear genes and/or their expression products. The phenotype investigated here is such an expression product. The concept requires to test taxonomic hypotheses by exploratory and hypothesis-driven data analyses and using the threshold principle to evaluate evolutionary divergence. It also requires to check individual samples for hybridization and intraspecific polymorphism if the data allow this.

Equipment and measuring

Two Leica M165C high-performance stereomicroscopes equipped with 1.6x (RS) or 2.0x (BS) planapochromatic objectives were used. The latter system allowed magnifications of 360x and a resolution of 1050 lines /mm. Pin-holding stages, permitting full rotations around X, Y, and Z axes were used for spatial adjustment of specimens. Schott KL 1500 cold–light sources equipped with two flexible, focally mounted light–cables providing light from variable directions, allowed sufficient illumination over the full magnification range and a clear visualization of silhouette lines. Schott KL 2500 LCD cold–light sources in combination with a Leica coaxial polarized–light illuminator provided optimal resolution of tiny structures and microsculpture at highest magnifications. Simultaneous or alternative use of the cold-light sources depending upon the required illumination regime was quickly provided by regulating voltage up and down. Leica cross-scaled ocular micrometers with 120 graduation marks ranging over 52 % of the visual field were used. To avoid the parallax error, its measuring line was constantly kept vertical within the visual field. Z-stack images of mounted specimens were produced with a KEYENCE VHX-7000 digital microscope using magnifications between 20 and 1000x. Bernhard Seifert collected most of the data in the *Formica cinerea* group and Roland Schultz collected most of the data in the *F. subpilosa* and *F. rufibarbis* groups.

Definition of morphometric characters

Twentyfour primary measurements were taken in workers. This included the linear measurements CL, CW, SL, EYE, OceD, MtSt, MtPpSt, MtMtp, PeW, GHL, RipD and sqPDG, the seta counts nGen, nCH, nGu, nPn, nMn, nPrMe, nPe, nHFex, nHFfl and nHT as well as the pigmentation characters PIGM and CONT. In bilaterally developed characters, arithmetic means of the data of both body sides were calculated – this refers to linear measurements as well as seta counts. All measurements were made on mounted and fully dried specimens. The reproducibility of NUMOBAT data recording in general is strongly dependent from carefully considering the character definitions given below. Resolution of the microscope and illumination of the object are important in characters such as RipD or sqPDG.

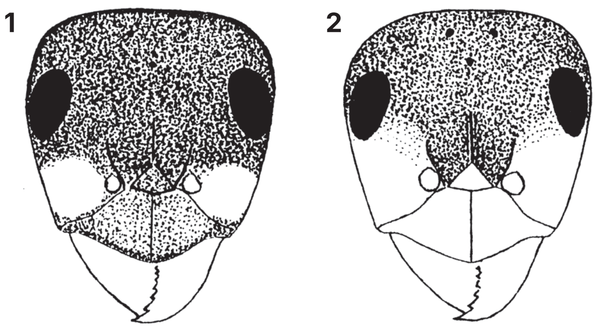
CL – maximum cephalic length in median line; the head must be carefully tilted to the position yielding the true maximum; excavations of hind vertex and/or clypeus reduce CL.

CONT – the contrast between the dark and the light pigmentation on genae, subjectively interpolated between the values 1.0 (Fig. 1) and 0 (Fig. 2). Do not use magnifications >100 x and test different angles of light incidence.

CW – maximum cephalic width; the maximum in Formica is found either behind (larger specimens) or across the eyes (smaller specimens).

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

EYE – eye-size index: the arithmetic mean of the large (EL) and small diameter (EW) of the elliptic compound eye.



Figures 1–2. Pigmentation pattern of dorsal head in a worker of (**1**) *F. cunicularia* showing the upper extreme of pigmentation contrast on genae (CONT = 1.0), and pigmentation pattern of dorsal head in a worker of (**2**) *F. clara* showing the lower extreme of pigmentation contrast on genae (CONT = 0).

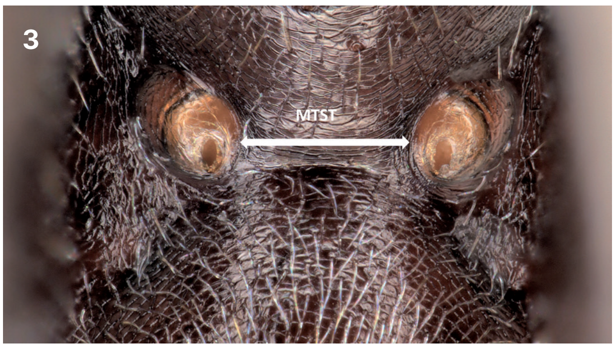


Figure 3. Minimal distance between the inner margins of the bulges of the metathoracal spiracles (MtSt).

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 excluding the row of setae immediately anterior of the hind tergite margin.

MtSt – minimal distance between the margins of the rings surrounding the metathoracal stigmata (Fig. 3). This is basically the width of the normally structured metathoracal surface.

MtPpSt – smallest distance between the outer bead margins of the metathoracal and propodeal stigma (Fig. 4)

MtMtp – distance of the caudoventral bead margin of the metathoracal stigma to most distant caudoventral margin point of metapleuron. Take care to determine the real metapleural margin if there is much pubescence (Fig. 5).

nCH – with the head in full face view, unilateral number of setae protruding more than 10 µm from posterior margin of vertex and the head sides anterior to level of anterior eye margin. To avoid the parallax error in

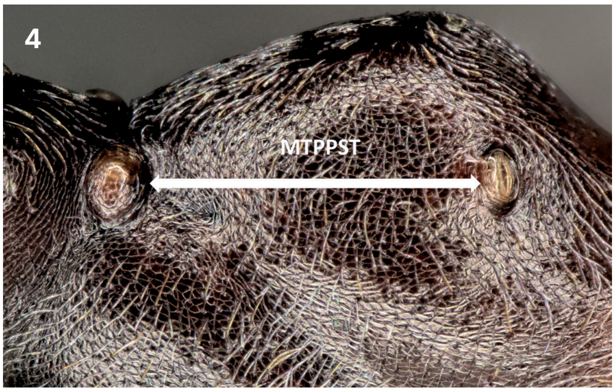


Figure 4. Minimal distance between the bulge margins of the metathoracal and propodeal spiracles (MtPpSt).

Figure 5. Minimal distance of the bulge margin of the metathoracal spiracle from the most distant caudoventral margin of metapleuron (MtMtp).

assesing protruding distance, rotate the head with the ocular micrometer kept vertically in the visual field. nGen – unilateral number of setae protruding more than 10 µm from genal margin with head in full face view. Take care to avoid the parallax error.

nGu – unilateral number of setae protruding more than 10 µm from underside of head (= "gula") as visible in lateral view.

nHFex – unilateral number of setae protruding more than 10 µm from cuticular silhouette of the extensor profile of hind femora. Apical setae with longitudinal orientation are excluded from the count. The correct spatial adjustment is given when the two edges along the distal flexor margin of the femur do exactly superimpose.

nHFfl – unilateral number of setae protruding more than 10 µm from cuticular silhoute of the flexor profile of hind femora with the spatial adjustment given in nHFex. If the preparation of the specimen prevents a view on the whole flexor margin, position the femur perpendicular, use higher magnifications and run from the distal to the proximal part of femur with a slow change of focus.

nHT – unilateral number of setae protruding more than 10 µm from the cuticular silhouette of the extensor profile of hind tibia. Apical setae with longitudinal orientation are excluded from the count. The correct spatial adjustment is given when the swivelling plane of the tibio-femoral hinge joint is in visual plane.

nMn – unilateral number of setae on mesonotum protruding more than 10 µm from cuticular surface

nPe – unilateral number of setae on protruding more than 10 µm from the dorsal and lateral silhouette of petiole as it is given (or would be given) in caudal or frontal viewing position. Only setae dorsal of the spiracle are considered. If adjusting to a frontal or caudal viewing position is difficult, which is often prevents an easy standardized counting of lateral setae, use the dorsal view and a high magnification and run down the margin under slow change of focus.

nPn – unilateral number of setae protruding more than 10 µm from cuticular surface of pronotum.

nPrMe – unilateral number of setae protruding more than 10 µm from cuticular surface on propodeum and lateral metapleuron (excluding weir hairs of the metapleural gland orifice and those on ventrolateral edge of metapleuron which are directed downwards.

nSc – unilateral number of setae protruding more than 10 µm from cuticular surface of dorsal scape. Apical setae with more or less longitudinal orientation are not counted.

OceD – distance between inner margins of posterior (lateral) ocelli.

PeW – maximum width of petiole.

PIGM – the percent ratio of the blackish or brownish pigmented surface of the mesosoma excluding the coxae as perceptible in lateral view. It is, in other words, the percentage of pigmentation which is not light reddish or yellowish red. A value of 0 means that the whole mesosoma is uniformly reddish or yellowish red. Do not use magnifications >100 x and test different angles of light incidence

RipD – average distance of microripples on dorsal plane of first gaster tergite crossing a longitudinal counting line. At least three counts along a 90 µm distance on different surface spots are averaged. Counting is performed at a magnification of at least 250x. Use clean surfaces and take care for optimal lighting. The measure applies to both ripple or network stuctures with irregular orientation.

Setae – all stronger hairs having at least twice the basal diameter of neighbouring pubescence hairs (typical for *Serviformica* are 3.5 µm diameter for pubescense and >8 µm for setae)

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

sqPDG – square root of 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. In order to normalise positively skewed distributions, the square root of PDG is calculated. Exact counting is promoted by clean surfaces and flat, reflexion-reduced illumination directed perpendicular to the axis of pubescence hairs. Counting is performed at a magnification of at least 250x. In each specimen 4-6 measuring-lines of 400 µm are averaged under exclusion of surface parts with apparently detached or, relative to the overall average, strongly reduced pubescence. If there are no transects with undamaged pubescence, PDG can be calculated by the formula $PDG = BD^2/PLG$ where BD is the mean distance of hair base punctures and PLG the mean length of pubescence hairs.

Removal of allometric variance

Similar to the situation in many other Formicine, Dolichoderine and Myrmicine ant genera, many shape and setae characters are significantly influenced in *Formica* by allometric effects. Removal of allometric variance (RAV) was performed with the procedure described by Seifert (2008). This allows to reveal in comparative tables which shape variables do really differ between the species independent from body size and improves the performance of principal component analyses (PCA). For example, the RAV calculations presented below reduce the coefficient of varition of the eye size index EYE /CS to 59% in *Formica cinerea* or to 68% in *Formica litoralis*. RAV was performed by a linear function for the assumtion of all individuals to have a cephalic size of CS = 1400 µm. The functions were calculated as the arithmetic mean of the species-specific functions of 44 Palaearctic *Serviformica* species for which data in more than 30 individuals were available. Calculating the functions for setae numbers excluded species with zero or close to zero setae in a character. In the extreme, the functions for nHFex were calculated only with the data of *Formica selysi* and *F. torrentium*. The RAV functions of 9 shape, 11 setae, one pubescence and two pigmentation characters are given below. The variable GHL /CS is given in per cent. In contrast to the improvement of the performance of a PCA by RAV, this is not the case in Linear Discriminant Analyses (LDA) because these analyses are able to rotate the axes of the variables in dependence to a size component. The results are the same if raw data, primary indices or RAV-corrected data are used in a LDA.

CL/CW_{1400} = CL / CW / (-0.1108*CS+1.2988)*1.1437
SL/CS_{1400} = SL / CS / (-0.1124*CS+1.2433)*1.0859
EYE/CS_{1400} = EYE / CS / (-0.0533*CS+0.3669)*0.2923
PeW/CS_{1400} = PeW / CS / (0.0842*CS+0.3079)*0.4258
$OceD/CS_{1400}$ = OceD / CS / (0.0113*CS+0.1505)*0.1663
$MtSt/CS_{1400}$ = MtSt /CS / (0.0412*CS+0.0723)*0.1299
$MtPpSt/CS_{1400}$=MtPpSt/CS/(-0.0224*CS+0.3880)*0.3566
$MtMtp/CS_{1400}$=MtMtp/CS/(-0.0245*CS+0.6870)*0.6527
GHL/CS_{1400} = GHL / CS / (0.131*CS+8.157)*8.340
nCH_{1400} = nCH / (12.43*CS-2.35)*15.06
nGu_{1400} = nGu / (5.50*CS-0.37)*7.33
$nGen_{1400}$ = nGen / (6.21*CS-2.08)*6.61
nPn_{1400} = nPn / (21.68*CS-14.49)*15.86
nMn_{1400} = nMn / (12.50*CS-10.59)*6.91
$nPrMe_{1400}$ = nPrMe / (11.75*CS-8.14)*8.31
nPe_{1400} = nPe / (8.38*CS-4.29)*7.44
$RipD_{1400}$ = RipD / (0.392*CS+5.16)*5.71
$sqPDG_{1400}$ = sqPDG / (+0.354*CS+3.352)*3.85
$nHFex_{1400}$ = nHFex / (7.81*CS-1.44)*9.49
$nHFfl_{1400}$ = nHFfl / (11.56*CS-4.19)*12.00
nHT_{1400} = nHT / (3.51*CS-1.56)*3.36
$PIGM_{1400}$ = PIGM / (-39.44*CS+78.6)*23.4
$CONT_{1400}$ = CONT / (-0.002*CS+0.17)*0.171

These RAV-corrected variables were used in the exploratory and hypothesis-driven data analyses.

Explorative and supervised data analyses, classification and statistical testing

The formation of species hypotheses was done by an interaction of exploratory data analyses (EDA) and a controlling linear discriminant analysis (LDA). The EDAs applied consisted of three variants of Nest Centroid Custering (NC-Clustering) and of principal component analysis (PCA). NC-clustering was run as hierarchical NC-Ward clustering, hierarchical NC-part.hclust clustering, non-hierarchical NC-part.means clustering and NC-NMDS.kmeans clustering. These methods were described in more detail by Seifert *et al*. (2013) and Csősz & Fisher (2016). NC-clustering will usually expose species hypotheses more clearly than a PCA but it is also more prone to distortion. The main weakness of NC-clustering is that hybrid samples are usually not exposed as separate cluster, even if making up much of the material, because many of them are absorbed by the clusters of either parental species (Seifert 2021, 2024, 2025). Similarly, rare species, represented by very few samples in the material, can be swallowed by the cluster of an abundant similar species. A sample-by-sample supervision in the simple vectorial space is needed here to avoid misleading indications. The less sensitive but more robust PCA, which operates in the simple vectorial space, provides a higher probability of exposing intermediate hybrid clusters and to spatially separate single samples of rare species from main clusters. For these reasons a PCA was always run in parallel to NC-clustering and in some cases preferred for hypothesis formation.

Establishment of final species hypothesis was done by checking the species hypothesis by a controlling LDA in which controversial samples were run as wild-cards. Controversial could mean disagreeing classification in two EDA methods or classifications proposed by a single EDA method which appeared unlikely due to zoogeography and other background information. Nest sample means of posterior probabilities for *n* considered species were obtained by firstly calculating the geometric means P_1, $P_2 ... P_n$ of the individual data. The posterior probability for species 1 is then given in the nest-sample mean as $p_1 = P_1/(P_1 + P_2 ... + P_n)$ and for the other species accordingly. The final classification ("final species hypothesis") was established by the LDA in the iterative procedure described by Seifert *et al*. (2013). Decisions if morphologically defined clusters can be considered as valid species were achieved according to the GAGE Species Concept which proposed, in an implementing provision, that the mean error of the applied exploratory data analyses determined by the controlling LDA should be $< 5\%$. This threshold proposal appeared reasonable to mitigate taxonomic splitting tendencies. PCA, LDA, and ANOVA tests were performed with the software package SPSS 15.0.

4 On subgenera and diagnosis of the *Formica cinerea*, *F. subpilosa* and *F. rufibarbis* species groups

A majority of contemporary evolutionists seem to agree that easy optical recognition of bifurcating phylogenetic trees outweighs their disadvantage that they represent only a rough, frequently distorted picture of true evolutionary processes. We admit that simplicity and parsimony are good initial approaches for treatment of complicated problems and it seems that, among all imperfect descriptions of evolution, no system is known providing better illustrations than classical trees. Anyway, we have to be aware that future developments of phylogenetic systems for classification of ants are difficult to predict for three main reasons.

The first reason is the uncomfortable fact that introgression of genes by hybridization is a major factor in ant evolution. Simple bifurcating trees cannot reflect complicated evolutionary networks (Seifert 2021). This causes ongoing disputes on whether to construct these trees by considering the "democratic majority" of all genes of the nuclear genome or by selecting a tiny percentage of nuclear genes showing the "deepest coalescence times between species" (see, for instance, discussion in Mallet et al. 2016). As a matter of fact, tree topologies achieved by these alternative approaches may radically differ (e.g., Fontaine et al. 2015).

The second reason for poor predictability of future phylogenetic systems is different treatment of paraphyletic groups. The hardcore phylogeneticists, being mentally caught within the construct of logical inclusiveness and banning the naming of any paraphyletic group, tend to collect species in megagenera (e.g., Ward et al. 2015). The other party, the pragmatic phylogeneticists, agree that the phylogenetic approach basically provides a useful backbone of systematics, but they pledge for nomenclatoric maintenance of those paraphyletic groups which form well-circumscribed clusters each sharing several strong autapomorphies that distinguish them from other clusters (e.g., see discussion in Seifert et al. 2016).

The third reason for instability of modern phylogenetic trees is incomplete sampling. This refers both to the

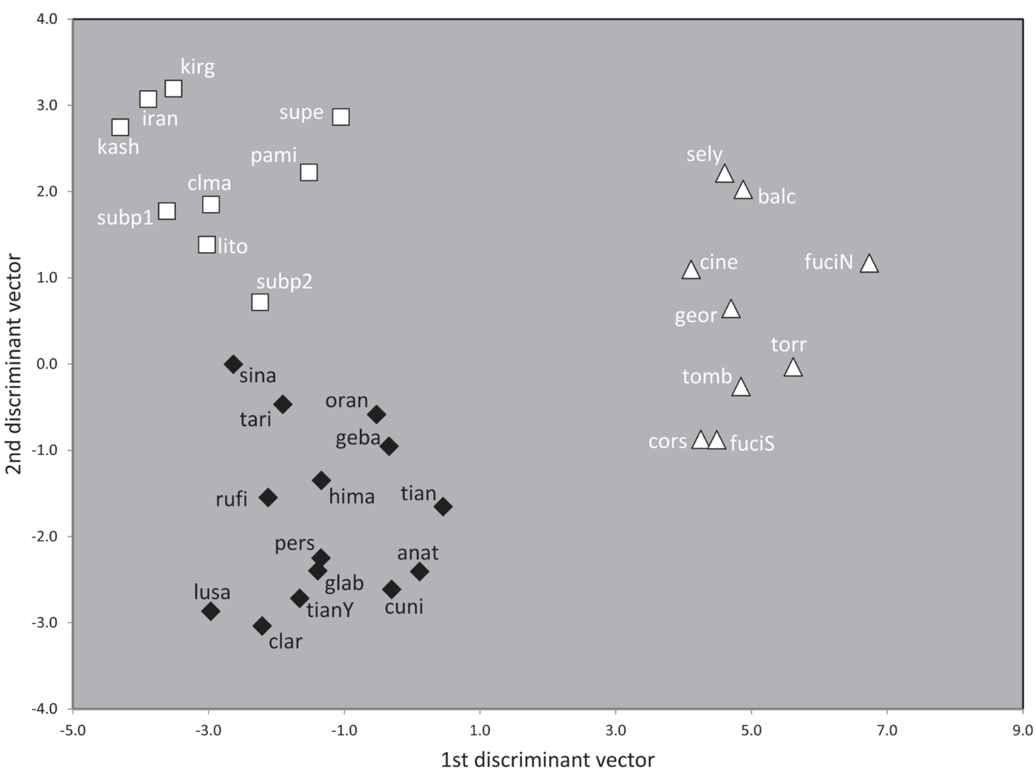


Figure 6. Linear discriminant analysis using as variables the first three principal components extracted from species means of eight shape and one seta character. Black rhombs: *Formica rufibarbis* group, white squares: *F. subpilosa* group, white triangles: *F. cinerea* group. Abreviations for species: anat – *anatolica*, balc – *balcanina*, cine – *cinerea*, clar – *clara*, clma – *clarissima*, cors – *corsica*, cuni – *cunicularia*, fuciN – *fuscocinerea* northern population, fuciS – *fuscocinerea* southern population, geba – *gebaueri* n.sp., geor – *georgica*, glab – *glabridorsis*, hima – *himalayensis* n.sp., iran – *iranica* n.sp., kash – *kashmirensis*, kirg – *kirgisica* n.sp., lito – *litoralis*, lusa – *lusatica*, oran – *orangea*, pami – *pamirica*, pers –*persica*, rufi – *rufibarbis*, sely – *selysi*, sina *sinae*, subp1 – *subpilosa* morph 1, subp2 – *subpilosa* morph 2, supe – *superpilosa* n.sp., tari – *tarimica*, tian – *tianshanica*, tianY – *tianshanica* Yunnan, tomb – *tombeuri*, torr – *torrentium*.

number of species included in a tree and the number of samples within a species as well as to missing elements (extinct species for which we have no data).

Being aware of these impediments, we avoid here any discussion if a subgeneric division of the genus *Formica* Linnaeus 1758 or raising subgenera to genus level makes sense from the perspective of a more flexible phylogeneticist. We give a pragmatic answer and collect here all Palaearctic *Formica* species under the subgenus *Serviformica* Forel 1913 that do not belong to the well circumscribed socially parasitic subgenera *Raptiformica* Forel 1913, *Coptoformica* Müller 1913 and *Formica* s.str. (=ants of the *Formica rufa* group). We also exclude from *Serviformica* four very deviating species with unique character combinations: the socially parasitic *Formica uralensis* Ruzsky 1895, the monospecific genus *Iberoformica* Tinaut 1990 (raised by Munoz-Lopez et al. 2012 to genus level), and the two strongly deviating species of the *Formica sentschuensis* group: *Formica sentschuensis* Ruzsky 1915 and *Formica tibetana* Schultz & Seifert 2025 from the east of the Tibetan plateau (Schultz & Seifert 2025). With exception of *Iberoformica* and the *Formica sentschuensis* group, the subgenus *Serviformica* deviates from all other *Formica* species by independent colony foundation throughout all phases of dispersal and population development – in particular no host species are needed when new localities are colonized (Seifert 2018, Borowiec et al. 2021).

Seifert & Schultz (2009a, b) provided evidence for a phenotypic separation of the *F. cinerea*, *F. subpilosa* and *F. rufibarbis* groups which included 5 shape and 8 setae characters. This approach risks misallocations due to the occasionally extreme variance of seta numbers within groups of closely related species (Seifert 2016, 2021). Here we use the species means of the 8 shape variables CL/CS_{1400}, SL/CS_{1400}, $OceD/CS_{1400}$, EYE/CS_{1400}, $MtSt/CS_{1400}$, $MtPpSt/CS_{1400}$, $MtMtp/CS_{1400}$ and PeW/CS_{1400} plus a single seta character $nHTFfl_{1400}$. In order to avoid an overfitting (the smallest class had only 9 elements), the LDA was run using the first three principal components extracted from these 9 characters. The resulting clusters were largely congruent with subjective assessment of relatedness by overall phenotypical impression (Fig. 6). Overall, the *Formica cinerea* group cluster is characterized by a combination of small PeW/CS_{1400}, large EYE/CS_{1400}, small $OceD/CS_{1400}$ and usually large $nHTFfl_{1400}$. The *F. rufibarbis* group members exibit a combination of large PeW/CS_{1400}, medium EYE/CS_{1400}, small $OceD/CS_{1400}$ and small $nHTFfl_{1400}$ whereas those of the *F. subpilosa* group combine medium PeW/CS_{1400}, small EYE/CS_{1400}, large $OceD/CS_{1400}$ and large $nHTFfl_{1400}$.

5 Key to workers

The key does not consider the *Serviformica* species *Formica fusca* Linnaeus 1758*, F. lemani* Bondroit 1917, *F. gagates* Latreille 1798, *F. picea* Nylander 1846, *F. gagatoides* Ruzsky 1904, *F. japonica* Motschulski 1866, *F. formosae* Emery 1925, *F. pyrenaea* Bondroit 1918, *F. maura* Santschi 1929 and *F. gerardi* Bondroit 1917. These species are characterized by a homogenously dark brown to jet black mesosoma without small patches of reddish pigmentation and by absence of setae surpassing the posterior margin of head. Within the species considered in the key, *Formica tombeuri* – a setae-reduced species of the *F. cinerea* group – and very dark *F. cunicularia* or *F. tianshanica* workers may match this diagnosis and additional characters such as eye size have to be considered. The key uses setae numbers as mean of both body halves, absolute measurements in mm (but RipD and sqPDG in µm) and geographic coordinates in decimal format (e.g. 3.03°W = -3.03; LON = longitude, LAT = latitude). Morphometric indices and setae numbers are raw data without allometric corrections with exception of couplet 18. This key is safe when the definitions for character recording are carefully considered and when the optical equipment is sufficient. However, we doubt that running through the key really saves working time with exception of the few easily identified species. As alternative we recommend to record all characters and to classify the test sample by a wild-card run of a LDA within the data frame provided by supplementary information SI2. A preselection which candidates have to be tested in the LDA can be done by studying the morphometric tables and geographic distribution.

1a Palaearctic west of 60°E **2**
1b Palaearctic east of 60°E **19**
2a Extensor profile of hind femur without setae **4**
2b Extensor profile of hind femur with semierect setae, Europe west of 17°E **3**
3a East of 2° E. Contact zone with 3b possibly in Massif Central (Figs 7-9). Discriminant $0.132*nHFex+0.143*nPrMe-17.182*EYE+0.427*LON+3.638 > 0$ [error 0% in 81 individuals]. Alpes and adjacent regions, Apennines. .... ***selysi***
3b West of 2° E. Pyrenees and SW France (Figs 10-12). Discriminant < 0 [error 0% in 84 individuals]. .... ***torrentium***

4a Posterior margin and underside of head without setae, flexor margin of hind tibia without or very few setae, eye smaller and petiole wider. Discriminant 0.203*nCH-0.052*nGu+0.10*nHFfl-10.57*PeW+24.06*EYE-5.347 < 0 [0% error in 591 nest sample means]. **10**

4b Posterior margin and underside of head with setae, flexor margin of hind tibia always with setae, eye larger and petiole narrower. Discriminant > 0 [0.4% error in 262 nest sample means]. **5**

5a Corsica. Posterior margin and underside of head with few setae, nGu+nCH 6.5 ± 2.3. Small species, CW 1.088 ± 0.086 mm. Endemite of Corsica. .... ***corsica***

5b Not in Corsica. Posterior margin and underside of head with more setae, nGu+nCH 32.6 ± 12.7. On average larger. **6**

6a Asia Minor, Caucasus, Iran. **7**

6b Outside this area. **8**

7a Propodeum and lateral metanotum with many setae, nPrMe 17.6 ± 5.2. Discriminant 0.317*nPrMe -0.264*nGen-0.042*nCH-0.091*nGu-0.076*nHFfl-0.728 > 0 [error 0% in 24 nest-sample means]. .... ***georgica***

7b Propodeum and lateral metanotum with fewer setae, nPrMe 5.6 ± 3.7. Discriminant < 0 [error 0% in 117 nest sample means]. .... ***cinerea***

8a Genae with many setae, nGen 7.4 ± 2.8. Discriminant 1.363*nGen+0.834*nGu-1.594*nPrMe+0.394*nHFfl+83.08 *SL-71.122 > 0 [error 0% in 57 nest sample means of non-hybrid samples; be aware of the hybrid zone with *F. cinerea* in Romania, see section 6.4]. Balkans only. .... ***balcanina***

8b Genae with no or very few setae nGen 0.66 ± 1.08. Discriminant < 0 [error 0% in 178 nest sample means of non-hybrid samples; be aware of the hybrid zone with *F. balcanina* in Romania].......... **9**

9a Discriminant 0.183*nGu+0.212*nHFfl+0.204*nPe-25.54*EYE-13.88*MtSt+12.62*MtPpSt+0.050*LON+2.79 > 0 [error 0% in 77 nest sample means]. .... ***cinerea***

9b Discriminant < 0 [error 0% in 57 nest sample means]. .... ***fuscocinerea***

10a Discriminant 0.152*nGu+0.086*nHFfl-4.149*CL+6.372*SL+20.016*PeW-61.61*EYE+11.316 < 0 [error 0% in 17 nest sample means]. Only Pyrenees and Iberian Peninsula (Figs 13-15). .... ***tombeuri***

10b Discriminant > 0 [error 0% in 629 nest sample means]. **11**

11a Discriminant 0.526*nPrME-0.100*nMn+0.418*nHFfl+0.287*RipD+7.528*SL-8.105*PeW-17.32*EYE -3.277 > 0 [error 0% in 52 nest sample means of at least two individuals]. **12**

11b Discriminant < 0 [error 0% in 517 nest sample means of at least two individuals]. **13**

12a Microsculpture of first gaster tergite very delicate, RipD > 7.3, surface despite dense pubescence rather shiny (Fig.18). Iran. (Figs 16-18). .... ***iranica* n.sp.**

12b Microsculpture of first gaster tergite much stronger, RipD 5.6 ± 0.4, surface impression matt (Fig. 19). Iran. Steppes, semideserts and rural habitats from E Turkey east to NE China. .... ***subpilosa***

13a Few setae on underside of head usually present, nGu 1.58 ± 0.86. Pronotum always with a number of setae, nPn 9.1 ± 6.1. Mesosoma usually with a large percentage of dark pigmentation, PIGM 74 ± 20. Eye large, EYE/CS 0.302 ± 0.013. Scape short, SL/CS 1.030 ± 0.034. Ocellar distance large, OceD/CS 0.170 ± 0.008. Discriminant 4.993*nGu+0.003*nPn+0.005*PIGM-3.932*SL+12.69*EYE +6.224*OceD-4.928 > 0 [error 0% in 15 nest sample means and 16% in 68 individuals]. Endemic in south-central Anatolia. .... ***anatolica***

13b Setae on underside of head fully absent. Character combination different. Discriminant < 0 [error 0% in 502 nest sample means and 0.2% in 1669 individuals]. **14**

14a Scape very short, SL/CS 1.025 ± 0.029. Distance of transverse ripples on dorsum of first gaster tergite large, RipD 6.75 ± 0.78. Head, mesosoma, coxae, all appendages and petiole homogenously reddish yellow; dark pigment strongly reduced, PIGM 4.2 ± 4.7. Discriminant 12.104*CW-9.922*SL-7.329*PeW+1.957*RipD -0.038*nPn-0.010*PIGM-7.597 > 0 [error 1.3% in 79 individuals]. Steppes, semideserts and rural areas from NE Iran to E Mongolia. .... ***orangea***

14b Scape longer, SL/CS 1.083 ± 0.039. Distance of transverse microsculpture on gaster tergites smaller, RipD 4.53 ± 0.44. Percentage of dark pigmentation on head and mesosoma variable but often larger, PIGM 36.1 ± 34.9. Discriminant < 0 [error 0.6% in 1590 individuals]. **15**

15a Scape very long, SL/CS 1.160 ± 0.033. Distance of transverse microsculpture on gaster tergites large, RipD 5.71 ± 0.48. Pronotum without setae, nPn 0.05 ± 0.20. Mesosoma with large areas of dark pigmentation, PIGM 69 ± 22. Discriminant 0.047*nPn+2.527*RipD-9.861*CL+14.138*SL-14.031*EYE-22.264*GHL-12.602 > 0 [error 0% for means of 32 nest samples and 4.6% for 87 individuals]. Humid regions of Turkey and N Iran. .... ***persica***

15b Scape shorter, SL/CS 1.078 ± 0.035. Distance of transverse microsculpture on gaster smaller, RipD 4.46 ± 0.32. Pronotum frequently with setae, nPn 4.52 ± 4.82. Pigmentation variable. Discriminant < 0 [error 0% for 442 nest sample means and 0.7% for 1502 individuals]. **16**

16a Pronotum, mesonotum, petiole scale above stigma and flexor profile of hind femur with more numerous setae, nPn 11.5 ± 5.1, nMn 6.6 ± 4.2, nPe 3.1 ± 1.6, nHFfl 2.64 ± 1.7. Discriminant 0.121*nPn+ 0.136*nMn+0.418*nHFfl +0.451*nPe+3.449*CL-6.299*CW-3.896*SL+11.042*OceD+3.822 > 0 [error 0% in 100 nest samples and 9% in 324 individual workers]. Pyrenees to West Siberia (86° E)........... ***rufibarbis***

16b Pronotum, mesonotum, petiole scale above stigma and flexor profile of hind femur only with few setae, nPn 2.6 ± 2.9, nMn 1.3 ± 1.7, nPe 0.6 ± 0.8, nHFfl 0.42 ± 0.67. Discriminant < 0 [error 0.3% in 342 nest samples and 1.4% in 1178 individual workers].......... **17**

17a Mesosoma usually with high percentage of dark pigmentation, PIGM 65 ± 29; pigmentation contrast on genae usually strong, CONT 0.58 ± 0.29. Pronotum and mesonotum without or only with very few setae, nPn 1.20 ± 1.79, nMn 0.68 ± 1.07. Eye larger, EYE/CS 0.301 ± 0.009. Discriminant 40.054*EYE-7.417*CW+6.659*MtSt -6.77*MtPpSt-0.115*nPn+0.032*nMn-0.238*nHFfl+0.144*nPe+1.932*CONT+0.033*PIGM-6.049 > 0 [error 3.7% in 134 nest samples] (Figs 20-22). .... ***cunicularia***

17b Mesosoma usually with low percentage of dark pigmentation, PIGM 10 ± 13; pigmentation contrast on genae usually weak, CONT 0.17 ± 0.24. Pronotum and mesonotum with more setae, nPn 4.2 ± 2.9, nMn 1.7 ± 1.8. Eye smaller, EYE/CS 0.288 ± 0.010. Discriminant < 0 [error 0.6% in 156 nest samples]. **18**

18a Determination difficult. It requires RAV-corrected data and an extended character set, see supplementary information SI1. With GHL/CS_{1400} in % and RipD and $sqPDG_{1400}$ in µm, discriminant $2.408*CS+18.63*CL/CW_{1400}-1.478*SL/CS_{1400}-2.304*OceD/CS_{1400}+20.221*EYE/CS_{1400}+0.003*PeW/CS_{1400}+13.424*MtSt/CS_{1400}+69.106*MtPpSt/CS_{1400}+6.98*MtMtp/CS_{1400}-0.354*GHL/CS_{1400}-0.024*nPn_{1400}+0.156*nMn_{1400}+0.073*nPe_{1400}-0.065*nHFfl_{1400}-0.712*sqPDG_{1400}-0.091*RipD_{1400}+0.007*PIGM_{1400}+0.545*CONT_{1400}-56.44 < 0$ [error 2.4% in 83 nest samples]. More southern latitudes, absent from Central Europe and southern Fennoscandia (Figs 23-25). .... ***clara***

18b Discriminant > 0 [error 0% in 73 nest samples]. More northern latitudes, going north to S Fennoscandia (Figs 26-28). .... ***lusatica***

19a Outside Tibetan Plateau. **20**

19b Tibetan Plateau **45**

20a Dorsal plane of scape always without setae. Genae without or only few setae, nGen 0.18 ± 0.61, at most 6.5. .... **21**

20b Dorsal plane of scape with many setae, nSc 11.0 ± 2.1 [8.5, 14.5]. All body parts extremely hirsute. Genae with many setae, nGen 7.3 ± 1.9 [5.3, 11.0]. Propodeo-metapleural surface with many setae 27.3 ± 5.2 [20, 34.5]. Tian Shan (Figs 29-31). .... ***superpilosa* n.sp.**

21a Posterior margin and underside of head very hirsute, nCH 22.9 ± 6.3, nGu 9.2 ± 2.8. Eye large, EYE/CS 0.312 ± 0.012, petiole rather narrow, PeW/CS 0.380 ± 0.028. Discriminant 0.296*nCH +0.382*nGu-0.175*nPrMe -7.899*PeW+19.551*EYE-7.753 > 0 [error 0.3% in 330 individuals]. Temperate zone of Siberia. Not in Tian Shan and Pamirs. .... ***cinerea***

21b Posterior margin and underside of head much less hirsute. Hirsute individuals of the *F. subpilosa* group species from Tian Shan and Pamirs may reach with nCH and nGu in the lower range of *F. cinerea* that, however, does not occur in these regions. Discriminant < 0 [error 0.1% in 2063 individuals]. **22**

22a Anteromedian margin of clypeus in dorsofrontal view not excavated. Scape shorter. Discriminant 17.018*SL -15.061*CL+0.489*RipD-8.397 < 0 [error 0% in 1947 individuals].......... **23**

22b Anteromedian margin of clypeus in dorsofrontal view slightly excavated (Fig. 32). Scape very long. Distance of transverse microsculpture on dorsum of 1st gaster tergite large, RipD 9.37 ± 0.52. Discriminant > 0 [error 0% in 38 individuals]. Myanmar and the adjacent part of Chinese province Yunnan .... ***rufolucida***

23a Himalayas. **24**

23b Outside Himalayas **26**

24a Flexor profile of hind femur with setae, nHFfl 7.5–10.5. Eye small, EYE/CS_{1400} 0.275–277. Only type sample from Kashmir known. .... ***kashmirica***

24b Flexor profile of hind femur only with occasional setae, nHFfl 0.5 ± 0.8. Eye larger, EYE/CS_{1400} 0.291 ± 0.006. .... **25**

25a Probably absent from the Himalayas (data here for comparison). Discriminant 32.856*MtMtp +21.672*MtPpSt +0.8639*PeW-5.588*SL-24.29*CW-5.752 > 0 [error 3.0% in 67 nest sample means] (Figs 23–25). .... ***clara***

25b Discriminant < 0 [error 0% in 16 nest sample means] (Figs 33-35). .... ***himalayensis* n.sp.**

26a China east of 98°E. **27**

26b Other regions. **31**
27a Very slender. SL/CS 1.185 ± 0.031, MtPpSt 0.397 ± 0.010, MtMtp 0.710 ± 0.011. Discriminant 33.549*CL -19.764*MtPpSt-46.024*MtMtp+0.521*RipD+0.557 < 0 [error 0% in 19 individuals]. .... ***glabridorsis***
27b Less slender. SL/CS 1.068 ± 0.039, MtPpSt 0.351 ± 0. 011, MtMtp 0.640 ± 0.014. Discriminant > 0 [error 0% in 375 individuals]. **28**
28a Distance of transverse ripples on dorsum of 1st gaster tergite small, RipD 4.24 ± 0.28. Pronotum with many setae, nPn 14.1 ± 4.2. Eye small, EYE/CS 0.286 ± 0.008. Discriminant 1.306*RipD+13.629*EYE -0.228*nPn-10.468 < 0 [error 0% in 276 individuals]. **29**
28b Distance of transverse ripples on dorsum of 1st gaster tergite larger, RipD 6.14 ± 0.65. Pronotum with very few setae, nPn 1.29 ± 1.28. Eye large, EYE/CS 0.303 ± 0.010. Discriminant > 0 [error 0% in 212 individuals]. **30**
29a Flexor profile of hind femur usually with few setae, nHTFfl 2.88 ± 1.51. Distance between metanotal stigma and caudal margin of metapleuron smaller, MtMtp/CS 0.631 ± 0.012. Distance between metanotal stigmata larger, MtSt/CS 0.128 ± 0.017. .... ***clarissima***
29b Flexor profile of hind femur usually without setae, nHTFfl 0.18 ± 0.26. Distance between metanotal stigma and caudal margin of metapleuron larger, MtMtp/CS 0.652 ± 0.015. Distance between metanotal stigmata smaller, MtSt/CS 0.114 ± 0.010. Bona species? Data based on type series only (Figs 36, 37). .... ***sinae***
30a Distance of pubescence hairs on dorsum of 1st gaster tergite large, sqPDG > 3.7. Gaster very shiny (Figs 38-40). .... ***gebaueri* n.sp.**
30b Distance of pubescence hairs on dorsum of 1st gaster tergite low, sqPDG < 3.7. Gaster not very shiny. Population in Yunnan, isolated from Central Asian main population (Figs 41-43). .... ***tianshanica***
31a Back of head almost always with setae, nCH 1.73 ± 2.41. Pronotum with many setae, nPn 19.6 ± 8.2. Eye smaller, EYE/CS 0.284 ± 0.009. Setae on 1st gaster tergite longer, GHL/CS 10.16 ± 1.73, Discriminant 23.693*EYE+0.218*nCH-0.124*nPn-23.986*GHL +0.509*RipD -7.674 < -0.74 [error 0% in 137 nest sample means]. *F. subpilosa* group. **32**
31b Discriminant within the interval [-0.74, 0.65]. **36**
31c Back of head only exceptionally with single setae, nCH 0.03 ± 0.14. Pronotum on average with fewer setae, nPn 4.1 ± 5.18.Eye larger, EYE/CS 0.295 ± 0.011. Setae on 1st gaster tergite shorter, GHL/CS 7.56 ± 1.18. Discriminant > 0.65 [error 0% in 383 nest sample means]. *F. rufibarbis* group. **39**
32a Distance between transverse microsculpture on gaster tergites larger, RipD 5.69 ± 0.45. Distance between metathoracal spiracles smaller, MtSt/CS 0.108 ± 0.013. Distance between metathoracal spiracle and hind margin of metapleuron larger, MtMtp/CS 0.647 ± 0.012. Discriminant 2.681*RipD-31.762*MtSt+11.55*MtMtp-18.082 > 0 [error 0% in 127 individuals]. East Turkey to NE China. .... ***subpilosa***
32b Distance between transverse microsculpture on gaster tergites smaller, RipD 4.28 ± 0.29**.** Distance between metathoracal spiracles larger, MtSt/CS 0.132 ± 0.018. Distance between metathoracal spiracle and hind margin of metapleuron smaller, MtMtp/CS 0.638 ± 0.015. Discriminant < 0 [error 0% in 429 individuals]. **33**
33a Siberia and Tibetan Plateau between 88°E and 127°E. Mesonotum and propodeo-metapleural surface with only few setae, nMn 4.50 ± 2.59, nPrMe 1.47 ± 1.27. Gaster setae shorter, GHL/CS 8.49 ± 1.19%. Discriminant 0.129*nPrMe+1.08*nMn+35.353*GHL-19.758*MtPpSt+1.958*sqPDG-2.977 < 0 [error0% in 47 nest sample means]. .... ***clarissima***
33b NW Himalayas, Pamirs, Tian Shan and margin of Tarim Bassin between 70°E and 82°E. Mesonotum and propodeo-metapleural surface with more setae nMn 11.51 ± 3.94, nPrMe 8.29 ± 4.12. Gaster setae longer, GHL/CS 10.72 ± 1.38. Discriminant > 0 [error 0% in 76 nest sample means]. **34**
34a Underside of head with very few setae nGu 0.65 ± 0.58. Setae number on pronotum less large, nPn 20.2 ± 4.6. Discriminant 0.494*nGu+0.116*nPn-17.152*PeW+9.266*MtMtp-2.3421 < 0 [error 0% in 41 nest sample means]. .... ***litoralis***
34b Underside of head with more setae nGu 2.70 ± 1.61. Setae number on pronotum larger, nPn 32.6 ± 8.7. Discriminant > 0 [error 0% in 35 nest sample means]. **35**
35a Seta numbers on underside of head and extensor profile of hind tibia less large, nGu 1.79 ± 0.83, nHT 3.31 ± 1.99. Petiole narrower PeW/CS 0.392 ± 0.024. Distance between the metathoracal spiracles and metathoracal and propodeal spiracle larger, MtSt/CS 0.139 ± 0.014, MtPpSt/CS 0.357 ± 0.008. Discriminant 0.318*nGu+0.091*nHT+21.06*PeW-45.574*MtSt-56.435*MtPpSt-17.479*CW-0.495 < 0 [error 0% in 21 nest sample means]. .... ***pamirica***
35b Seta numbers on underside of head and extensor profile of hind tibia large, nGu 3.86 ± 1.61, nHT 10.36 ± 5.58. Petiole wider PeW/CS 0.425 ± 0.025. Distance between the metathoracal spiracles and metathoracal and

propodeal spiracle lower, MtSt/CS 0.123 ± 0.015, MtPpSt/CS 0.336 ± 0.009. Discriminant > 0 [error 0% in 14 nest sample means] (Figs 44-46). .... ***kirgisica* n.sp.**

36a Pronotum and propodeo-metapleural surface always with setae, nPn 13.9 ± 6.0, nPrMe 2.3 ± 2.8. Percentage of dark mesosomal pigmentation usually low, PIGM 15.1 ± 19.4. Discriminant 9.793*PeW-30.865*EYE-0.138*nPn-0.249*nPrMe+0.328*nPe+0.149*mHFfl+5.144> 0 [error 0% in 238 nest sample means]. **37**

36b Pronotum and propodeometapleural surface usually without or with very few setae, nPn 1.44 ± 1.30, nPrMe 0.03 ± 0.0. Percentage of dark mesosomal pigmentation usually large, PIGM 83.1 ± 13.7. Discriminant < 0 [error 0% in 42 nest sample means]. Tian Shan, Tarbagatai, Saur and Bogda Shan mountains (Figs 41-43). ... ***tianshanica***

37a Distance between transverse microsculpture on gaster tergites smaller, RipD 4.35 ± 0.33. Petiole wider, PeW/CS 0.454 ± 0.035. Number of setae on flexor profile of hind femur smaller, nHFfl 2.76 ± 1.61. Discriminant 2.054*RipD -13.194*PeW+6.136*SL+0.255*nHFfl-9.85 < 0 [error 0.3% in 595 individuals]. **38**

37b Distance between transverse microsculpture on gaster tergites larger, RipD 5.62 ± 0.46. Petiole narrower, PEW/CS 0.393 ± 0.022. Number of setae on flexor profile of hind femur larger, nHFfl 6.7 ± 2.4. Discriminant > 0 [error 0% in 194 individuals]. East Turkey to NE China (Fig. 19). .... ***subpilosa***

38a Palaearctic from 4°W to 86°E. Distance between metanotal and propodeal spiracle larger, MtPpSt/CS 0.369 ± 0.012. Eye larger, EYE/CS 0.290 ± 0.010. Petiole wider, PeW/CS 0.473 ± 0.027 . Discriminant 40.787*MtPpSt+80.048*EYE+8.853*PeW-31.505*CW +0.128*nPn-14.267 [error 0% in 28 nest sample means]. .... ***rufibarbis***

38b Palaearctic from 88°E to 127°E. Distance between metanotal and propodeal spiracle smaller, MtPpSt/CS 0.347 ± 0.010. Eye smaller, EYE/CS 0.286 ± 0.008. Petiole narrower, PeW/CS 0.431 ± 0.027. Discriminant < 0 [error 4.2% in 47 nest sample means]. .... ***clarissima***

39a Distance between transverse microsculpture on gaster tergites large, RipD 7.93 ± 0.82. Pronotum always with many setae, nPN 11.9 ± 3.0. Distance between metathoracal spiracles low, MtSt/CS 0.118 ± 0.013. Discriminant 0.205*nPn+0.933*RipD-12.506*MtSt-5.579 > 0 [error 0% in 106 individuals]. Lowland and mountains at the northern margin of Tarim Bassin. .... ***tarimica***

39b Character combination different. If nPn similarly large, RipD much smaller. If RipD similarly large, nPn much smaller. Distance between metathoracal spiracles larger. Discriminant < 0 [error 0.8% in 993 individuals] **40**

40a Mesosoma with many setae, nPn 11.07 ± 4.81, nMn 6.69 ± 4.13, nPrMe 0.80 ± 1.15. Flexor profile of hind tibia with a low number of setae, nHFfl 2.66 ± 1.69. Discriminant 0.234*nPn-0.283*nPrMe +0.307*nHFfl-3.622*CW+ 0.553*nPe+0.076*nMn+1.942 > 0 [error 1% in 100 nest sample means]. .... ***rufibarbis***

40b Mesosoma and flexor profile of hind femur with much fewer setae, Pn 1.42 ± 1.75, nMn 0.72 ± 1.13, nPrMe 0.02 ± 0.12, nHFfl 0.37 ± 0.63. Discriminant < 0 [errror 0.3% in 321 nest sample means]...................................... **41**

41a Distance of transverse microsculpture on dorsum of 1st gaster tergite larger, RipD 6.78 ± 0.81. Whole head, mesosoma, coxae, all appendages and petiole in typical cases reddish yellow; sometimes in smaller specimens diffuse brown spots may occur on posterior vertex and dorsal promesonotum, PIGM 4.4 ± 4.6. Discriminant 19.457*MtPpSt-6.071*CW+0.022*PIGM-1.071*RipD+4.828 < 0 [error 3.1% in 64 Individuals and 0% in 23 nest sample means]. Steppes and semideserts from NE Iran to E Mongolia. .... ***orangea***

41b Character combination different. If having similarly large RipD, then PIGM > 17. If having similarly low PIGM, then RipD much smaller. Discriminant > 0 [error 0.2% in 845 individuals and 0% in 254 nest sample means]. **42**

42a Distance of transverse microsculpture on dorsum of 1st gaster tergite larger, RipD 6.04 ± 0.61. Distance between metanotal and propodeal spiracle and between metanotal spiracle and caudalmost point of metapleuron smaller, MtPpSt/CS 0.351 ± 0.010, MtMtp/CS 0.644 ± 0.012. Discriminant 2.158*RipD+12.206*CL-13.902*MtPpSt-14.704*MtMtp-9.06 > 0 [error 3.2% in 155 individuals]. Mountain areas of Tian Shan, Tarbagatai, Saur, Bogda Shan (Figs 41-43) .... ***tianshanica***

42b Distance of transverse microsculpture on dorsum of 1st gaster tergite smaller, RipD 4.43 ± 0.33. Distance between metanotal and propodeal spiracle and between metanotal spiracle and caudalmost point of metapleuron larger, MtPpSt/CS 0.372 ± 0.013, MtMtp/CS 0.671 ± 0.015. Discriminant < 0 [error 0.6% in 690 individuals]. **43**

43a Mesosoma usually with high percentage of dark pigmentation, PIGM 65 ± 29; pigmentation contrast on genae usually strong, CONT 0.58 ± 0.29. Eye larger, EYE/CS 0.301 ± 0.009. Setae on 1st gaster tergite shorter, GHL/CS 6.76 ± 0.83%. Pronotum and mesonotum without or only with very few setae, nPn 1.20 ± 1.79, nMn 0.68 ± 1.07. Discriminant 0.032*PIGM+2.182*CONT-9.706*CW-6.864*PeW+40.992*EYE

-0.084*OceD+7.93*MtSt-13.888*MtPpSt-9.038*GHL-0.164*nHFfl +0.19*nPe+7.334*CL- 5.6217 > 0 [error 1.5% in 134 nest sample means]. Only known so far from Manrak Mountains, E Kazakstan (Figs 20–22). .... ***cunicularia***

43b Mesosoma usually with low percentage of dark pigmentation, PIGM 8 ± 12; pigmentation contrast on genae usually low, CONT 0.23 ± 0.23. Eye smaller, EYE/CS 0.288 ± 0.009. Setae on 1st gaster tergite longer, GHL/CS 7.37 ± 0.95%. Pronotum and mesonotum with few setae, nPn 2.04 ± 1.95, nMn 0.88 ± 1.25. Discriminant < 0 [error 1.3% in 77 nest sample means]. **44**

44a Setae on pro-mesonotum very few, nPn 1.64 ± 1.57, nMn 0.65 ± 0.91. Discriminant 0.213*nPn+0.32*nMn+0.321*nPe-0.029*PIGM+2.575*CONT-10.619*CW-0.126*OceD -22.527*MtSt+23.704*MtMtp-6.471 < 0 [error 0% in 67 nest sample means] (Figs 23–25). .... ***clara***

44b Setae numbers on pro-mesonotum larger, nPn 3.87 ± 2.62, nMn 2.15 ± 2.17. Discriminant > 0 [error 0% in 10 nest sample means]. Not in Tian Shan (Figs 26–28). .... ***lusatica***

45a Underside and posterior margin of head without or with only few setae; nGu 0.49 ± 0.53, maximum 4; nCH 0.43 ± 0.60, maximum 3. Scape longer, SL/CS 1.063 ± 0.043. Discriminant 0.369*nCH+1.326*nGu-0659*SL-4.658 < 0 [error 0% in 331 individuals]. **46**

45b Underside and posterior margin of head always with setae, nGu 7.8 ± 1.7, nCH 10.0 ± 4.5. Scape short, SL/CS 0.988 ± 0.023. Discriminant > 0 [error 0% in 22 individuals] (Figs 47–49). W Tibet. .... ***lhasaensis***

46a Dorsum of 1st gaster tergite shiny, with dilute pubescence and wide distance of transverse microriples; RipD 6.44 ± 0.65, at least 5.0; sqPDG 7.35 ± 1.66, at least 3.94. Pronotum without or very few setae, nPn 0.9 ± 1.2. Chinese provinces Quinghai, Gansu, Shaanxi and Sichuan (Figs 38–40). .... ***gebaueri* n.sp.**

46b Dorsum of 1st gaster tergite matt, with dense pubescence and low distance of transverse microripples; RipD 4.25 ± 0.29, at most 4.9; sqPDG 3.20 ± 0.17, at most 3.67. Pronotum usually with setae, nPn 14.1 ± 4.3. ... ***clarissima***

6 The species of the *Formica cinerea* group

6.1 *Formica cinerea* Mayr 1853

***Formica cinerea* Mayr 1853** [type investigation]

This taxon has been described from Bozen (Bolzano) in South Tyrol / Italy. Ivestigated was one type worker, labelled “*Tirol G.Mayr \ zu G.Mayr Bd. III. p. 101, 277 \ Type \ Form. cinerea det.G.Mayr* “, NHM Wien. The specimen is allocated to the *Formica cinerea* cluster with p=0.9731 in a wild-card run of a 3-class LDA considering the taxa *F. cinerea*, *F. fuscocinerea* and *F. selysi* (see supplementary information SI3, setting 1).

***Formica cinerea* var. *imitans* Ruzsky 1902** [zoogeography, redescription by Dlussky (1967)]

This taxon has been described from Orenburg/ W Siberia. The synonymy is obvious as *F. cinerea* is the only *F. cinerea* group species found in this region.

***Formica cinerea* var. *armenica* Ruzsky 1905** [type investigation]

This taxon has been described from the region of Mount Ararat / Turkey. Investigated was the lectotype worker 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. The lectotype is allocated to the *Formica cinerea* cluster with p=0.9997 in a wild-card run of a 3-class LDA considering the species *F. cinerea*, *F. balcanina* and *F. georgica* (see supplementary information SI3, setting 2)

Formica cinerea cinereoimitans Ruzsky 1905 [zoogeography]

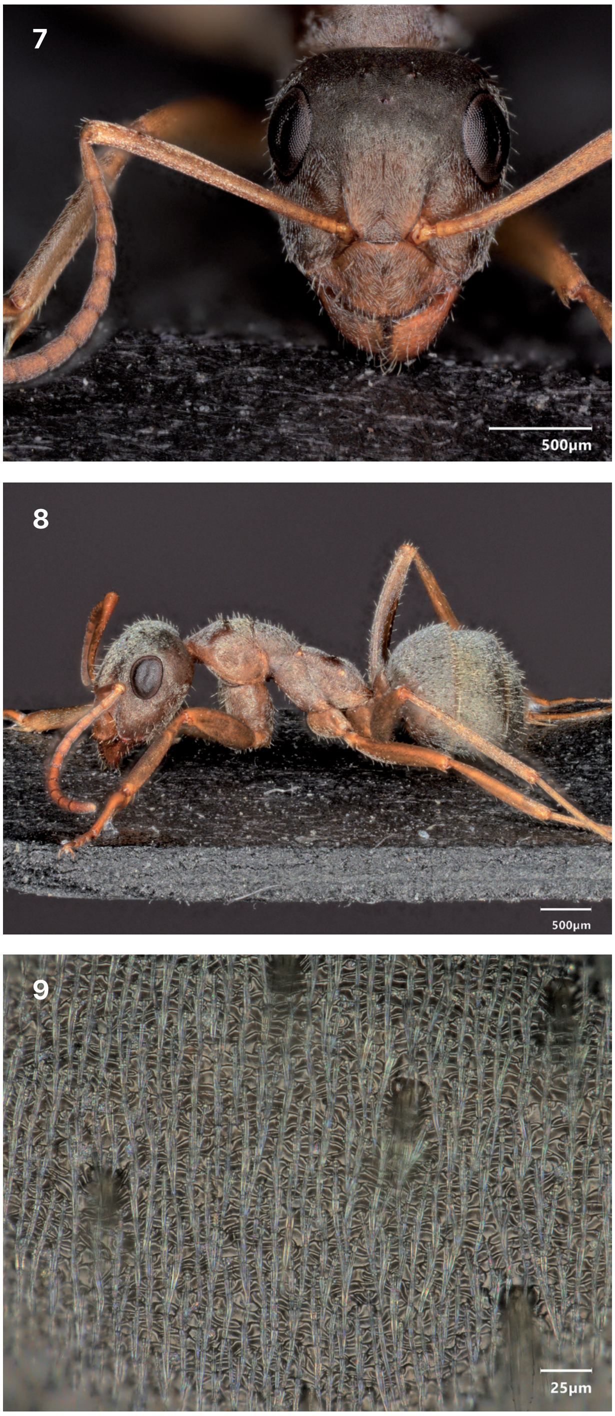
This name was introduced by Ruzsky within the section treating *Formica cinerea var. imitans* on page 405. Full text in translation from the Russian: “Transitional forms (*cinereo-imitans* m.) with dark legs, dark brown patches on head and thorax or with the whole thorax darkened” (Ruzsky 1905). Identification of type specimens seems impossible as no type locality was given, but the synonymy is very likely as *Formica cinerea* is the only *F. cinerea* group species occuring in the geographic region considered by Ruzsky.

***Formica cinerea* var. *subrufoides* Forel 1913** [type investigation]

This taxon has been described from Bolzano (Bozen) / Italy. Investigated were 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. The specimens are allocated to the *Formica cinerea* cluster with p=0.9994 in a wild-card run of a 3-class LDA considering the species *F. cinerea*, *F. fuscocinerea* and *F. selysi* (see supplementary information SI3, setting 1).

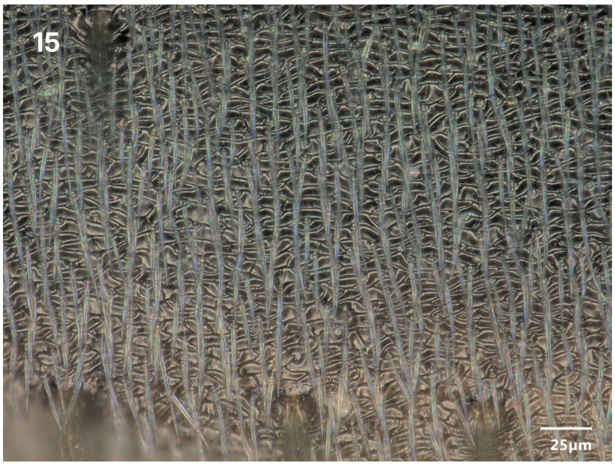
***Formica cinerea* var. *cinereoglebaria* Kulmaticky 1922** [zoogeography]

This taxon is a *nomen nudum* and has been reported from Poland: “Nizina Wielkopolsko-Kujawska”. The

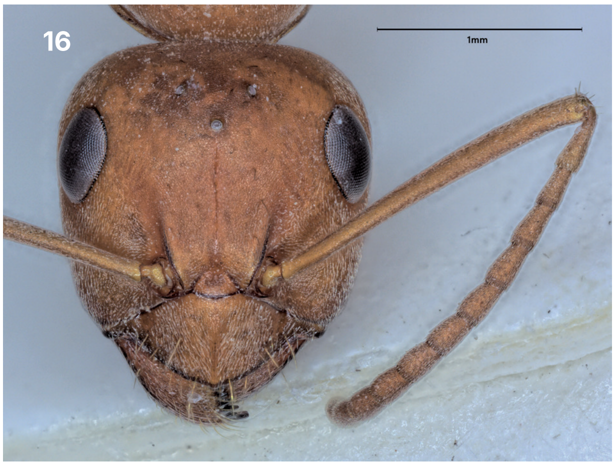


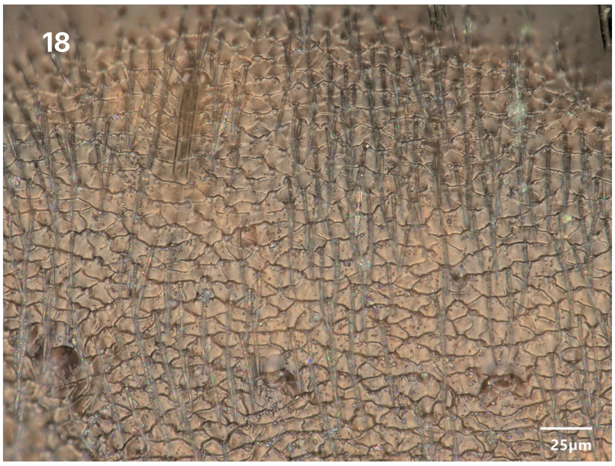
Figures 7–9. *Formica selysi* / Buisson / France, 2014-07-07; (**7**) head, (**8**) lateral (horizontally mirrored), (**9**) 1st gaster tergite.

Figures 10-12. *Formica torrentium*, Castiello de Jaca / Spain, 2025-05-16; (**10**) head, (**11**) lateral, (**12**) 1st gaster tergite.



Figures 13–15. *Formica tombeuri*, Rio Cinca / Spain, 2012-06-14; (**13**) head, (**14**) lateral (horizontally mirrored), (**15**) 1st gaster tergite.





Figures 16-18. *Formica iranica* n.sp., holotype, Kashan, Komjan / Iran, 2012-05-09; (**16**) head, (**17**) lateral, (**18**) 1st gaster tergite.

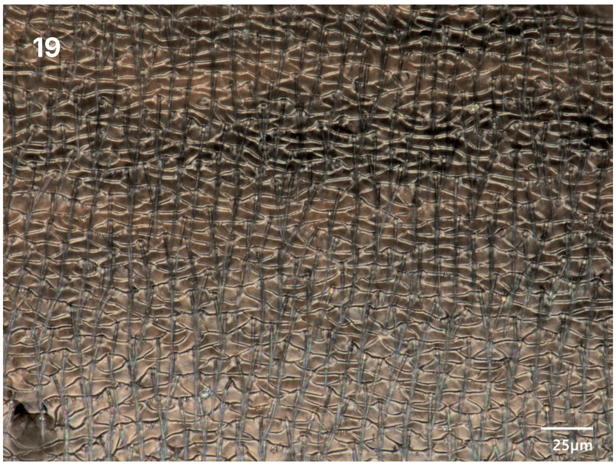
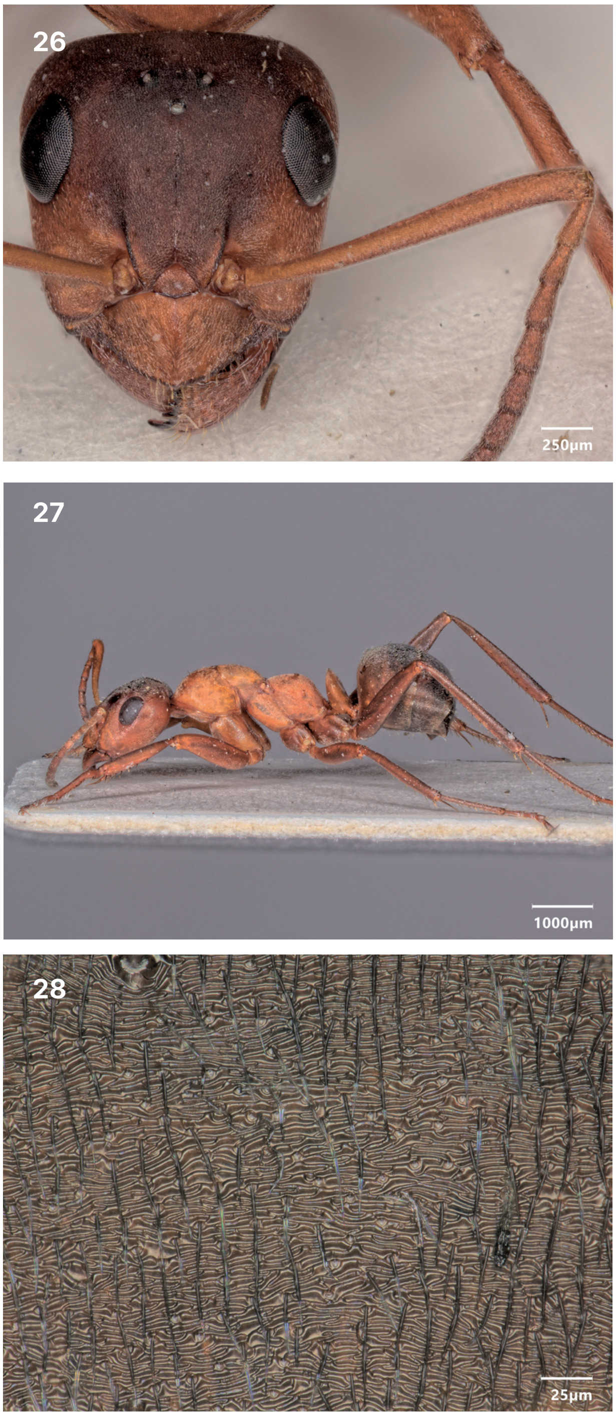


Figure 19. *Formica subpilosa*, Lepsy river / Kazakhstan, 2001-07-18; 1st gaster tergite.

Figures 20–22. *Formica cunicularia*, neotype, Fumel / France, 2008-07-25; (**20**) head, (**21**) lateral (horizontally mirrored), (**22**) - 1st gaster tergite.

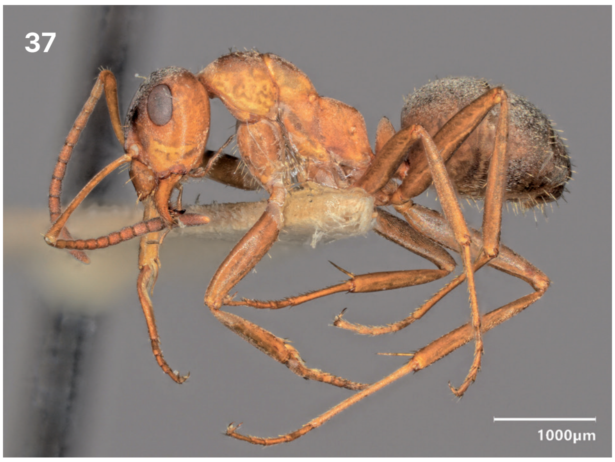
Figures 23–25. *Formica clara*, Abkenar / Iran, 2016-01-15; (**23**) head, (**24**) lateral, (**25**) 1st gaster tergite.



Figures 26–28. *Formica lusatica*, Halbendorf / Germany, 1992-07-30; (**26**) head, (**27**) lateral, (**28**) 1st gaster tergite.

Figures 29–31. *Formica superpilosa n.sp.*, holotype, Kok-Bel / Kyrgyzstan, 2004-07-31; (**29**) head, (**30**) lateral, (**31**) 1st gaster tergite.

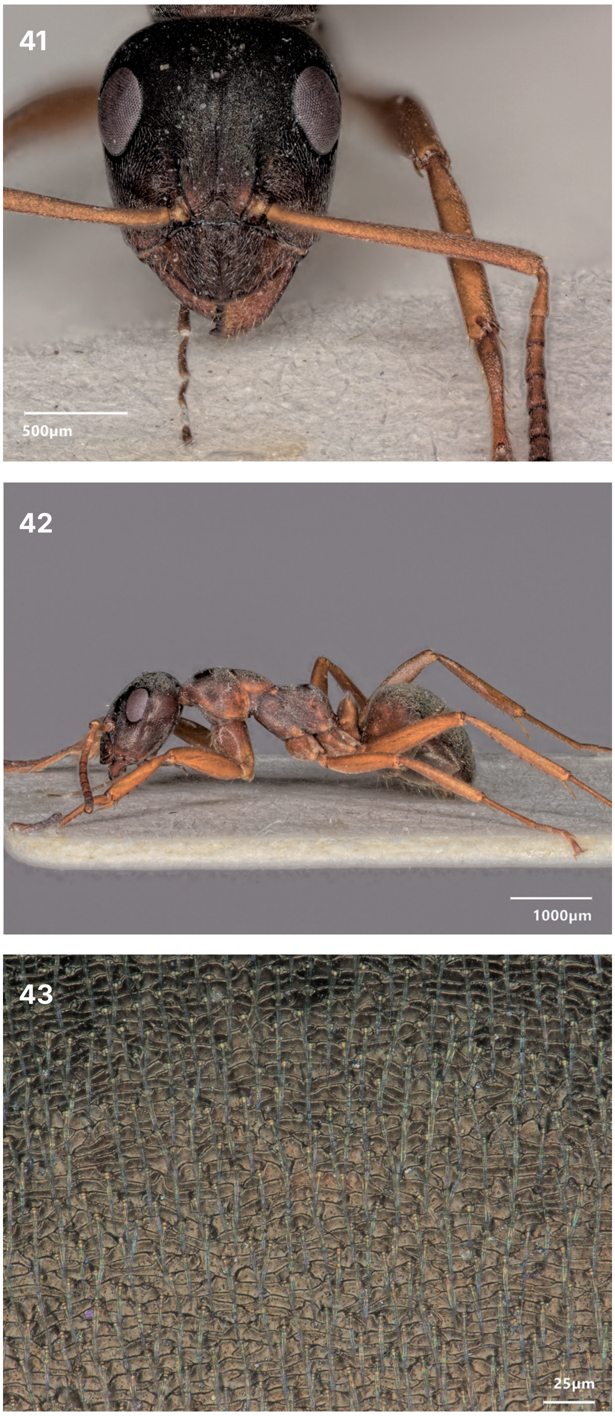
Figure 32. *Formica rufolucida*, Niutoushan / China, 2010-06-01; clypeus.



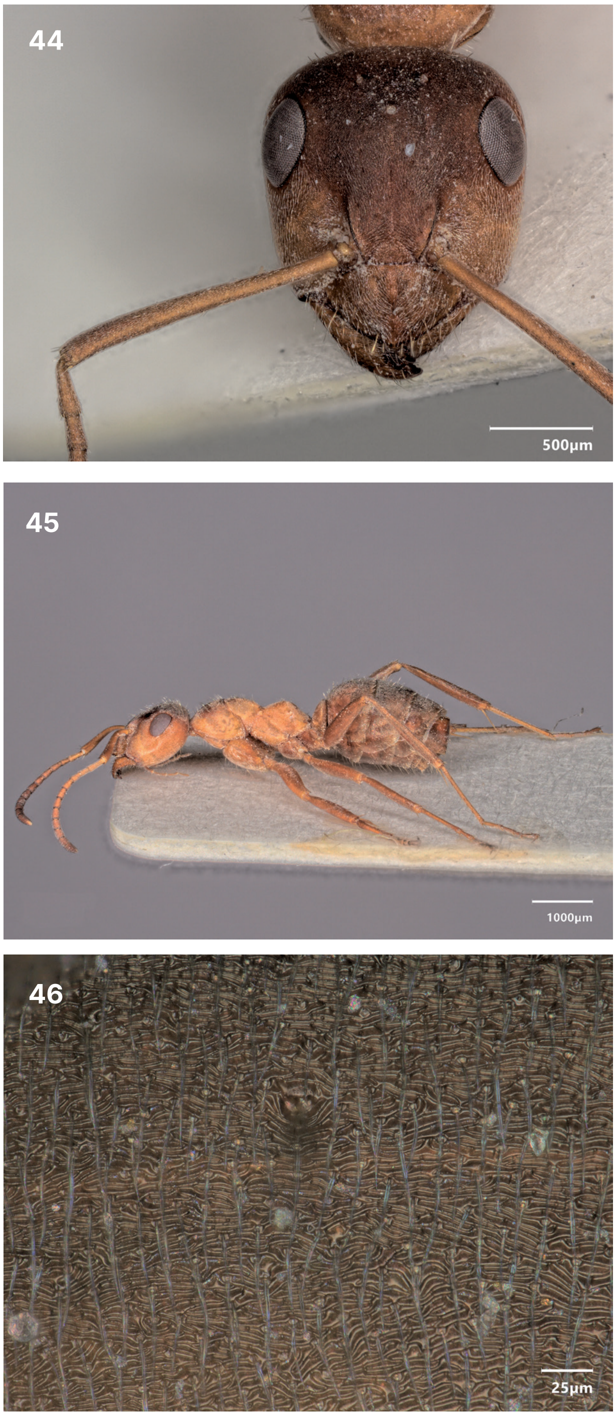
Figures 33–35. *Formica himalayensis n.sp.*, holotype, Fagu / India, 1996-09-29; (**33**) head, (**34**) lateral, (**35**) 1st gaster tergite.

Figures 36, 37. *Formica sinae* stat.nov., type, Shantung / China, 1922-08-24; (**36**) head, (**37**) lateral.

Figures 38–40. *Formica gebaueri n.sp.*, holotype, Fagu / India, 1996-09-29; (**38**) head, (**39**) lateral, (**40**) 1st gaster tergite.



Figures 41–43. *Formica tianshanica*, holotype, Kap Tshigai valley / Kyrgyzstan, 1998-07-16; (**41**) head, (**42**) lateral (horizontally mirrored), (**43**) 1st gaster tergite.



Figures 44–46. *Formica kirgisica n.sp.*, holotype, Kolnysh-Kyja / Kyrgyzstan, 1998-07-28; (**44**) head, (**45**) lateral (horizontally mirrored), (**46**) 1st gaster tergite.

Figures 47–49. *Formica lhasaensis n.sp.*, holotype, Lhasa / China, 2012-08-29; (**47**) head, (**48**) lateral, (**49**) 1st gaster tergite.

synonymy is obvious as *F. cinerea* is the only *F. cinerea* group species found in this region.

***Formica cinerea* var. *brevisetosa* Karavajev 1927** [zoogeography, unavailable name]

This taxon has been described from Crimea, Ukraine but the name is an unresolved junior primary homonym of *Formica rufa brevisetosa* Ruzsky 1926. The type locality indicates that this ant can only belong to *Formica cinerea*.

***F. cinerea* var. *sabulosa* Karavaiev, 1931** [type investigation]

This taxon has been described from near Cherson / Ukraine. Karavajev (1931) gave the following data for the type series „Korsunskij Monasteri, Stramniederugen, 13.ix.1928, Nr. 4177“. Investigated were 6 syntype workers labelled “4177. Coll. Karavaievi” and “Syntypus Formica cinerea var. sabulosa Kar.” (written by Kostyuk appr. 1975), ZI Kiev. The type sample is allocated to the *Formica cinerea* cluster with p=1.0000 in a wild-card run of a 3-class LDA considering the species *F. cinerea*, *F. balcanina* and *F. georgica* (see supplementary information SI3, setting 2)

***Formica cinerea* var. *ochracea* Karavajevi 1937** [type investigation]

This taxon has been described from Rybalchanska Dacha in Ukraine. Investigated were 3 syntype workers labelled “Rybaltsa Dacha. Kinb. Karavaev” (in Cyrillic), “360. Coll. Karavaievi”, “Form.(Serviformica) cinerea v. ochracea Karav. Typus” and “Syntypus Formica cinerea var. ochracea Kar.” (written by Kostyuk appr. 1975), ZI Kiev and 3 syntype workers labelled “360. Coll. Karavaievi” and “Syntypus Formica cinerea var. ochracea Kar.” (written by Kostyuk appr. 1975), all in ZI Kiev. The type sample is allocated to the *Formica cinerea* cluster with p=0.9998 in a wild-card run of a 3-class LDA considering the species *F. cinerea*, *F. balcanina* and *F. georgica* (see supplementary information SI3, setting 2)

***Formica cinerea* var. *novaki* Kratochvil 1941** (in Novák & Sadil 1941) [zoogeography]

This taxon has been described from Czechia within a key without giving a type locality. It apparently belongs to the *cinerea* group, but the discrimination to other taxa is based on useless characters of mesosomal shape and color. By zoogeographic indication it can only be a synonym of either *Formica cinerea* or *F. fuscocinerea*. The synonymy supposed here is based on the much higher abundance of *F. cinerea* in Czechia.

All material examined. Numeric phenotypical data were taken in 121 nest samples with 350 workers. The material came from Austria (4 samples), Azerbaijan (1), Bulgaria (1), Belarus (1), Finland (3), Germany (22), Iran (2), Italy (12), Poland (2), Romania (20), Russia (6), Slovakia (2), Sweden (2), Switzerland (13), Turkey (6), Ukraine (24). For details see supplementary information SI1 and SI2.

Geographic range. It has by far the largest range of any species of the *Formica cinerea* group species extending from 6° E in Central Europe to 86°E in West Siberia. The northern distributional border in Finland is currently at 65.3°N. The Caucasian-East Anatolian population extends in southeastern direction to NW Iran (38.2°N, 44.8°E). It ascends in the Alps to 1400 m at 46°N, in the Apennine to 1564 m at 42°N and in E Anatolia to 2300 m at 40°N. The postglacial immigration to Central Europe most probably occurred very soon and rapidly along sand banks of outwash plains and ancient river valleys.

Description: --Worker (Tab. 2-4; key). Medium-sized, CS 1348 ± 145 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape moderately long, CL/CW 1.127 ± 0.020, SL/CS 1.051 ± 0.026. Eye large, EYE/CS 0.309 ± 0.006. Ocellar distance moderately large, OceD/CS 0.165 ± 0.011. Distance between metathoracal spiracles low, MtSt/CS 0.129 ± 0.017. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt 0.338 ± 0.012, MtMtp/CS 0.630 ± 0.012. Petiole scale rather wide PeW/CS 0.384 ± 0.024. Setae on first gaster tergite of medium length, GHL/CS 8.53 ± 0.80%. Genae without or few standing setae, nGen 1.06 ± 1.24. Margin of hind vertex and gula with numerous standing setae, nCH 24.1 ± 6.0, nGu 9.6 ± 2.8. Pronotum and mesonotum with many standing setae, nPn 43.6 ± 10.7, nMn 11.5 ± 4.9. Number of standing setae on propodeum plus upper surfaces of metapleuron moderate, nPrMe 5.9 ± 3.5. Number of setae on petiole scale above the stigma moderate, nPe 7.8 ± 2.2; within all these fringe setae, setae projecting dorsad about as numerous as those projecting laterad, the latter almost always present. Setae on extensor profile of hind femur and extensor profile of hind tibia nearly absent, nHFex 0.02 ± 0.12, nHT 0.21 ± 0.41; those on flexor profile of hind femur rather numerous nHFfl 12.6 ± 3.0. Head, mesosoma, petiole, and gaster covered by a dense silvery pubescence. Distance of transverse ripples and of pubescence hairs on dorsum of first gaster tergite rather low, RipD 5.50 ± 0.64, sqPDG 3.05 ± 0.14. 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. Lateral mesonotum anterior of metathoracic spiracle densely microcarinulate, with a mean carinular crest distance of 4.8-5.5 µm; mean width of carinulae aproximately as wide as the interspaces. 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. 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. The reddish color morph is rather rare in the Central European population whereas it is dominating in specimens from the Ukrainian and South Russian steppes (var. *imitans* Ruzsky).

Habitat and Biology. See Seifert (2018).

Taxonomic comments: The *Formica cinerea* populations from Central and East Europe, from the Balkans, Asia Minor and Caucasus are unseparable by any exploratory data analysis. There is a hybrid zone with *F. balcanina* in Central Romania (see section 6.5) and occasional hybridization with *F. selysi* in the Alps (see section 6.7). *Formica cinerea* is similar to *F. fuscocinerea*. Both species are sympatric in the Apennines, in the Alps and foothills of the Alps. The separation of *F. cinerea* and *F. fuscocinerea* by exploratory data analyses is generally strong in the sympatric area which is west of 17°E (Fig. 50). Considering the 15 characters CS, CL/CW_{1400}, $Oced/CS_{1400}$, EYE/CS_{1400}, SL/CS_{1400}, $MtSt/CS_{1400}$, $MtPpSt/CS_{1400}$, $MtMtp/CS_{1400}$, PeW/CS_{1400}, $nGen_{1400}$, nCH_{1400}, nGu_{1400}, $nPrMe_{1400}$, $nHFfl_{1400}$ and nPe_{1400}, the error of exploratory data analyses within 99 nest samples is 0% in the PCA, NC-part.kmeans and NC-NMDS.kmeans, and 2.0% in NC-Ward. The classification error in the LDA considering the same characters is 3.0% in 297 worker individuals. However, this clear separation is mitigated when *F. cinerea* samples from the whole Palaearctic range are included. Beginning in SE Poland, E Slovakia and W Romania, the eastern population of *F. cinerea* shows some samples with reduced seta numbers on propodeum, metapleuron and petiole which might be confused with *F. f. fuscocinerea* (Sample No 1200, 1203, 1274, 1584, 1588, 1594). This reduction is interpreted here as geographic variation because the population average of the eastern populations clearly indicates a *F. cinerea* morphology and because a PCA considering all 18 characters does not suggest any reasonable cluster separation.

6.2. *Formica cinerea iberica* Finzi 1928

***Formica cinerea* var. *iberica* Finzi 1928** [type investigation]

This taxon has been described from the Pyrenees. Investigated was one 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. The specimen is allocated to the *Formica cinerea* cluster with p=0.9982 in a wild-card run of a 3-class LDA considering the species *F. cinerea*, *F. torrentium* and *F. selysi* (see supplementary information SI3, setting 3 and section 6.4).

All material examined. Numeric phenotypical data were taken in 2 samples with 5 workers. The material came from the Spanish Pyrenees. For details see supplementary information SI1 and SI2.

Geographic range. Only known in two samples from the Pyrenees. The sample from Castiello de Jaca (42.63°N, 0.55°W) is from about 900 m a.s.l.

Description: --Worker (Tab.1). Medium-sized, CS 1300 ± 163 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head moderately long, CL/CW 1.127 ± 0.010. Scape shorter than in *cinerea*, SL/CS 1.029 ± 0.026. Eye large, EYE/CS 0.313 ± 0.008. Ocellar distance moderately large, OceD/CS 0.168 ± 0.003. Distance between metathoracal spiracles larger than in *cinerea*, MtSt/CS 0.143 ± 0.018. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt 0.336 ± 0.003, MtMtp/CS 0.630 ± 0.009. Petiole scale narrower than in *cinerea* PeW/CS 0.361 ± 0.010. Setae on first gaster tergite of medium length, GHL/CS 8.02 ± 0.83%. Genae without or few standing setae, nGen 0.38 ± 0.35. Margin of hind vertex and gula with numerous standing setae, nCH 21.6 ± 2.3, nGu 8.7 ± 1.3. Pronotum and mesonotum with many standing setae. Number of standing setae on propodeum plus upper surfaces of metapleuron moderate, nPrMe 8.0 ± 3.1. Number of setae on petiole scale above the stigma moderate, nPe 9.5 ± 2.4. In difference to *cinerea*, few small setae on extensor profile of hind femur and extensor profile of hind tibia present, nHFex 1.96 ± 1.36, nHT 0.68 ± 0.65; those on flexor profile of hind femur rather numerous nHFfl 13.3 ± 3.7.

Habitat and Biology. No data are available but it is supposed to have inhabited river banks at the southern slope of the Pyrenees.

Taxonomic comments: Despite of weak morphological separation from the nominal form, we maintained this taxon on subspecific level because its status is questionable and has to be checked. Firstly, if really being conspecific with *F. cinerea*, it would represent a widely disjunct Iberian population – the next verified site of the main population is some 630 km NE. Secondly, only two old samples of *F. c. iberica* are known: the type specimen from about 1860 and a sample from Castiello de Jaca /Pyrenees collected by Collingwood in 1966. More recent collections in riverine habitats of the terra typica yielded only *Formica torrentium* and *F. tombeuri* as members of the *F. cinerea* group. This raises the

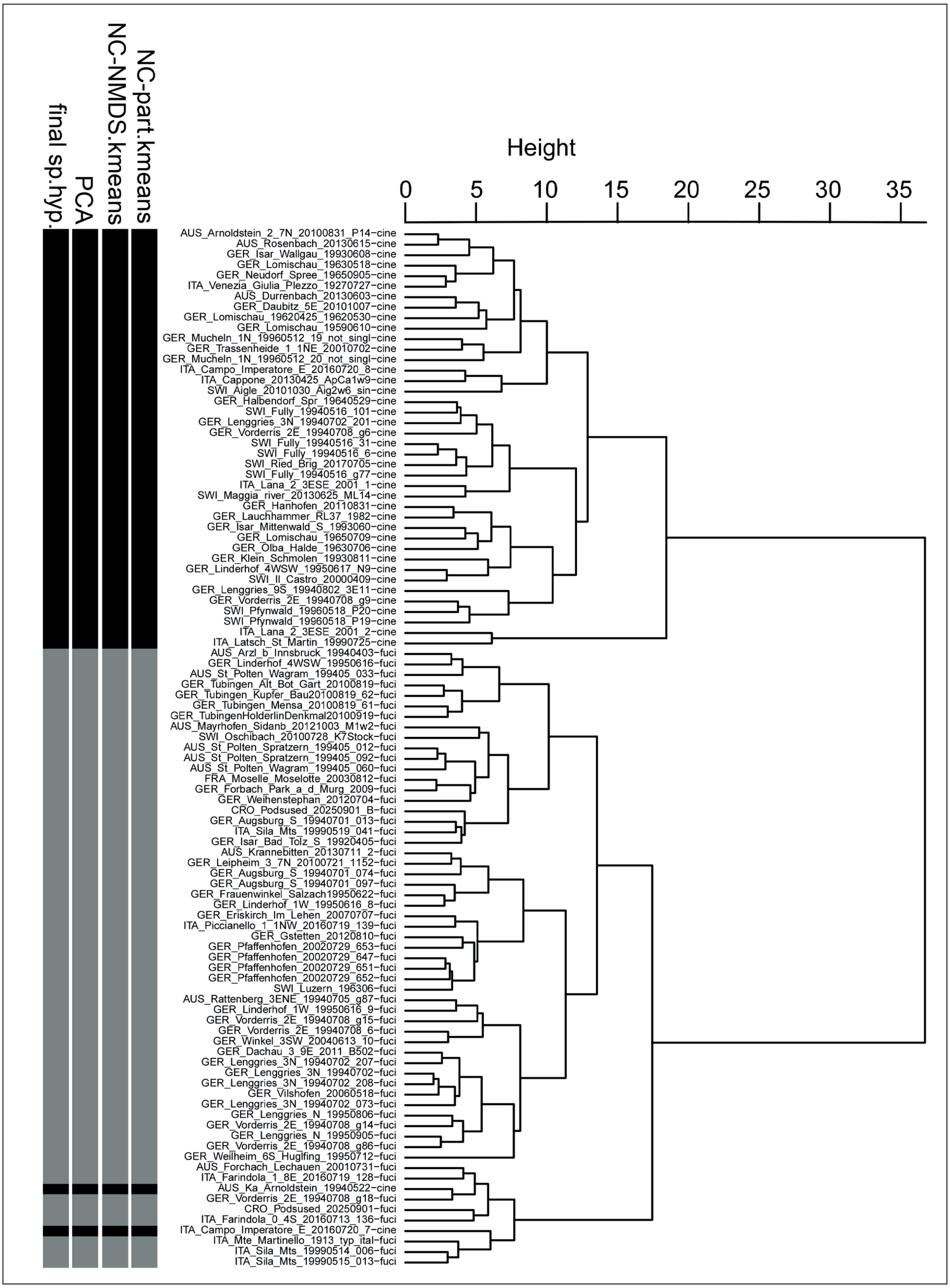


Figure 50. Four variants of exploratory data analyses (EDAs) of nest samples of *Formica cinerea* (n=42) and *F. fuscocinerea* (N=57) from their sympatric area in the Apennines, Alpes and their foothills. NC-Ward dendrogram shown. The mean error of four EDAs relative to the final species hypothesis is 0.5%.

question, if the small and isolated population of *F. c. iberica* became extinct just recently through competive displacement by the other two species or was hybridized to extinction by *F. torrentium*. The hybridization theory is supported by the fact that just those six characters in which the *iberica* workers differ more strongly from those of *cinerea* show mean values approaching the *F. torrentium* condition (Tab. 1).

Table 1. RAV-corrected morphological data of three taxa of the *Formica cinerea* group. Data of a one-tailed ANOVA are placed in the column between the two compared taxa *F. cinerea* and *F. cinerea iberica*.

	cinerea (n=220)	ANOVA $p,F_{1,223}$	***cinerea iberica*** (n=5)	***torrentium*** (n=84)
$nHFex_{1400}$	0.01±0.07	0.000,485.3	1.96±1.36	4.7±2.1
nHT_{1400}	0.22±0.44	0.021,5.40	0.68±0.65	1.3±1.00
SL/CS_{1400}	1.054±0.026	0.037,4.38	1.029±0.017	1.039±0.019
$nPrMe_{1400}$	5.4±2.9	0.055,3.73	8.0±3.1	9.6±2.6
nPe_{1400}	7.6±2.2	0.063,3.50	9.5±2.4	11.3±2.7
$MTST/CS_{1400}$	0.129±0.018	0.087,2.95	0.143±0.008	0.157±0.010
PeW/CS_{1400}	0.376±0.022	n.s.,2.33	0.361±0.010	0.347±0.018
GHL/CS_{1400}	8.39±0.75	n.s.,1.143	8.02±0.83	7.55±0.63
$nGen_{1400}$	0.76±1.04	n.s.,0.65	0.38±0.35	3.5±2.1
$nHFfl_{1400}$	12.2±2.8	n.s.,0.62	13.3±3.7	16.4±2.8
EYE/CS_{1400}	0.311±0.006	n.s.,0.53	0.313±0.008	0.308±0.006
$OceD/CS_{1400}$	0.165±0.011	n.s.,0.41	0.168±0.003	0.159±0.011
nCH_{1400}	23.0±5.8	n.s.,0.27	21.6±2.3	24.1±3.
CS[µm]	1331±137	n.s.,0.26	1300±163	1302±139
$MTPPST/CS_{1400}$	0.338±0.012	n.s.0.22	0.336±0.003	0.327±0.010
nGu_{1400}	8.9±2.6	n.s.,0.025	8.7±1.3	15.3±3.1
$MTMTP/CS_{1400}$	0.630±0.012	n.s.,0.009	0.630±0.009	0.622±0.012
CL/CW_{1400}	1.127±0.022	n.s.,0.001	1.127±0.010	1.142±0.016

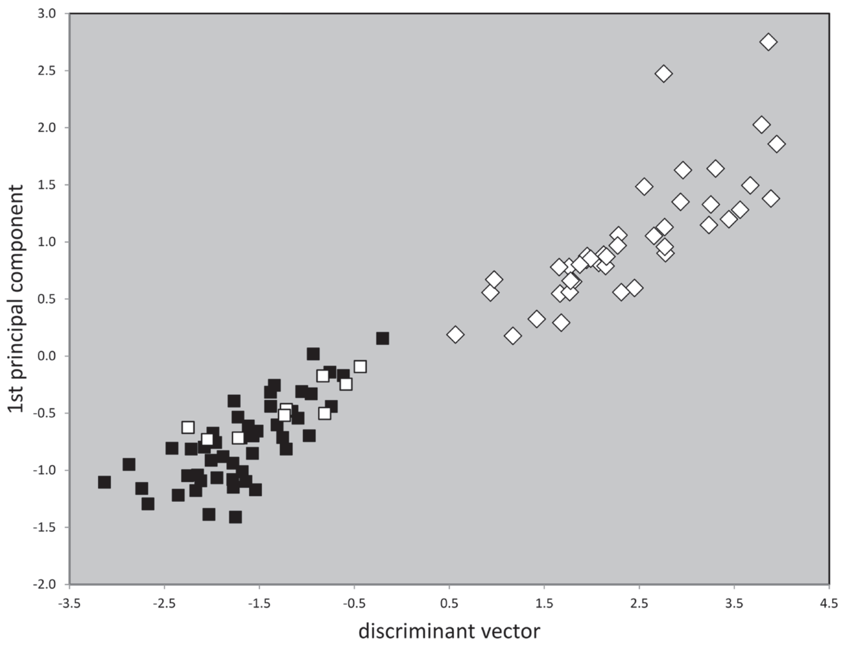


Figure 51. Plot of nest sample means of the first principal component against the linear discriminant vector of workers of *Formica cinerea* (white rhombs), *F. fuscocinerea* northern population (black squares) and of *Formica fuscocinerea* southern population (white squares).

6.3 *Formica fuscocinerea* Forel 1874

***F. fusca var. fuscocinerea* Forel 1874** [type investigation] This taxon has been described from Einsiedeln near Zürich and Zürich. Investigated was 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 paratype worker and 2 paratype gynes on another pin labelled by Forel "*cinerea ♀, Zürich; F.fusco-cinerea Forel*"; all material stored in MHN Genève. The lectotype sample is allocated to the *Formica fuscocinerea* cluster with p=0.9962 in a wild-card run of a 3-class LDA considering the taxa *F. cinerea*, *F. fuscocinerea* and *F. selysi* (see supplementary information SI3, setting 1). Note: Two workers and one gyne labelled by Forel himself "Z.hôpital"\"F.cinereo-rufibarbis"\"Type", stored in MHN Genève belong to *Formica rufibarbis.*

***Formica lefrancoisi* Bondroit 1918** [type investigation]

This taxon has been described from Grande Chartreuse / France. Investigated were 1 lectotype, worker designated by Seifert in 1994, and labelled "Zurich Forel"; 2 paralectotype workers with locality label "Grande Chartreuse", all material stored in IRSN Bruxelles. The lectotype is allocated to the *Formica fuscocinerea* cluster with p=0.9987 in a wild-card run of a 3-class LDA considering the taxa *F. cinerea, fuscocinerea* and *selysi* (see supplementary information SI3, setting 1).

***Formica cinerea* var. *italica* Finzi 1928** [type investigation]

This taxon has been described from Monte Martinello in Calabria / Italy. Investigated were two worker syntypes labelled "*Mte. Martinello Stauder 5.6.13 \ Tipo \ F. cinerea var. italica Finzi 28 \ M.C.Z. CoType 28814* ", MCZ Cambridge. The lectotype is allocated to the *Formica fuscocinerea* cluster with p=0.9977 in a wild-card run of a 2-class LDA considering the taxa *F. cinerea* and *F. fuscocinerea* (see supplementary information SI3, setting 4).

All material examined. Numeric phenotypical data were taken in 66 nest samples with 217 workers. The material came from Austria (12 samples), Croatia (3), France (2), Germany (36), Italy (8) and Switzerland (5). For details see supplementary information SI1 and SI2.

Geographic range. The northern population of *F. fuscocinerea* is confined to the Alps from 5.8°E (Grenoble region) to 16.9°E (Hainburg, Lower Austria, Wagner et al. 2019). Following rivers leaving the Alps, this population extends south to 44.5°N (Emilia-Romagna). In the north, there is an ongoing range expansion in Bavaria and Baden-Württemberg along the tributaries of the Danube that reached north to 48.7°N in the year 2009. The altitudinal range in Germany, Switzerland and Austria extends from 200 to 1550 m, but the main population is found below 800 m. A strong population in the city of Tübingen was most probably anthropogenically introduced with riverine gravel from the Alps in the mid 1970s. *F. fuscocinerea* seems to be absent from areas east of the Alps – probably due to competitive pressure of *F. cinerea*. The southern population is known from the Apennines and north Croatia at elevations from near sea level to 1210 m and goes east to 17.2°E. The current distribution and the mode of dispersal suggests a glacial refuge situated in low, sunny river valleys of the southeastern Alps and/or at the bottom of the northern Adria which fell dry during the glacial maximum.

Description: --Worker (Tab. 3; key). All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Slightly smaller than *cinerea*, CS 1321 ± 136 µm. Head and scape moderately long, CL/CW 1.129 ± 0.021, SL/CS 1.044 ± 0.021. Eye larger than in *cinerea*, EYE/CS 0.316 ± 0.008. Ocellar distance moderately large, OceD/CS 0.165 ± 0.010. Distance between metathoracal spiracles larger than in *cinerea*, MtSt/CS 0.142 ± 0.014. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt/CS 0.333 ± 0.011, MtMtp/CS 0.621 ± 0.011. Petiole scale narrower than in *cinerea*, PeW/CS 0.369 ± 0.020. Setae on first gaster tergite of medium length, GHL/CS 8.27 ± 0.83%. Genae without standing setae, nGen 0.09 ± 0.27. Margin of hind vertex and gula with fewer standing setae than in *cinerea*, nCH 16.4 ± 6.4, nGu 4.7 ± 1.8. Pronotum and mesonotum with many standing setae. Number of standing setae on propodeum plus upper surfaces of metapleuron smaller than in *cinerea*, nPrMe 1.5 ± 1.5. Number of setae on petiole scale above the stigma smaller than in *cinerea*, nPe 3.6 ± 1.8; within all these fringe setae, setae projecting dorsad clearly more numerous than those projecting laterad, the latter frequently entirely absent. Setae on extensor profile of hind femur and extensor profile of hind tibia absent, nHFex 0.01 ± 0.07, nHT 0.13 ± 0.28; those on flexor profile of hind femur less numerous than in *cinerea*, nHFfl 7.6 ± 2.0. Head, mesosoma, petiole, and gaster covered by a dense silvery pubescence. Distance of transverse ripples and of pubescence hairs on dorsum of first gaster tergite rather low, RipD 5.86 ± 0.67, sqPDG 2.89 ± 0.13. 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. In the northern population, microsculpture frontal of the metathoracal stigma in contrast to *cinerea* in the form of a fine network of elongated meshes. The inner surface of the meshes is shining; the average small diameter of a mesh is about 9-11 µm - i.e. the ratio of sculptured surface against shining surface is much smaller than in *cinerea*. 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. Colour polymorphism. Morphs with a yellowish-red colour component on mesosoma and anterior head more frequent than in Central European population of *cinerea*; entirely dark, intermediate, or patchily coloured morphs can occur syntopically.

Habitat and Biology. For the northern population see Seifert (2018). The southern population forms a similar ecological niche. It was mainly found on river banks but also in sunny road embankments, a limestone quarry, a fallow of arable land and a sand dune.

Taxonomic comments: *Formica fuscocinerea* shows similarities to *F. cinerea* and is sympatric with the latter in the Alps, in areas closely adjacent to the Alps and in the Apennines. The southern population of *F. fuscocinerea* differs from the northern population by smaller eyes, longer scape and a wider petiole thus approaching the *F. cinerea* condition but remains separable from the latter by the lower seta numbers and the larger MtSt/CS (see section 6.1 and Figs 50, 51). Confusion might arise with some samples of the eastern population of *F. cinerea* which have reduced setae numbers on propodeum, metapleuron and petiole scale thus approaching phenotypically to *F. fuscocinerea* (see section 6.1).

6.4 *Formica balcanina* Petrov & Collingwood 1993

Formica balcanina **Petrov & Collingwood 1993** [zoogeography, paratype investigation]

This taxon has been described from Serbia, Montenegro, North Macedonia, Greece and Turkey. The holotype sample, collected in the Nature Reserve Deliblato Sands [44.90°N 21.09°E] in Serbia, was not available, but the identity of the taxon is already clear from original description and the reported geographical distribution. Three paratype workers labelled "North Greece Drosopyghi leg. Collingwood 1984.09.01", stored in SMN Görlitz were allocated with p=1.000 to the *F. balcanina* cluster when run as wild-cards in a 3-class LDA comparing the species *F. cinerea, F. balcanina* and *F. georgica* (supplementary information SI3, setting 2).

All material examined. Numeric phenotypical data were taken in *Formica balcanina* in 57 nest samples with 167 workers. The material came from Bosnia (11 samples), Bulgaria (20), Croatia (1), Greece (1), North Macedonia (7), Romania (14) and Serbia (3). Phenotypical data of hybrids *F. balcanina X cinerea* were taken in 6 samples with 21 workers from Romania. For details see supplementary information SI1 and SI2.

Geographic range. The known range of *Formica balcanina* is not larger than 500,000 km² and has its westernmost point in Bosnia (18°E), its southernmost point in Greece (39.5°N), its easternmost point in Bulgaria (28.1°E) and its northernmost point in Romania (47.0°N). The altitudinal distribution ranges from near sea level at the Black Sea coast up to 1300 m in Bulgaria. Sympatric occurrence with *F. cinerea* is known in Romania within an area of about 120,000 km² but hybrids are documented so far only in a small zone of some 40,000 km² in western Romania (Fig. 52).

Description: --Worker (Tabs. 3, 4; key). Medium-sized, CS 1321 ± 105 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head moderately long, CL/CW 1.133 ± 0.015; scape shorter than in *cinerea* SL/CS 1.022 ± 0.020. Eye slightly larger than in *cinerea*, EYE/CS 0.312 ± 0.006. Ocellar distance moderately large, OceD/CS 0.169 ± 0.009. Distance between metathoracal spiracles larger than in *cinerea*, MtSt/CS 0.141 ± 0.013. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt/CS 0.331 ± 0.010, MtMtp/CS 0.626 ± 0.012. Petiole scale rather wide PeW/CS 0.383 ± 0.023. Setae on first gaster tergite longer than in *cinerea*, GHL/CS 9.41 ± 0.65%. Genae in stark contrast to *cinerea* with many standing setae, nGen 7.9 ± 2.9. Margin of hind vertex with numerous standing setae, nCH 34.1 ± 6.4, standing setae on gula more numerous than in *cinerea,* nGu 18.4 ± 3.6. Pronotum and mesonotum with many standing setae, nPn 40.7 ± 7.3, nMn 10.3 ± 3.6. Number of standing setae on propodeum plus upper surfaces of metapleuron moderate, nPrMe 4.6 ± 2.3. Number of setae on petiole scale above the stigma moderate, nPe 9.0 ± 2.4. Setae on extensor profile of hind femur and extensor profile of hind tibia nearly absent, nHFex 0.10 ± 0.29, nHT 0.18 ± 0.39; setae on flexor profile of hind femur more numerous than in *cinerea*, nHFfl 21.7 ± 3.8. Sculpture and pubescence on body surfaces as in *cinerea*. Distance of transverse ripples and of pubescence hairs on dorsum of first gaster tergite rather low, RipD 5.55 ± 0.64, sqPDG 3.07 ± 0.14. 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 data of hybrids *F. balcanina X cinerea* see Tab. 4

Habitat and Biology. The habitat selection is comparable to *Formica cinerea*. It prefers open habitats with much bare ground such as sand and gravel banks along rivers and lakes, road embankments, or margins of strip mines. It may also occur in dry grassland with low vegetation height or in vineyards and is frequently found in centers of cities and villages with much surface sealing. The colony size ranges from small (and probably monogynous) to very large, polygynous and supercolonial. No data on the time of sexual eclosion and swarming are known.

Taxonomic comments: Recognizing the species status of *Formica balcanina* is a problematic descision as *balcanina* forms a hybrid zone with *cinerea* in Romania which is some 40,000 km² large (Fig. 52). We checked the situation by analysing all samples of both species from the range of *F. balcanina* and from all geographic regions adjacent or close to this range. These were 121 nest samples with 371 worker individuals from the eastern parts of Austria, Poland, Slovakia, Venezia-Giulia (NE Italy), the Balkan countries, the Ukraine and Turkey for which data of the 13 characters CS, CL/CW_{1400}, SL/CS_{1400}, EYE/CS_{1400}, PeW/CS_{1400}, $nGen_{1400}$, nCH_{1400}, nGu_{1400}, $nPrMe_{1400}$, $nHFex_{1400}$, $nHFfl_{1400}$, nHT_{1400} and nPe_{1400} were

Table 2. Comparison of data of *Formica balcanina* and *F. cinerea* for geographic areas with sympatric and allopatric distribution. Data of a one-tailed ANOVA are placed in the line between the compared populations.

	Dis_6	SL/CS_{1400}	$nGen_{1400}$	nGu_{1400}	$nHFfl_{1400}$
***balcanina*, allopatric range (n=115)**	2.843±1.126	1.024±0.022	8.16±2.79	18.69±3.66	22.46±3.31
ANOVA $F_{1,163}$, p	8.55,**0.004**	n.s.	n.s.	4.09,**0.045**	22.34,**0.000**
***balcanina*, sympatric range (n=48)**	2.261±1.227	1.018±0.016	7.22±3.02	17.45±3.39	19.61±3.95
***cinerea*, allopatric range (n=171)**	-2.356±0.772	1.048±0.024	1.34±1.30	10.06±2.85	12.31±3.33
ANOVA $F_{1,185}$, p	4.67,**0.032**	4.14,**0.043**	n.s.	n.s.	n.s.
***cinerea*, sympatric range (n=17)**	-1.916±1.060	1.036±0.024	1.81±1.50	10.48±2.15	10.99±2.71

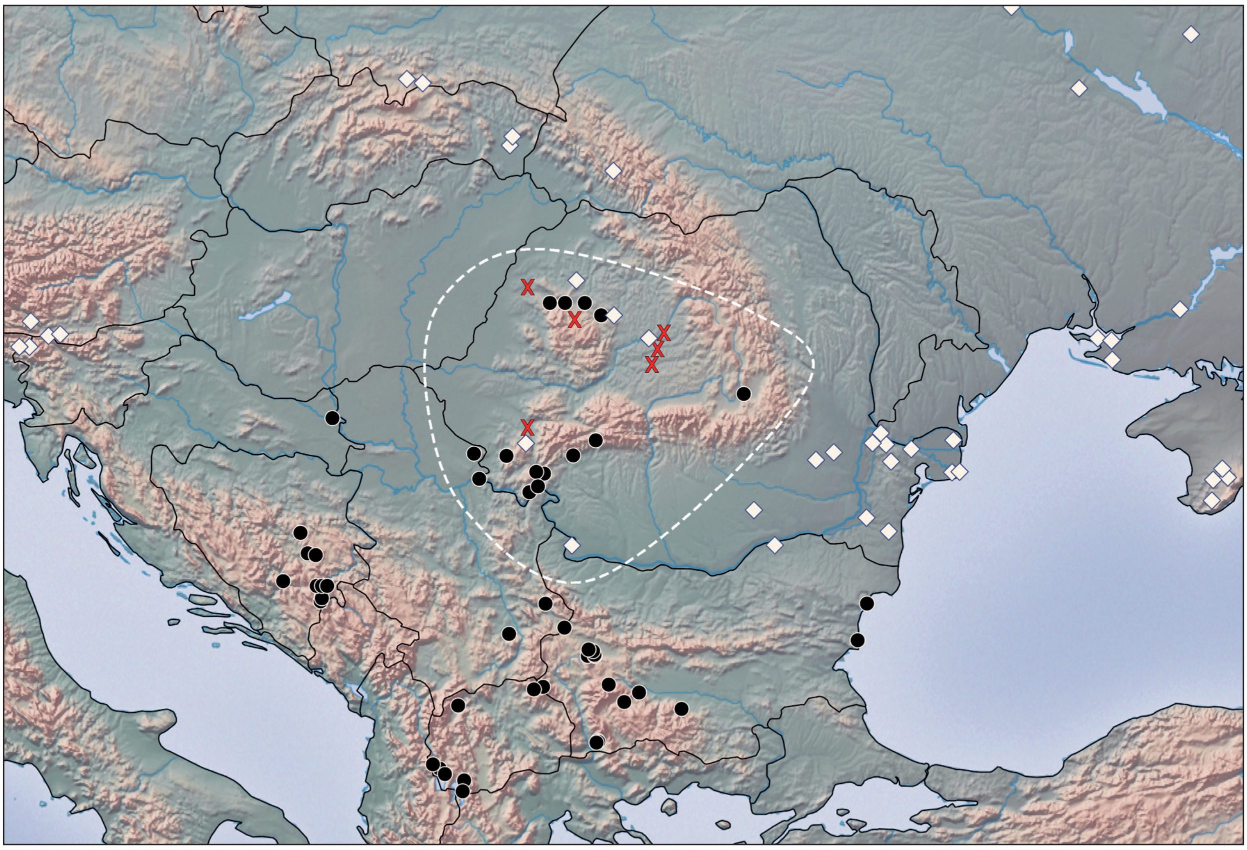


Figure 52. Geograpic distribution of *Formica cinerea* (white rhombs), *Formica balcanina* (black dots) and of hybrids *F. balcanina x cinerea* (red X). The dashed line circumscribes the supposed area of sympatric occurrence.

available. In a first step, the exploratory data analyses NC-part.hclust and NC-part.kmeans both suggested two clusters. Thereafter, an LDA was run with the classification hypothesis suggested by NC-part.kmeans, which was preferred as it shows no tendency to over-splitting. In order to detect problematic samples of possible hybrid identity, the distribution of posterior probabilities was checked within each nest sample. All samples with within-sample disagreements of $p > 0.9$ for *F. balcanina* and $p > 0.9$ for *F. cinerea* were set as wild-cards in a second run of the LDA. Samples with a sample mean of posterior probabilities > 0.95 were supposed to represent the parental species and no longer run as wild-cards. This procedure was repeated in additional LDA runs until no further sample of parental species could be identified according to the threshold p > 0.95 This resulted in 56 samples of *F. balcanina,* 59 samples of *F. cinerea*, and 6 samples *F. balcanina* X *cinerea*. Finally, a character-reduced LDA using the six key characters SL/CS_{1400}, PeW/CS_{1400}, $nGen_{1400}$, nGu_{1400}, $nPrMe_{1400}$, and $nHFfl_{1400}$ was run which classified 99.4% of 350 individuals of the parental species correctly whereas the classifications within all hybrid samples remained controversial. The classification errors of the exploratory data analyses NC-part.kmeans and NC-Ward for the

Table 3. RAV-corrected morphological data of workers of the *Formica cinerea* group. This table includes only specimens for which data on petiole width and eye size were available. Only specimens with available data on petiole width and eye size are included. Sequence of data: arithmetic mean ± standard deviation [minimum, maximum]. Numbers following the maximum indicate a reduced sample size for the given character.

	fuscocinerea (n=188)	***cinerea*** (n=339)	***balcanina*** (n=166)	***torrentium*** (n=84)	***selysi*** (n=81)	***georgica*** (n=71)
CS[µm]	1321±136 [1027,1754]	1348±145 [969,1741]	1321±105 [1066,1619]	1302±139 [1049,1640]	1344±123 [1046,1657]	1356±141 [1069,1731]
CL/CW_{1400}	1.129±0.021 [1.068,1.169]	1.127±0.020 [1.039,1.202]	1.133±0.015 [1.077,1.169]	1.142±0.016 [1.098,1.178]	1.137±0.018 [1.087,1.179]	1.127±0.014 [1.102,1.159]
SL/CS_{1400}	1.044±0.021 [0.977,1.093]	1.051±0.026 [0.978,1.183]	1.022±0.020 [0.899,1.075]	1.039±0.019 [0.971,1.100]	1.057±0.021 [0.983,1.106]	1.046±0.021 [0.986,1.100]
EYE/CS_{1400}	**0.316**±0.008 [0.300,0.365]	0.309±0.006 [0.289,0.330]	0.312±0.005 [0.297,0.325]	0.308±0.006 [0.296,0.319]	0.303±0.005 [0.290,0.317]	0.308±0.005 [0.297,0.319]
$OceD/CS_{1400}$	0.165±0.010 [0.138,0.193] 182	0.165±0.011 [0.137,0.208] 232	0.169±0.009 [0.144,0.191] 153	0.159±0.011 [0.123,0.180]	0.160±0.006 [0.146,0.175]	0.171±0.007 [0.161,0.188] 23
$MTST/CS_{1400}$	**0.142**±0.014 [0.105,0.185] 182	0.129±0.017 [0.087,0.183] 226	0.141±0.013 [0.112,0.189] 143	**0.157**±0.010 [0.123,0.180]	0.134±0.013 [0.103,0.180]	0.131±0.012 [0.110,0.152] 20
$MTPPST/CS_{1400}$	0.333±0.011 [0.298,0.366] 182	0.338±0.012 [0.284,0.367] 226	0.331±0.010 [0.298,0.361] 142	0.327±0.010 [0.305,0.352]	0.333±0.010 [0.309,0.353]	0.339±0.009 [0.316,0.355] 20
$MTMTP/CS_{1400}$	0.621±0.011 [0.594,0.657] 182	0.630±0.012 [0.597,0.676] 226	0.626±0.012 [0.594,0.660] 142	0.622±0.012 [0.596,0.658]	0.630±0.012 [0.606,0.665]	0.625±0.010 [0.607,0.641] 20
PeW/CS_{1400}	**0.369±**0.020 [0.307,0.417]	0.384±0.024 [0.318,0.448]	0.383±0.023 [0.320,0.430]	0.347±0.018 [0.308,0.402]	0.329±0.016 [0.292,0.365]	0.392±0.020 [0.343,0.444]
GHL/CS_{1400}	8.27±0.83 [6.30,10.50] 171	8.53±0.80 [6.31,11.13]336	9.41±0.65 [8.02,11.21]	7.55±0.63 [5.66,8.94]61	7.69±0.61 [5.87,9.12]	9.21±1.01 [5.60,11.77]
$nGen_{1400}$	0.09±0.27 [0,2.1]	1.06±1.24 [0.0,5.9]	7.9±2.9 [**0.0**,13.5]	3.5±2.1 [0.5,10.8]	8.9±2.4 [4.3,15.4]	0.3±0.4 [0.0,2.3]
nCH_{1400}	16.4±6.4 [2.2,35.8]	24.1±6.0 [8.4,46.9]	34.1±6.4 [12.3,51.8]	24.1±3.3 [11.0,30.6]	29.7±3.9 [21.2,38.9]	23.3±4.5 [3.4,31.8]
nGU_{1400}	**4.7**±1.8 [0.5,11.0]	9.6±2.8 [0.0,19.7]	18.4±3.6 **[**10.1,28.4]	15.3±3.1 [6.7,20.8]	20.4±4.6 [11.3,39.5]	8.3±1.8 [3.3,13.2]
$nPrMe_{1400}$	**1.5**±1.5 [0.0,7.2]	5.9±3.5 [0.0,19.2]	4.6±2.3 [0.0,11.3]	9.6±2.6 [2.0,15.6]	19.1±5.7 [8.4,38.6]	**19.0**±4.9 [7.6,33.0]
nPe_{1400}	**3.6±**1.8 [0.0,7.9]	7.8±2.2 [0.0,14.8]	9.0±2.4 [0.6,14.4]	11.3±2.7 [3.6,17.7]	17.8±4.9 [5.3,35.1]	9.9±2.0 [5.3,14.9]
$nHFEX_{1400}$	0.01±0.07 [0.0,0.5]	0.02±0.12 [0.0,1.6]	0.10±0.29 [0.0,2.1]	4.7±2.1 [1.4,11.5]	14.7±4.2 [6.0,24.2]	0.05±0.21 [0.0,1.1]
$nHFfl_{1400}$	7.6±2.0 [1.5,13.8]	12.6±3.0 [2.5,22.0]	21.7±3.8 [6.7,31.7]	16.4±2.8 [7.9,22.2]	25.3±4.3 [14.9,36.3]	14.6±3.4 [3.8,25.1]
nHT_{1400}	0.13±0.28 [0.0,1.2]126	0.21±0.41 [0.0,2.0]	0.18±0.39 [0.0,2.9]	1.3±1.00 [0.0, 4.3]	5.75±2.30 [1.9,12.0]	0.10±0.30 [0.0,1.7]
$Ripd_{1400}$	5.86±0.67 [4.0,7.3]44	5.50±0.64 [4.4,6.7]25	5.55±0.64 [4.5,6.7]24	6.29±0.57 [5.4,7.2] 21	4.93±0.42 [4.4,5.7] 22	6.00±0.56 [4.6,6.8] 20
$sqPDG_{1400}$	2.89±0.13 [2.61,3.15] 44	3.05±0.14 [2.67,3.39] 25	3.07±0.21 [2.50,3.40] 24	2.80±0.12 [2.52,3.05]21	2.77±0.20 [2.42,3.10] 22	2.98±0.16 [2.75,3.32]20

Table 4. RAV-corrected morphological data of workers of the *Formica cinerea* group. Columns with hybrids placed between those of the parental species. Only specimens with available data on petiole width and eye size are included. Sequence of data: arithmetic mean ± standard deviation [minimum, maximum]. Numbers following the maximum indicate a reduced sample size for the given character.

	selysi n=81	***cinerea x selysi*** (n=4)	***cinerea*** n=339	***balcanina x cinerea*** n=21	***balcanina*** n=166	***corsica*** n=35	***tombeuri*** n=55
CS[µm]	1344±123 [1033,1657]	1312±94 [1187,1396]	1348±145 [969,1741]	1287±90 [1142,1422]	1321±105 [1066,1619]	1193±91 [1051,1419]	1375±146 [1119,1724]
CL/CW_{1400}	1.137±0.018 [1.087,1.179]	1.133±0.010 [1.121,1.145]	1.127±0.020 [1.039,1.202]	1.130±0.024 [1.070,1.170]	1.133±0.015 [1.077,1.169]	1.140±0.021 [1.094,1.184]	1.130±0.018 [1.085,1.165]
SL/CS_{1400}	1.057±0.021 [0.976,1.106]	1.060±0.007 [1.051,1.067]	1.051±0.026 [0.978,1.183]	1.031±0.024 [0.990,1.074]	1.022±0.020 [0.899,1.075]	1.050±0.019 [1.006,1.089]	1.055±0.024 [0.992,1.124]
EYE/CS_{1400}	0.303±0.005 [0.290,0.317]	0.305±0.002 [0.303,0.307]	0.309±0.006 [0.289,0.330]	0.313±0.006 [0.299,0.325]	0.312±0.005 [0.297,0.325]	0.311±0.006 [0.303,0.324] 18	0.311±0.006 [0.298,0.323]
$OceD/CS_{1400}$	0.160±0.006 [0.146,0.175]	0.164±0.008 [0.158,0.175]	0.165±0.011 [0.137,0.208] 232	0.174±0.011 [0.156,0.193]	0.169±0.009 [0.144,0.191] 153	0.156±0.012 [0.136,0.177] 17	0.161±0.009 [0.132,0.176]
$MTST/CS_{1400}$	0.134±0.013 [0.103,0.180]	0.125±0.008 [0.117,0.133]	0.129±0.017 [0.087,0.183] 226	0.147±0.012 [0.120,0.178]	0.141±0.013 [0.112,0.189] 143	0.126±0.014 [0.090,0.143] 17	0.132±0.013 [0.090,0.166] 52
$MTPPST/CS_{1400}$	0.333±0.010 [0.309,0.353]	0.346±0.005 [0.340,0.352]	0.338±0.012 [0.284,0.367] 226	0.330±0.007 [0.318,0.350]	0.331±0.010 [0.298,0.361] 142	0.338±0.012 [0.312,0.356] 17	0.336±0.011 [0.317,0.354] 52
$MTMTP/CS_{1400}$	0.630±0.012 [0.606,0.665]	0.645±0.011 [0.635,0.656]	0.630±0.012 [0.597,0.676] 226	0.620±0.010 [0.599,0.638]	0.626±0.012 [0.594,0.660] 142	0.628±0.016 [0.604,0.650] 17	0.631±0.012 [0.602,0.655] 52
PeW/CS_{1400}	0.329±0.016 [0.292,0.365]	0.349±0.012 [0.332,0.357]	0.384±0.024 [0.318,0.448]	0.378±0.026 [0.336,0.430]	0.383±0.023 [0.320,0.430]	0.394±0.022 [0.364,0.441] 17	0.379±0.017 [0.325,0.420]
GHL/CS_{1400}	7.69±0.61 [5.87,9.12]	8.16±0.33 [7.68, 8.45]	8.53±0.80 [6.31,11.13] 336	8.38±0.87 [6.14, 9.70]	9.41±0.65 [8.02,11.21]	8.09±0.98 [6.54,10.99] 17	7.57±0.69 [5.04, 8.81]
$nGen_{1400}$	8.9±2.4 [4.3,15.4]	4.40±1.50 [2.5,5.7]	1.06±1.24 [0.0,5.9]	4.3±1.8 [1.0,8.0]	7.9±2.9 [0.0,13.5]	0.00±0.00 [0,0.0]	0.00±0.00 [0,0.0]
nCH_{1400}	29.7±3.9 [21.2,38.9]	28.3±7.2 [21.5,38.2]	24.1±6.0 [8.4,46.9]	27.3±7.3 [11.8,37.5]	34.1±6.4 [12.3,51.8]	7.0±2.6 [1.5,11.1]	0.03±0.14 [0.0,0.7]
nGU_{1400}	20.4±4.6 [11.3,39.5]	17.0±4.1 [13.1,22.5]	9.6±2.8 [0.0,19.7]	13.5±3.8 [3.2,19.9]	18.4±3.6 [10.1,28.4]	1.3±0.8 [0.0, 3.3]	0.01±0.08 [0,0.6]
$nPrMe_{1400}$	19.1±5.7 [8.4,38.6]	10.3±2.1 [7.5,12.3]	5.9±3.5 [0.0,19.2]	4.8±3.6 [0.6,12.7]	4.6±2.3 [0.0,11.3]	0.7±1.5 [0.0,5.8]	0.01±0.05 [0.0,0.4]
nPe_{1400}	17.8±4.9 [5.3,35.1]	13.3±0.7 [12.5,14.0]	7.8±2.2 [0.0,14.8]	7.0±2.9 [0.0,10.5]	9.0±2.4 [0.6,14.4]	3.6±1.8 [0.0,8.0]	0.13±0.30 [0.0,1.1]
$nHFEX_{1400}$	14.7±4.2 [6.0,24.2]	3.75±1.34 [2.4,5.5]	0.02±0.12 [0.0,1.6]	0.01±0.04 [0.0,0.2]	0.10±0.29 [0.0,2.1]	0.00±0.00 [0.0,0.0]	0.00±0.00 [0,0.0]
$nHFfl_{1400}$	25.3±4.3 [14.9,36.3]	18.9±3.4 [16.5,23.9]	12.6±3.0 [2.5,22.0]	17.2±2.2 [12.9,21.7]	21.7±3.8 [6.7,31.7]	6.9±1.8 [2.9,9.8]	0.20±0.37 [0.0,1.8]
nHT_{1400}	5.75±2.30 [1.9,12.0]	2.65±0.47 [2.1,3.2]	0.21±0.41 [0.0,2.0]	0.16±0.25 [0.0,0.6]	0.18±0.39 [0.0,2.9]	0.10±0.29 [0.0,1.2]	0.00±0.00 [0.0,0.0]
$Ripd_{1400}$	4.93±0.42 [4.4,5.7] 22		5.50±0.64 [4.4,6.7] 25	5.13±0.51 [4.2,6.1]	5.55±0.64 [4.5,6.7] 24	5.00±0.57 [3.5,6.0] 17	5.34±0.50 [4.5,6.8]
$sqPDG_{1400}$	2.77±0.20 [2.42,3.10] 22		3.05±0.14 [2.67,3.39] 25	2.92±0.19 [2.55,3.24]	3.07±0.21 [2.50,3.40] 24	3.09±0.25 [2.36,3.46] 17	2.90±0.14 [2.57,3.19]

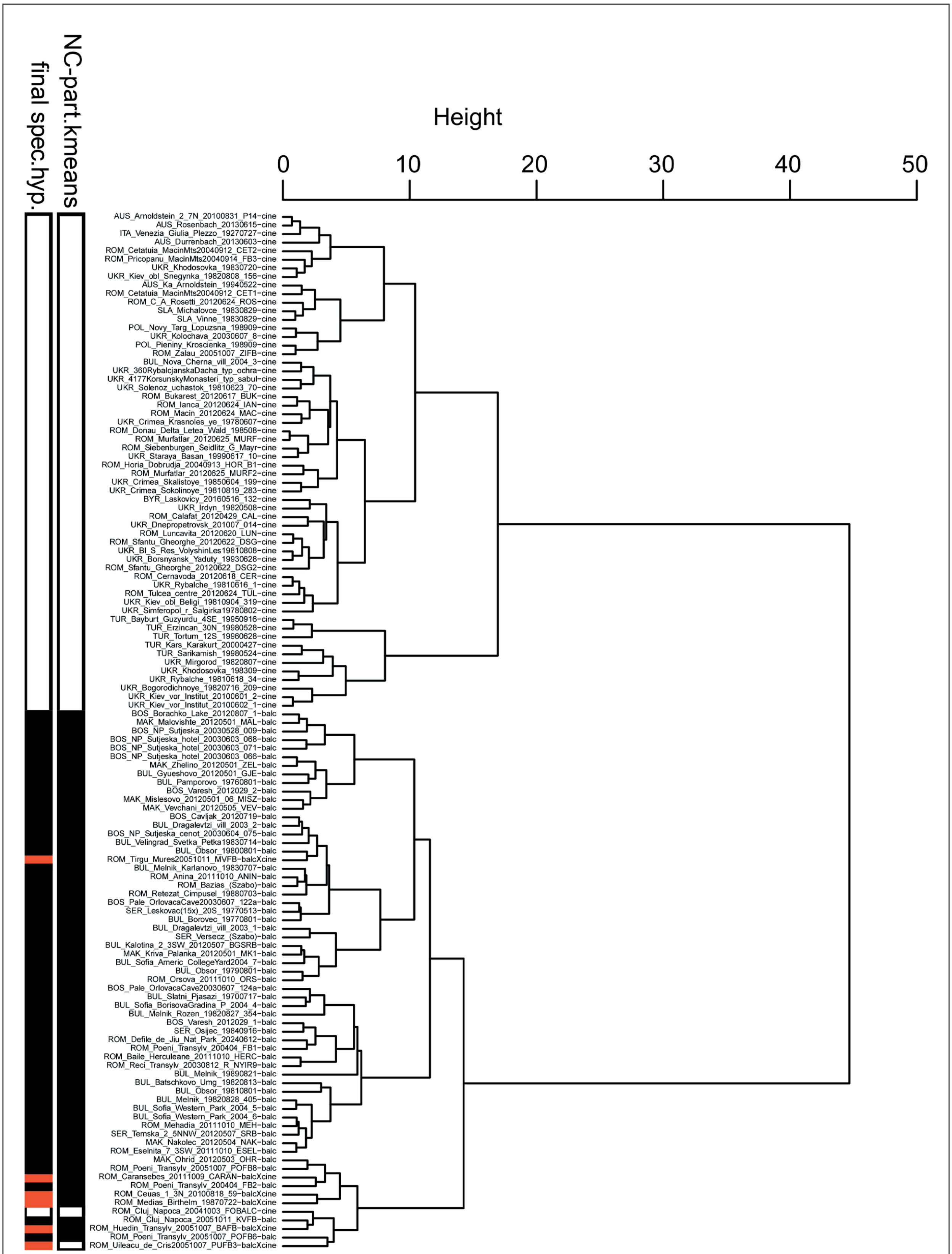


Figure 53A: Classification of worker samples of *Formica balcanin*a (black bars), *F. cinerea* (white bars) and hybrids *F. balcanina x cinerea* (red bars) by the exploratory data analyses NC-Ward and NC-part.kmeans. Excluding the hybrid samples, the classification error of the EDAs relative to the final species hypothesis 1.1 and 0%.

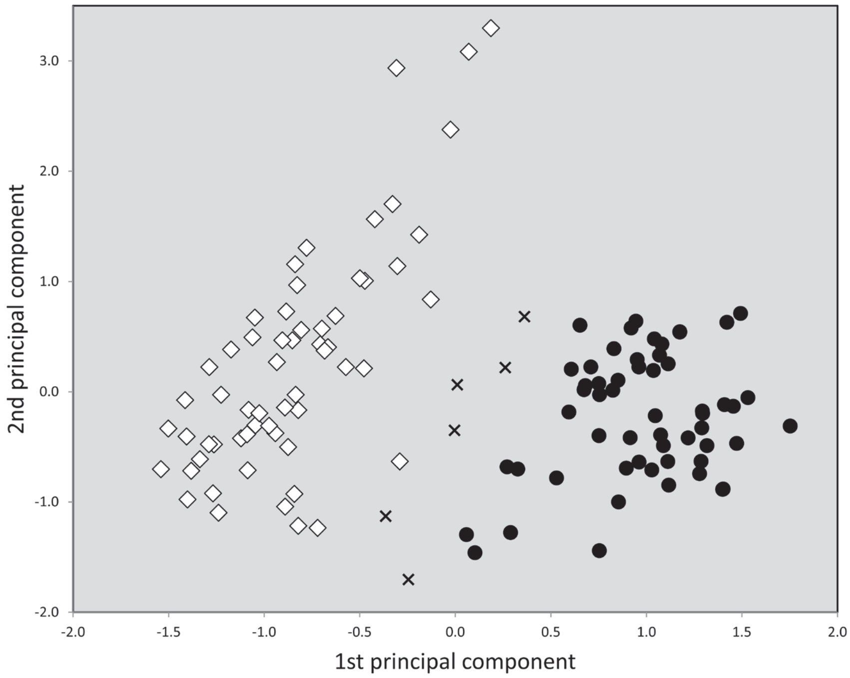


Figure 53B. Nest sample means of a principal component analysis of *Formca cinerea* (white rhombs), *F. balcanina* (black dots) and of hybrids *F. balcanina* x *cinerea* (crosses)

parental species were 0 and 0.9% using this character set (Fig. 53A). Yet, all hybrid samples were placed in these two analyses within the *balcanina* cluster. This is an example showing the failure NC clustering to present evidence for hybridization. Instead, the real situation is approximated by a PCA which places all hybrid samples and one *cinerea* sample in an intermediate position between the parental clusters (Fig. 53B). This outlier illustrates that our identification of hybrid samples should be understood as tentative – the more as backcrosses of hybrids with either parental species cannot be identified with our morphological method.

In order to assess if there are signals for introgression in the samples classified as parental species, the situation within the sympatric and allopatric ranges of both species was compared.

Considering the six key characters given above, the sympatric population of *F. balcanin*a shows convergence to *F. cinerea* in the discriminant vector Dis_6 (p=0.004), nGu_{1400} (p=0.045) and $nHFfl_{1400}$ (p=0.000) whereas the sympatric *F. cinerea* population converges only slightly in the discriminant vector (p=0.032) and SL/CS_{1400} (p=0.043, Tab. 2). In conclusion, phenotype signalizes moderate introgression of genes into *F. balcanina* but only weak or absent introgression in *F. cinerea*.

6.5 *Formica georgica* Seifert 2003

***Formica georgica* Seifert 2003** [type investigation]
This taxon has been described from Georgia. Investigated were the 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"; 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. The holotype series was allocated with p=0.9999 to the *F. georgica* cluster when run as wild-cards in a 3-class LDA comparing the species *F. cinerea, F. balcanina* and *F. georgica* (supplementary information SI3, setting 2).

All material examined. Numeric phenotypical data were taken in 24 nest samples with 71 workers. The material came from Armenia (6 samples), Georgia (17) and Turkey (1). For details see supplementary information SI1 and SI2.

Geographic range. The known range of *Formica georgica* extends over NE Turkey, Armenia and Georgia from near Sukhumi (40.9°E) east to Shenako (45.7°E) and

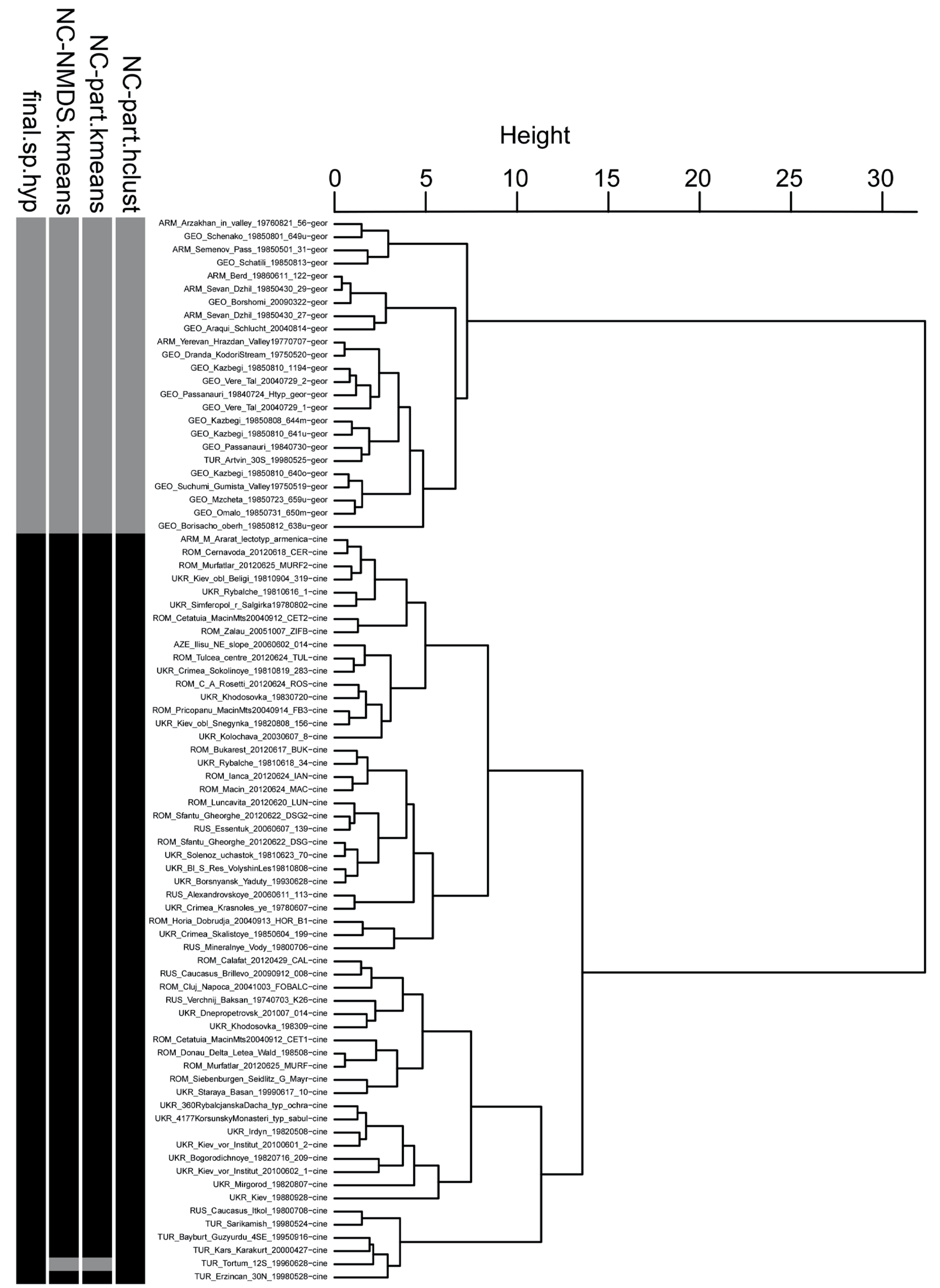


Figure 54. Four variants of exploratory data analyses (EDAs) of 57 nest samples of the eastern population of *Formica cinerea* (black bars) and of 24 nest samples of *F. georgica* (grey bars). NC-Ward dendrogram shown. The mean error of four EDAs relative to the final species hypothesis is 0.5%.

is not larger than 90,000 km². The altitudinal distribution ranges from near sea level at the Black Sea up to 2034 m in Armenia.

Description: --Worker (Tab. 3; key). Medium-sized, CS 1356 ± 141 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape moderately long, CL/CW 1.127 ± 0.014, SL/CS 1.046 ± 0.021. Eye large, EYE/CS 0.309 ± 0.005. Ocellar distance rather large, OceD/CS 0.171 ± 0.007. Distance between metathoracal spiracles rather small, MtSt/CS 0.131 ± 0.012. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt/CS 0.339 ± 0.009, MtMtp/CS 0.625 ± 0.010. Petiole scale rather wide PeW/CS 0.392 ± 0.020. Setae on first gaster tergite longer than in *cinerea*, GHL/CS 9.21 ± 1.01%. Genae without or with only few setae, nGen 0.3 ± 0.4. Margin of hind vertex with numerous standing setae, nCH 23.3 ± 4.5. Standing setae on gula not very numerous, nGu 8.3 ± 1.8. Pronotum and mesonotum with numerous standing setae. Number of standing setae on propodeum plus upper surfaces of metapleuron much larger than in *cinerea*, nPrMe 19.0 ± 4.9. Number of setae on petiole scale above the stigma moderate, nPe 9.9 ± 4.9. Setae on extensor profile of hind femur and extensor profile of hind tibia nearly absent, nHFex 0.05 ± 0.21, nHT 0.10 ± 0.30; setae on flexor profile of hind femur moderately large, nHFfl 14.6 ± 3.4. Sculpture and pubescence on body surfaces as in *cinerea*. Distance of transverse ripples and of pubescence hairs on dorsum of first gaster tergite rather low, RipD 6.00 ± 0.56, sqPDG 2.98 ± 0.16. Colour polymorphism. 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.

Habitat and Biology. It typically follows rivers where it occurs on sand and gravel banks or meager pastures. It is also found in road embankments or along the shore line of lakes. 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. Sexuals were observed in the Caucasus July 31, 1985 (at 1650 m) and August 8, 1985 (at 1850 m). Concluded from repeated observation of single-queen claustral colony foundation and nest population size many colonies should be monogynous. Large supercolonies are not known so far.

Taxonomic comments: *Formica cinerea* is the only species of the *F. cinerea* group occurring in geographic neighborhood of *F. georgica* and showing sympatry with the latter in East Turkey and Armenia. Among five exploratory data analyses tested under inclusion of 24 samples of *georgica* and 57 samples of the eastern population of *cinerea* and considering 14 characters (see SI3, setting 5), NC-part.kmeans and NC-NMDS.kmeans provided the clearest separation in two clusters. The controlling LDA took over this hypothesis and changed the classification in 3.7% of the samples. Based on this final species hypothesis 98.4% of 245 individuals were classified correctly and 97.5% of 81 nest sample means showed posterior probabilities p > 0.95. Using only the five characters PeW/CS_{1400}, $nGen_{1400}$, nCH_{1400}, nGu_{1400} and $nPrMe_{1400}$, which contributed most to cluster separation, the disagreement between the two exploratory data analyses and the controlling LDA was reduced to a single sample (Sample No 1601 TUR: Tortum, see Fig. 54). This sample was classified with p=0.8162 as *F. cinerea* when run as wild-card in a LDA. Overall, there is a strong separation of the two species and no clear indication for hybridization.

6.6 *Formica selysi* Bondroit 1918

***Formica selysi* Bondroit 1918** [type investigation]
This taxon has been described from France: Alpes Maritimes: Saint Etienne de Tinée. Investigated were 8 worker syntypes labelled "*St. Etienne de Tinée Alp. mar. \ 1150 m \ Formica v. selysi type Bondr.*", IRSN Bruxelles. The holotype series was allocated with p=1.0000 to the *F. selysi* cluster when run as wild-cards in a 3-class LDA comparing the species *F. cinerea, F. selysi* and *F. torrentium* (supplementary information SI3, setting 3).

All material examined. Numeric phenotypical data were taken in 39 nest samples with 100 workers. The material came from Austria (3 samples), France (14), Germany (12), Italy (1) and Switzerland (9). For details see supplementary information SI1 and SI2.

Geographic range. The range of *Formica selysi* basically extends over the Alps and its northern, southern and western foothills west to the Massif Central (Fig. 55). The westernmost range border goes along 2.7°E in the Massiv Central and the easternmost one along 14.6° E in Slovenia and Austria (Bračko 2023, Wagner 2014). It follows the rivers leaving the Alpes in the north to 48.83°N (Iffezheim) and in the south down to 43.5°N (Cannes). Two single specimens from Bologna and Imola (coll. Gustav Mayr) suggest the existence of an (isolated?) population in the northern Apennines. In the Alps and its outlands, it occurs at significantly larger elevations than *F. fuscocinerea*: 730 ± 356 [8, 1780] m for 72 sites of *selysi* and 575 ± 224 [72, 1550] m for 63 sites of *fuscocinerea* (Seifert 2018). The postglacial spreading probably started from a refuge in southern France and/or northern Italy.

Figure 55. Geographic distribution of *Formica selysi* (white rhombs) and *F. torrentium* (black dots)

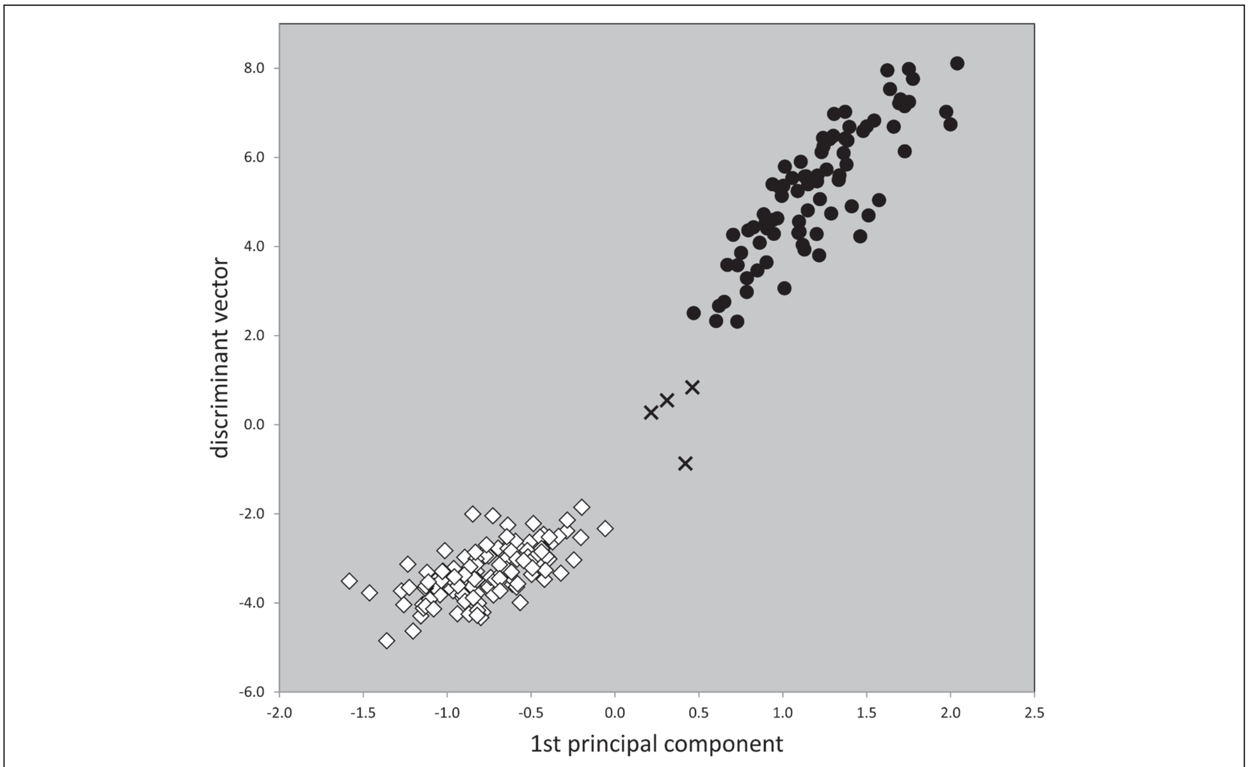


Figure 56. Principal component and linear discriminant vectors of 81 workers from 31 nest samples of *Formica selysi* (black dots), 129 workers from 45 nest samples of *F. cinerea* (white rhombs) and 4 workers from a single nest sample of hybrids *F. cinerea* x *selysi* (black X) based on material from France, Switzerland, Austria, Italy and Germany. The hybrid sample was run in the LDA as wild-cards.

Habitat and Biology. Primary habitat is gravel and sand banks of rivers with no or very sparse vegetation cover. *Formica selysi* can be expected in such places throughout its whole range. It colonizes bank reinforcements (also those completely made of concrete), light *Pinus* forests, embankments of roads or railway lines and sites subject to very strong anthropogenous movement of soil material. Clearly more abundant than *cinerea* and *fuscocinerea* on gravel banks and islands in rivers flooded a number of times per year. It is better adapted to higher stream velocities and coarser bank material than *cinerea* and *fuscocinerea*. For a synopsis of knowledge on special biology see Seifert (2018).

Taxonomic comments: As a combination of low petiole width, large eye, rich pilosity on all body surfaces and presence of many setae on extensor profile of hind femur, *Formica selysi* is not to confuse with any Palaearctic *Formica* species with exception of *F. torrentiu*m (for differences to the latter see section 6.7) or of hybrids (see below).

Purcell et al. (2016) have thoroughly investigated a hybrid zone of *Formica selysi* with *F. cinerea* in the upper Rhone valley in the Swiss Alps: Occurrence of backcrossed individuals signalized that hybrid queens are fertile and the presence of *F. cinerea* mtDNA in 97% of hybrids indicated that successful F_1 hybrids almost always had *F. cinerea* mothers and *F. selysi* fathers and that gene flow was unidirectional.

Yet, according to our phenotypical data, the overall frequency of hybridization between *Formica cinerea* and *F. selysi* appears to be low. We investigated samples from France, Switzerland, Austria, Italy and Germany for which the 13 characters CS, CL/CW_{1400}, SL/CS_{1400}, EYE/CS_{1400}, PeW/CS_{1400}, $nGen_{1400}$, nCH_{1400}, nGu_{1400}, $nPrMe_{1400}$, $nHFex_{1400}$, $nHFfl_{1400}$, nHT_{1400} and nPe_{1400} were available – 45 nest samples with 129 workers of *F. cinerea*, 31 nest samples with 81 workers of *F. selysi* and one nest sample with 4 workers later identified as F1 hybrids. The separation of the two species by several exploratory and hypothesis-driven data analyses was extremely strong. However one sample from the German Alps (Sample No 1266 GER: Krün) was placed in the PCA and a wild-card run of the LDA between the two clearly demarcated clusters of *F. cinerea* and *F. selysi* (Fig. 56). This is a strong indication for a hybrid identity. Considering only those 62 samples from regions where *F. cinerea* and *selysi* are sympatric, the overall frequency of hybrid samples in the Alps and its foothills would be 1.6%. However, the probability of the two species to hybridize under situations of direct encounter is certainly higher because syntopic occurrence is not given in all regions of the sympatric range.

6.7 *Formica torrentium* Bernard 1967

Formica torrentium **Bernard 1967** [zoogeography, topotypical material]

This taxon has been described from Barèges in the High Pyrenees, France [42.897°N, 0.065°E] on the basis of two gynes which are deposited in MNHN Paris. These two gynes, the lectotype and the paratype on the same pin labelled "*Bareges 4.7. 7.46 \ types ♀ de torrentium \ No. 169 Formica torrentium*" were investigated based on a loan in the year 2000. According to a message of the curator Quentin Rome of March 18, 2025 no workers from the type locality can be identified in the MNHN Paris collection. In contrast to the situation in workers, gynes of *F. torrentium* are difficult to separate from those of selysi. The sparse gyne material available, 7 specimens of *F. torrentium* and 13 of *F. selysi*, did not allow to develop a reliable means for numeric separation of the two species in this caste. However, there is a strong zoogeographic argument to name the western population *F. torrentium*: according to the clear determination of worker samples (see below), *F. selysi* is completely absent from the Pyrenees. The nearest site of *F. selysi* is situated 370 km NE of the type locality of *F. torrentium* (Fig. 55). Furthermore there is a topotypical worker series of *F. torrentium* available (Sample No 2437 FRA: Col de Tourmalet, leg. L. Fraysse 2019.08.22) which is allocated to the *F. torrentium* cluster with p=0.9994 in a wild-card run of a 3-class LDA considering the species *F. cinerea*, *F. torrentium* and *F. selysi* (see supplementary information SI3, setting 3).

All material examined. Numeric phenotypical data were taken in 27 nest samples with 86 workers. The material came from, France (21 samples) and Spain (6). For details see supplementary information SI1 and SI2.

Geographic range. *Formica torrentium* is found in the French and Spanish Pyrenees and in France west of 2°E with the main population occurring along the Atlantic shoreline north to 47.6°N. According to the data currently available *F. torrentium* and *F. selys*i appear to be allopatric, but a contact zone could possibly exist in Massif Central along the 2°E meridian. The Pyrenean population was found at elevations between 797 and 1470 m.

Description: --Worker (Tab. 3; Figs 10-12; key). Medium-sized, CS 1302 ± 139 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape moderately long, CL/CW 1.142 ± 0.016, SL/CS 1.039 ± 0.019. Eye large, EYE/CS 0.308 ± 0.006. Ocellar distance moderate, OceD/CS 0.159 ± 0.011. Distance between metathoracal spiracles larger than in *selysi*, MtSt/CS 0.157 ± 0.010. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt/

CS 0.333 ± 0.010, MtMtp/CS 0.630 ± 0.012. Petiole scale wider than in *selysi*, PeW/CS 0.329 ± 0.020. Transition between dorsal and caudal profiles of propodeum convex. Setae on first gaster tergite rather short, GHL/CS 7.55 ± 0.63%. Genae with setae, but significantly fewer than in *selysi*, nGen 3.5 ± 2.1. Margin of hind vertex with numerous standing setae, nCH 24.1 ± 3.3. Underside of head with numerous setae, nGu 15.3 ± 3.1. Pronotum and mesonotum with very numerous standing setae. Number of standing setae on propodeum plus upper surfaces of metapleuron much smaller than in *selysi*, nPrMe 9.6 ± 2.6. Number of setae on petiole scale above the stigma large but smaller than in *selysi*, nPe 11.3 ± 2.7. Some setae on extensor profile of hind femur and single setae on extensor profile of hind tibia usually present but less numerous and shorter than in *selysi*, nHFex 4.7 ± 2.1, nHT 1.3 ± 1.0; setae number on flexor profile of hind femur large, but smaller than in *selysi* nHFfl 16.4 ± 2.8. Head, mesosoma, petiole, and gaster covered by a dense, appressed pubescence. Distance of transverse ripples on dorsum of first gaster tergite larger than in *selysi*, RipD 6.29 ± 0.57; pubescence distance on tergite small, sqPDG 2.80 ± 0.12. Coloration of vertex, mesosoma, petiole and gaster usually dark brown, coxae, appendages, lateral and anterior part of head medium or lighter brown.

Habitat and Biology. Main and natural habitat of the Atlantic coast population are both white dunes with patches of vegetation and gray dunes but also margins of dune forests. Records from anthopogenous habitats include quarries and sand pits, sometimes located far from the coast, a park lawn with sparse vegetation, a graveled parking area with bushes and some greenery, and a margin of an asphalt road with trees. According to Clément Gouraud (pers. comm. 2024) populations are fragmented by dense urban areas and by the retreat of the coastline caused by erosion dynamics. The Pyrenean population strickly follows rivers where it is mainly found on gravel banks and stony pastures, but also along road embankments, in an urban park, a paved city center and a ruderal area.

Taxonomic comments: The phenotypic separation of *Formica torrentium* from *F. selysi* is very strong in the worker caste when a more complex character system is used. Considering 79 nest samples of *F. cinerea* from its whole Palaearctic range, 31 samples of *F. selysi* and 27 samples of *F. torrentium* and the 17 characters CS, CL/CW_{1400}, SL/CS_{1400}, EYE/CS_{1400}, $OceD/CS_{1400}$, $MtSt/CS_{1400}$, $MtPpSt/CS_{1400}$, $MtMtp/CS_{1400}$, PeW/CS_{1400}, $nGen_{1400}$, nCH_{1400}, nGu_{1400}, $nPrMe_{1400}$, $nHFex_{1400}$, $nHFfl_{1400}$, nHT_{1400} and nPe_{1400}, the mean error rate of the exploratory data analyses NC-Ward, NC-part.kmeans and NC-NMDS. kmeans was 1.0% (Fig. 57). Running the LDA under use of the final species hypothesis classified 98.0 % of 396 worker individuals correctly and provided a very strong separation based on sample means (Fig. 58). The separation of *F. torrentium* from *F. cinerea* was also clear using this complex character system, but there is a problem with the *F. torrentium* sample No 2452 from Castiello de Jaca 2022.07.24 providing a rather strong signal for *F. cinerea* (p_{cine} = 0.2732, p_{torr} =0.7268, p_{sely} =0.0000). This sample might possibly represent an introgression with *F. cinerea iberica* (see also discussion in section 6.2).

6.8 *Formica tombeuri* Bondroit 1917

***Formica tombeuri* Bondroit 1917** [type investigation]
Bondroit (1917) gave only "Portugal" as type locality. Investigated were 4 syntype workers labelled "Porto de G." and "Formica tombeuri Type Bondr.", depository IRSNB Bruxelles. The exact geographic situation of the type locality is unknown.

***Formica decipiens* Bondroit 1918** [type investigation]

This taxon has been described from the Eastern Pyrenees. Bondroit gave as localities "Prades, Taurinya, vallees infererieures du Canigou". Investigated were 3 syntype workers labelled "*Taurinya Pyr.or.\ Formica decipiens Type Bondr.*", IRSNB Bruxelles. The *F. decipiens* types show no difference to the types of *F. tombeuri* in any shape, pilosity or surface character and they are placed with any component of a PCA in the same cluster together with the types of *F. tombeuri*.

All material examined. Numeric phenotypical data were taken in 17 nest samples with 55 workers. The material came from France (2 samples), Portugal (1) and Spain (14). For details see supplementary information SI1 and SI2.

Geographic range. The main population of *Formica tombeuri* is found in the French and Spanish Pyrenees and NW Spain (Cantabria) and North (?) Portugal. The findings based on the samples determined by us and on credible records of Fede García are found in a very narrow band stretching from 6.1°W to 2.4°E with most southern and northern points at 42.2°N and 42.8° N. The elevation of 20 sites in that area is 1054 ± 386.5 [588, 1920] median 990 m. A probably isolated population could be confirmed for the Sierra de las Cabras [38.0897°N, 2.3423°W, 1784 m] – 550 km south of the main range.

Description: --Worker (Tab. 4; Figs 13-15; key). Rather large, CS 1375 ± 146 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape moderately long, CL/CW 1.130 ± 0.018, SL/CS 1.055 ± 0.024. Eye large, EYE/CS 0.311 ± 0.006. Ocellar distance moderate, OceD/CS 0.161 ± 0.009. Distance between metathoracal spiracles relatively small, MtSt/

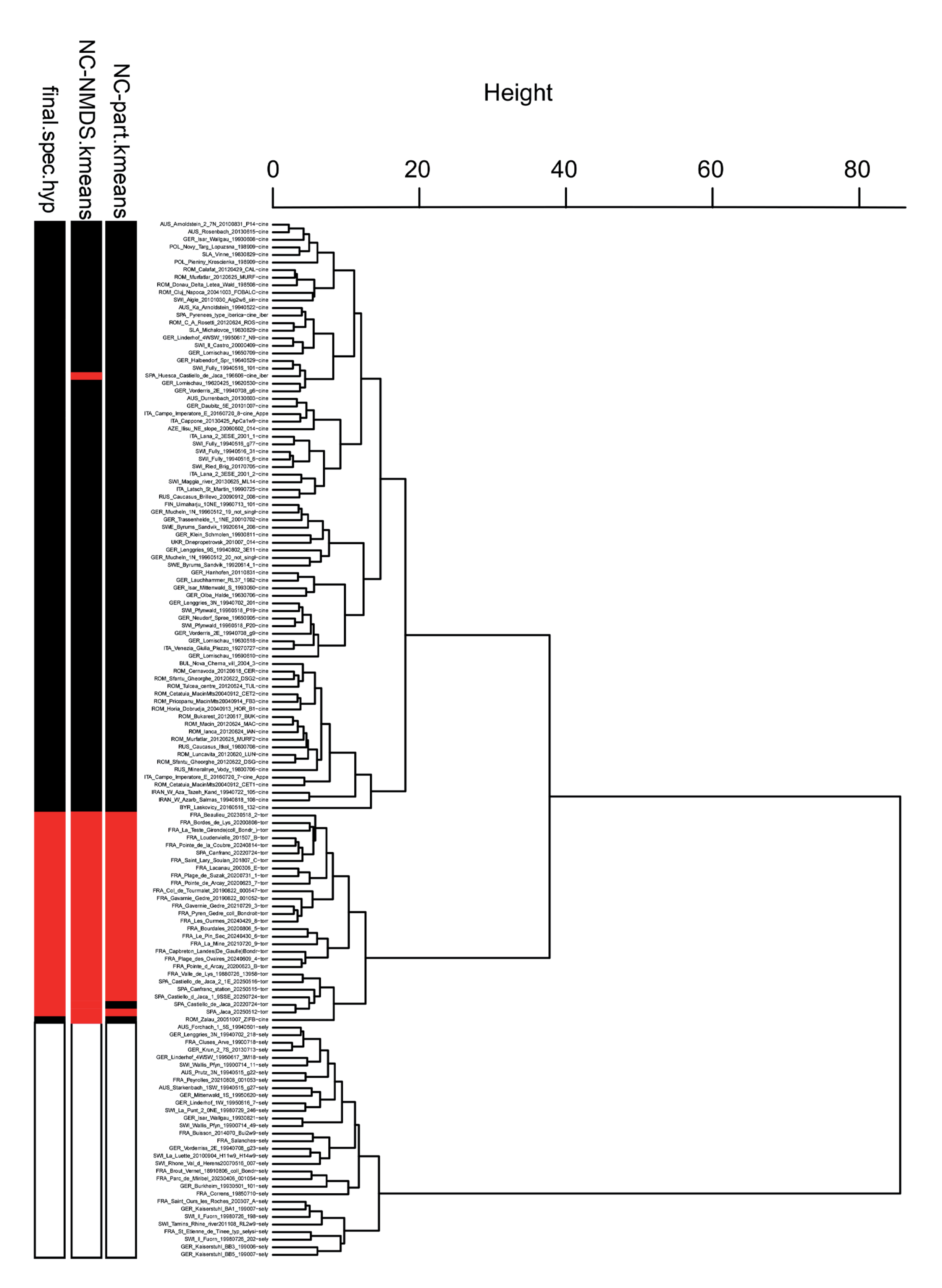


Figure 57. NC-clustering of nest samples of *Formica cinerea* (n=79, black bars), *F. selysi* (n=31, white bars) and *F. torrentium* (n=27, red bars). The mean error of NC-Ward (tree shown), NC-part.kmeans and NC-NMDS.kmeans was 1.0%.

CS 0.132 ± 0.013. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt/CS 0.336 ± 0.011, MtMtp/CS 0.631 ± 0.012. Petiole scale moderately wide, PeW/CS 0.379 ± 0.017. Setae on first gaster tergite rather short, GHL/CS 7.57 ± 0.69%. Genae, margin of hind vertex and underside of head completely without setae, nGen 0.0 ± 0.0, nCH 0.03 ± 0.14, nGu 0.01 ± 0.08. Pronotum always with some setae, nPn 6.2 ± 238.1; mesonotum with occasional setae, nMn 0.36 ± 0.64. Propodeum plus upper surfaces of metapleuron, petiole scale, extensor profile of hind femur, extensor profile of hind tibia completely without setae. Flexor profile of hind femur only with occasional setae, nHFfl 0.20 ± 0.37. Whole dorsum of gaster tergites with setae. Frontal triangle with strong transversal microripples. Whole head, mesosoma and gaster matt, because of strong microsculpture; in some specimens interspaces between microripples or microreticulum shining – hence appearing less matt in overall impression. Petiole scale in lateral view rather thickset, as high or nearly as high as propodeum; in frontal view narrow, its dorsal crest rounded or obtusely angulate (130-150°). Pubescence hairs on gaster tergites rather thick (2.4-4.6 µm) and silvery. Whole body blackish brown; antennae, mandibles and tibiae reddish brown. Lighter specimens: Vertex and posterior head blackish brown, genae, clypeus, mesosoma, coxae and gaster light brown; scape and mandibles yellowish.

Habitat and Biology (with much information by Fede García, pers. comm. August 10, 2025). One of the main natural habitats of *Formica tombeuri* are river banks where it competes in the Pyrenees with *F. torrentium* but it is as frequently found in light pine forests along the sun-exposed borders of pathways or in grasslands. In the latter habitats the colonies are smaller and not so dominant as those frequently found in urban zones which sometimes appear to be supercolonial. The urban habitats are often characterized by much surface sealing with concrete or stony pavement.

Alates were found June 26 and July 5. The sample from the Sierra de las Cabras came from a true supercolony covering an area of at least 7.12 ha of a light pine forest (Catharineu et al. 2021). *Formica tombeuri* made up 99.9% of 9300 pitfall-traped ants within the area of this supercolony.

Taxonomic comments: Big eye size, small petiole width, moderate occelli distance as well as the dense and strong microsculpture and dense silvery pubescence of head and mesosoma clearly indicate that *Formica tombeuri* is a member of the *F. cinerea* group. However, it is exceptional within this group by an extreme reduction of pilosity on head, mesosoma and legs. The separation from *F. lemani*, which is similar in seta counts and might occur syntopic at higher elevations in the Pyrenees, is easily done by morphometry.

6.9 *Formica corsica* Seifert 2003

Formica corsica **Seifert 2003** [type investigation]
This taxon has been described from Corsica. Investigated were the holotype and 2 paratype workers labelled *"CORSICA: Asco, 2000 m leg. A. Delestrade 1991.06.19*

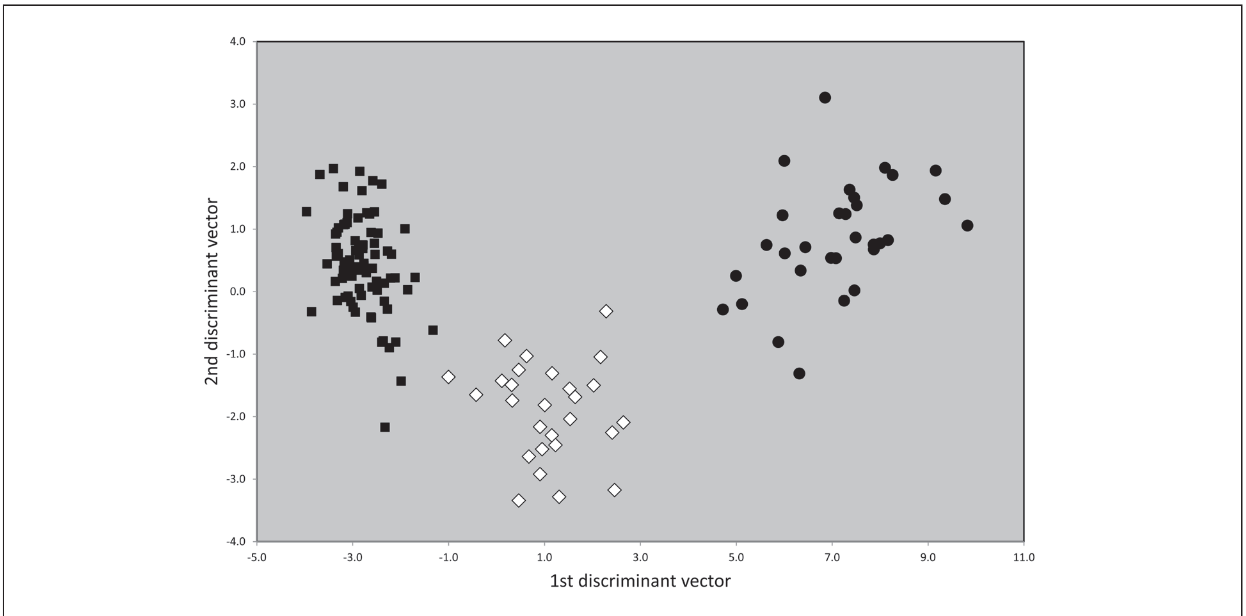


Figure 58. Nest sample means of linear discriminant scores of *Formica cinerea* (n=79, black squares), *F. selysi* (n=31, black dots) and *F. torrentium* (n=27, white rhombs).

No 1514"; depository SMN Görlitz, 3 paratypes MNHN Paris. Seven paratype workers labelled *"CORSICA: Niolo, 2000 m Mte Albanu leg. A. Delestrade 1992.09.13 No 1659*"; depositories MNHN Paris, SMN Görlitz. Nine paratype workers labelled *"CORSICA: Bavela, 1900 m leg. A. Delestrade 1991.09.21 No 1518*"; depositories MNHN Paris, SMN Görlitz. 16 paratype workers labelled *"CORSE MONTE-ROTONDO 2400 m 7-VII-1974 J-P.HEBRARD REC.*"; depositories MNHN Paris, SMN Görlitz.

All material examined. Numeric phenotypical data were taken in 11 nest samples with 35 workers. All material came from Corsica (France). For details see supplementary information SI1 and SI2.

Geographic range. *Formica corsica* is an endemite of Corsica found in elevations between 1000 and 2400 m.

Description: --Worker (Tab. 4; key). Smallest species of the *F. cinerea* group, CS 1193 ± 91 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape moderately long, CL/CW 1.140 ± 0.021, SL/CS 1.050 ± 0.019. Eye large, EYE/CS 0.311 ± 0.005. Ocellar distance small, OceD/CS 0.156 ± 0.012. Distance between metathoracal spiracles small, MtSt/CS 0.126 ± 0.014. Distance between metathoracal and propodeal stigma as well as between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt/CS 0.338 ± 0.012, MtMtp/CS 0.628 ± 0.016. Petiole scale rather wide PeW/CS 0.394 ± 0.022. Setae on first gaster tergite moderately long, GHL/CS 8.09 ± 0.98%. Genae without setae, nGen 0.0 ± 0.0. Margin of hind vertex with few setae, nCH 7.0 ± 2.6. Gula without or with very few setae, nGu 1.3 ± 0.8. Propodeum plus upper surfaces of metapleuron without or only very few setae, nPrMe 0.7 ± 1.5. Number of setae on petiole scale above the stigma low, nPe 3.6 ± 1.8. Setae on extensor profile of hind femur and extensor profile of hind tibia nearly absent, nHFex 0.0 ± 0.0, nHT 0.10 ± 0.29. Setae number on flexor profile of hind femur low, nHFfl 6.9 ± 1.8. Distance of transverse ripples and of pubescence hairs on dorsum of first gaster tergite rather low, RipD 5.00 ± 0.57, sqPDG 3.09 ± 0.25.

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 – that is, the ratio of sculptured surface against shining surface is about 2:1 and similar to the situation in *F. cinerea*. 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.

Habitat and Biology. Differing from the situation in the other species of the *Formica cinerea* group, 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. According to J. Casevitz-Weulersse (pers. comm. June 8, 2001), 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 the rather short time for larval development. Nest populations are small.

Taxonomic comments: *Formica corsica* is the only *F. cinerea* group species known from Corsica. Apart from the zoogeographic argument it is not to be confused due to its small size and setae numbers on posterior margin of vertex and underside of head which are larger than in *F. tombeuri* but smaller than in the remaining species of the *cinerea* group (Tab. 3). *Formica clara* and *F. cunicularia*, which also occur in Corsica, differ strikingly in setae numbers on hind margin of vertex, eye size, petiole width and pigmentation pattern (Tab. 7).

7. The species of the *Formica subpilosa* group

7.1 *Formica subpilosa* Ruzsky 1902

***Formica rufibarbis* ssp. *subpilosa* Ruzsky 1902** [type investigation]

This taxon has been described from Lake Aral in Kazakhstan. Investigated were the lectotype worker (labelled by Dlussky as "Lectoergatotype") and 4 paralectotype workers labelled "Karachingil ust. Syr Dari 29/ VI. 1900. L.S.Berg" and "F. rufibarbis F. v. subpilosa Ruz.(claro-subpilosa R.)"; depository ZMLSU Moskva. The lectotype sample is allocated to the *Formica subpilosa* cluster with p=1.0000 in a wild-card run of a 3-class LDA considering the species *F. subpilosa*, *F. tarimica* and a cluster collecting *F. clarissima, F. litoralis, F. pamirica* and *F. kirgisica n.sp.* (see supplementary information SI3, setting 6).

Formica cinerea* var. *bipilosa Karavajev 1926 [type investigation]

This taxon has been described from near to the Caspian Sea coast in Azerbaijan. Investigated were 11 syntype workers labelled "Vataga Khurshud bl. Salyan'. 20.III.1907 Shmidt i Shelkovnikov", "3306. Coll. Karavaiev", "F.(Serviformica) cinerea Mayr v. bipilosa Karav. typus" [white label] and "Syntypus Formica cinerea var. bipilosa Kar." [red label]; depository ZMU Kiev. The syntype sample is allocated to the *Formica subpilosa* cluster with p=1.0000 in a wild-card run of a 3-class LDA considering the species *F. subpilosa*, *F. tarimica* and a cluster collecting *F. clarissima, F. litoralis, F. pamirica* and *F. kirgisica n.sp.* (see supplementary information SI3, setting 6).

All material examined. Numeric phenotypical data were taken in 52 nest samples with 200 workers. The material came from Afghanistan (9 samples), Azerbaijan (3), China (2), Iran (1), Kazakhstan (3), Kyrgyzstan (24), Russia (4), Tajikistan (1), Turkmenistan (3), Turkey (1) and Uzbekistan (1). For details see supplementary information SI1 and SI2.

Geographic range. *Formica subpilosa* is found from East Turkey (40.2°N, 43.1°E) to Xinjiang in NW China (44.1°N, 88.0°E). The northernmost point of the range is marked by the type locality (46.1°N, 62.3°E) in Kazakhstan and the southernmost site is in Afghanistan (31.6°N, 65.7°E). The altitudinal range goes from -24 m in Azerbaijan up to 1513 m Kyrgyzstan. We referred the single record from the "Pamir" region (full text of Forel's label) to a place at the western margin of the Pamirs - only there we find altitudes below 2000 m a.s.l. Regarding the morphologically well separable morphs, there is no clear geographic pattern visible (Fig. 59).

Description: --Worker (Tab. 5; Fig. 19; key). Rather large, CS 1376 ± 133 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape rather long, CL/CW 1.151 ± 0.016, SL/CS 1.075 ± 0.024. Eye medium-sized, EYE/CS 0.278 ± 0.005. Ocellar distance smaller than in other members of the *subpilosa* group, OceD/CS 0.168 ± 0.009. Distance between metathoracal spiracles smaller than in other members of the *subpilosa* group, MtSt/CS 0.109 ± 0.011. Mesonotum in lateral aspect more slender than in other species. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt/CS 0.349 ± 0.010, MtMtp/CS 0.647 ± 0.012. Petiole moderately wide, PeW/CS 0.396 ± 0.023. Setae on first gaster tergite rather long, GHL/CS 11.35 ± 1.22%. Genae without setae, nGen 0.02 ± 0.10. Margin of hind vertex and underside of head without or very few standing setae, nCH 1.4 ± 1.3, nGu 0.27 ± 0.45. Pronotum, mesonotum and propodeum plus upper surfaces of metapleuron with setae number polymorphism (Tab. 6); pooled data of both morphs: nPn 18.7 ± 6.2, nMn 8.1 ± 3.7, nPrMe 5.9 ± 3.2. Number of setae on petiole scale above the stigma moderate, nPe 4.8 ± 1.7. Extensor profile of hind femur and extensor profile of hind tibia without or very few standing setae, nHFex 0.7 ± 1.0, nHT 1.5 ± 1.6. Setae

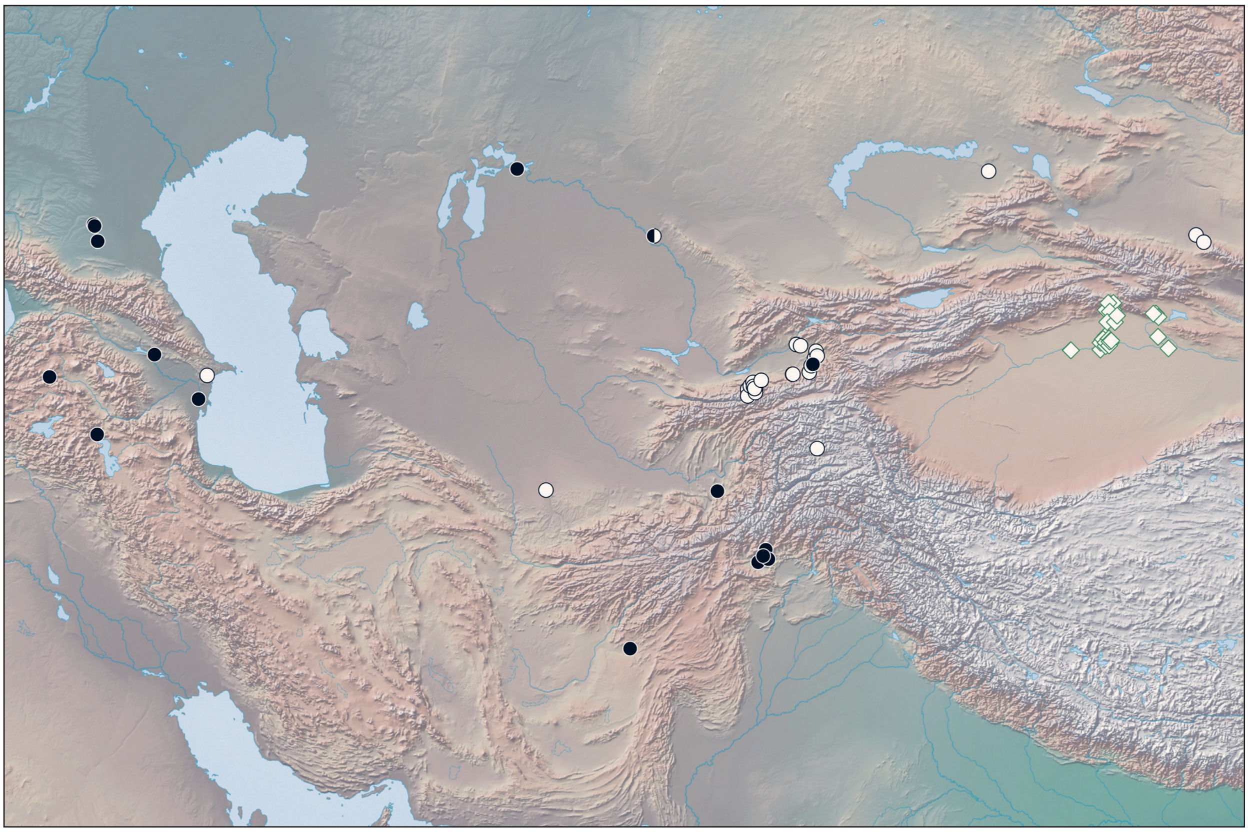


Figure 59. Geographic distribution of *Formica subpilosa* morph 1 (black dots), *Formica subpilosa* morph 2 (white dots) and of *F. tarimica* (white rhombs).

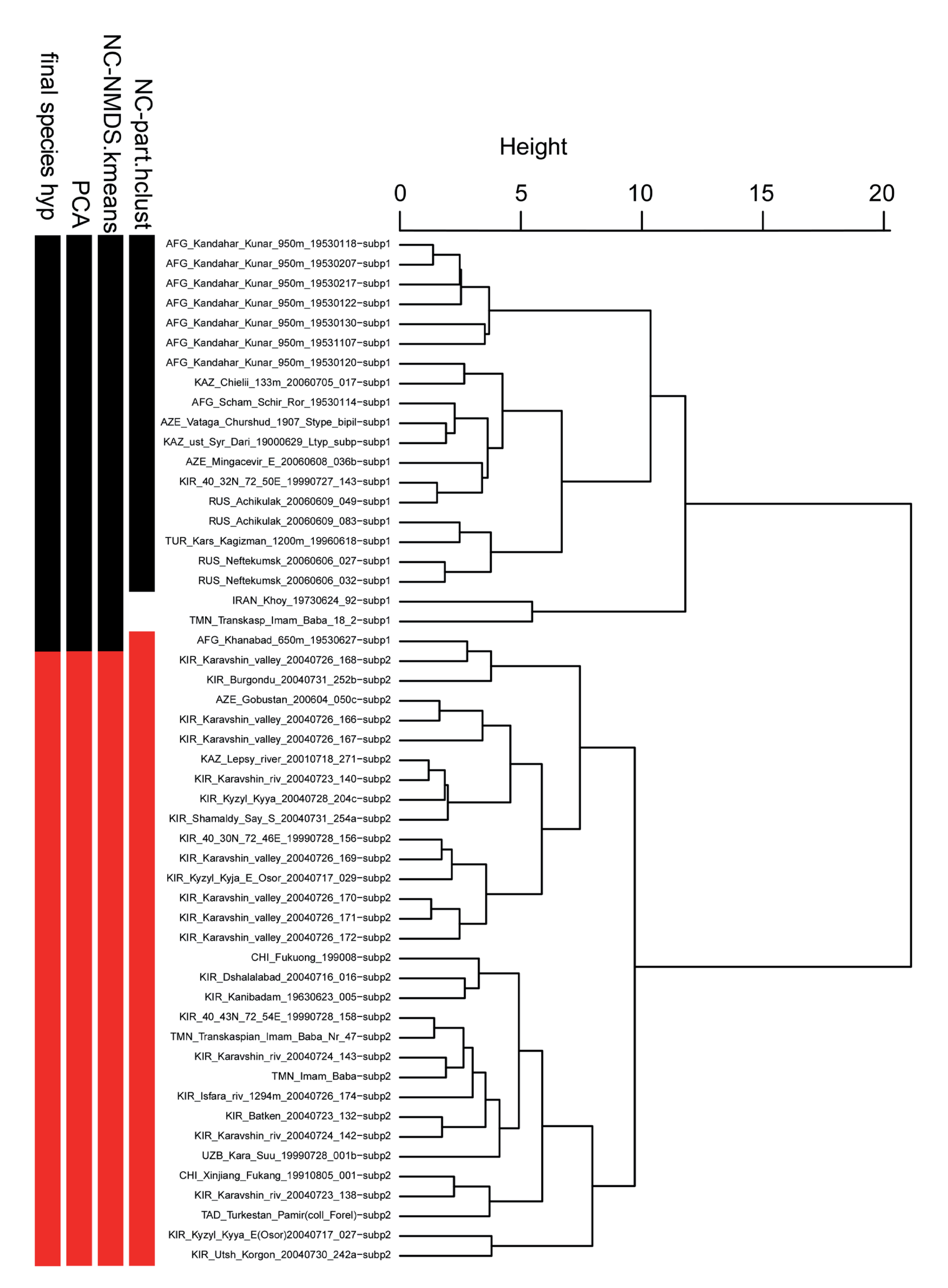


Figure 60. Exploratory data analyses separating nest samples of *Formica subpilosa* morph 1 (n=21, black bars) and of *F. subpilosa* morph 2 (n=31, red bars). The mean error of the four exploratory analyses is 1%. Empty bars are outliers in NC.part. hclust.

on flexor profile of hind femur always present, nHFfl 6.9 ± 2.1. Distance of transverse ripples on dorsum of first gaster tergite larger than in other members of the *subpilosa* group with exception of *F. iranica* n.sp., RipD 5.64 ± 0.46 (Fig. 19). Gaster covered by a dense silvery pubescence, sqPDG 3.00 ± 0.20. Pubescence on head, mesosoma and petiole clearly less dense. Whole head, mesosoma, coxae, all appendages and petiole in typical case light yellowish red; dark brown spots may occur on posterior vertex and dorsal promesonotum, particularly in smaller specimens. Gaster always dark brown.

Habitat and Biology. Compared to related species, *F. subpilosa* is apparently more thermophilic, occurring in lower altitudes and penetrating the true desert zone along moist river valleys or in oases. It is typical for irrigated soils and hence frequent in urban and agricultural regions. The main natural habitat is semidesert or transitions to dry steppe. It constructs big and very deep soil nests in the oases (Dlussky 1967). Due to its aggressiveness it can coexist with *Lasius neglectus* (see Schultz & Seifert 2005).

Taxonomic comments: As a combination of low ocelli distance, low distance between metathoracal spiracles, moderate seta number on propodeum-metapleuron, moderate seta number on flexor margin of hind femur and rather high ripple distance on 1st gaster tergite, *Formica subpilosa* is well separable from other species of the *subpilosa* group by any exploratory data analysis. *Formica tarimica*, a species of the *F. rufibarbis* group, is similar in all shape characters but can be separated by the strong reduction of setae on propodeum-metapleuron and flexor margin of hind femur and a higher distance of ripples on 1st gaster tergite (Tabs. 5 and 8).

A taxonomic conflict arises from the polymorphism within the entity named here *F. subpilosa* (Tab. 6). Firstly, the two morphs can be fully separated on worker individual level by an iterative LDA using the characters CS, CL/CW_{1400}, SL/CS_{1400}, $OceD/CS_{1400}$, EYE/CS_{1400}, PeW/CS_{1400}, GHL/CS_{1400}, $RipD_{1400}$, $sqPDG_{1400}$, nCH_{1400},, nPn_{1400}, nMn_{1400}, $nPrMe_{1400}$, $nHFfl_{1400}$ and nPe_{1400}. Secondly, the exploratory data analyses NC-Ward, NC-Part.hclust, NC-NMDS.kmeans and PCA confirm the classification of 52 nest samples established by the controlling LDA in the mean of the four analyses by 99.0% after character reduction to CL/CW_{1400}, $OceD/CS_{1400}$, EYE/CS_{1400}, PeW/CS_{1400}, nCH_{1400},, nPn_{1400}, nMn_{1400} and $nHFfl_{1400}$ (Fig. 60). These data would provide a sufficient argumentation to split *F. subpilosa* in two species. However, this hypothesis is strongly challenged by a nest sample (Sample No 689 KAZ: Chielii, 20060705-017) that was mixed with seven morph 1 and three morph 2 workers – all clearly determined when run as wild-cards in an LDA with p >0.95. A stereomicroscopic scrutiny of these ten workers did not provide any suggestion of differences in shape, pigmentation, surface structure or body size which could indicate accidental mixing of two different nest samples during collecting in the field. According to this finding and the absence of a clear geographic structure, we suppose that morph 1 and morph 2 should not be described as different species and represent an intraspecific polymorphism.

7.2 *Formica iranica* n.sp.

Etymology: The name is given according to the terra typica.

Type material

Holotype and one paratype worker on the same pin labelled "IRAN: 33.6165°N, 51.7280°E, Kashan Komjan, 1596 m, road side, stone semidesert, 2012.05.09-1017" and "Holotype (top) and paratype *Formica iranica* Schultz & Seifert"

All material examined. Only the type sample was available. For details see supplementary information SI1 and SI2.

Geographic range. Only known from the type locality.

Description: --Worker (Tab. 5; Figs 16-18; key). Rather large, CS 1424 ± 263 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm and are based on only two specimens. Head rather short but scape longer than in other members of the *subpilosa* group, CL/CW 1.127 ± 0.008, SL/CS 1.106 ± 0.015. Eye rather small, EYE/CS 0.272 ± 0.004. Ocellar distance larger than in other members of the *subpilosa* group, OceD/CS 0.192 ± 0.002. Distance between metathoracal spiracles rather large, MtSt/CS 0.140 ± 0.005. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt/CS 0.346 ± 0.001, MtMtp/CS 0.654 ± 0.007. Petiole moderately wide, PeW/CS 0.396 ± 0.004. Setae on first gaster tergite rather long, GHL/CS 11.40 ± 0.76%. Genae without setae, nGen 0.0 ± 0.0. Margin of hind vertex with single setae and underside of head without setae, nCH 1.05 ± 0.21, nGu 0.0 ± 0.0. Pronotum and mesonotom with moderate seta numbers, nPn 12.2 ± 1.8, nMn 6.1 ± 0.4. Propodeum-metapleuron without or only single setae, nPrMe 0.8 ± 1.1. Number of setae on petiole scale above the stigma low, nPe 2.4 ± 1.8. Extensor profile of hind femur and extensor profile of hind tibia without setae, nHFex 0.0 ± 0.0, nHT 0.0 ± 0.0. Seta number on flexor profile of hind femur much higher than in the similar colored *F. tarimica* and *orangea*, nHFfl 7.3 ± 0.3. Microsculpture on dorsum of 1st gaster tergite much finer than in *F. subpilosa*, surface despite dense pubescence rather shiny. Distance of transverse ripples larger than in all other members of the *subpilosa* group, RipD 9.30 ± 0.71. Gaster covered by a very dense silvery pubescence, sqPDG 2.49 ± 0.20. Pubescence on head, mesosoma and

Table 5. RAV-corrected morphological data of workers of the *Formica subpilosa* group. Only specimens with available data on petiole width and eye size are included. Sequence of data: arithmetic mean ± standard deviation [minimum, maximum]. Numbers following the maximum indicate a reduced sample size for the given character.

	iranica n.sp. (n=2)	***subpilosa*** (n=194)	***pamirica*** (n=69)	***kirghisica*** n.sp. (n=53)	***litoralis*** (n=283)	***clarissima*** (n=274)
CS[µm]	1424±263 [1238,1610]	1376±133 [1071,1699]	1297±116 [989,1528]	1326±83 [1146,1480]	1291±116 [964,1554]	1276±105 [1053,1550]
CL/CW_{1400}	1.127±0.008 [1.121,1.133]	1.151±0.016 [1.112,1.204]	1.144±0.018 [1.099,1.187]	1.126±0.014 [1.095,1.155]	1.124±0.019 [1.048,1.169]	1.128±0.021 [1.075,1.182]
SL/CS_{1400}	1.106±0.015 [1.096,1.117]	1.075±0.024 [0.998,1.131]	1.055±0.022 [1.009,1.111]	1.051±0.019 [1.010,1.084]	1.040±0.022 [0.963,1.091]	1.036±0.024 [0.949,1.096]
EYE/CS_{1400}	0.272±0.004 [0.270,0.275]	0.278±0.005 [0.264,0.292]	0.284±0.005 [0.274,0.299]	0.276±0.003 [0.267,0.284]	0.280±0.006 [0.264,0.302]	0.279±0.006 [0.265,0.295]
$OceD/CS_{1400}$	0.192±0.002 [0.191,0.194]	0.168±0.009 [0.135,0.192]	0.182±0.008 [0.161,0.195]	0.187±0.008 [0.171,0.205]	0.182±0.012 [0.158,0.220]	0.182±0.011 [0.152,0.215] 272
$MTST/CS_{1400}$	0.140±0.005 [0.137,0.144]	0.109±0.011 [0.082,0.165] 127	0.144±0.013 [0.107,0.176] 68	0.126±0.013 [0.104,0.160]	0.138±0.017 [0.102,0.205] 149	0.134±0.016 [0.092,0.171] 159
$MTPPST/S_{1400}$	0.346±0.001 [0.345,0.346]	0.349±0.010 [0.327,0.380] 127	0.354±0.007 [0.336,0.370] 68	0.335±0.009 [0.312,0.349]	0.342±0.010 [0.319,0.370] 149	0.344±0.009 [0.321,0.371] 159
$MTMTP/S_{1400}$	0.654±0.007 [0.649,0.659]	0.647±0.012 [0.617,0.695] 127	0.656±0.012 [0.630,0.695] 68	0.630±0.010 [0.605,0.656]	0.637±0.011 [0.604,0.659] 149	0.628±0.012 [0.594,0.666] 159
PeW/CS_{1400}	0.396±0.004 [0.393,0.399]	0.396±0.023 [0.314,0.448]	0.397±0.018 [0.347,0.436]	0.431±0.022 [0.375,0.489]	0.440±0.023 [0.375,0.521]	0.442±0.026 [0.387,0.535]
GHL/CS_{1400}	11.40±0.76 [10.87,11.94]	11.35±1.22 [3.59,14.08]	11.70±1.32 [7.14,15.04]	10.64±1.42 [7.70,13.05]	10.49±1.27 [5.63,14.96] 278	8.49±1.19 [5.61,12.54]
$nGen_{1400}$	0.0±0.0 [0.0,0.0]	0.02±0.10 [0.0,1.0] 187	0.11±0.30 [0.0, 1.2]	0.52±0.87 [0.0,3.4]	0.10±0.25 [0.0,1.3]	0.07±0.27 [0.0,2.6] 269
nCH_{1400}	1.05±0.21 [0.9,1.2]	1.4±1.3 [0.0, 8.3]	4.0±2.1 [1.1,12.3]	8.05±3.55 [2.5,16.4]	1.56±1.25 [0.0, 6.1] 278	0.57±0.70 [0.0, 3.4]
nGU_{1400}	0.00±0.00 [0.0,0.00]	0.27±0.45 [0.0,2.0]	1.95±0.88 [0.0, 4.1]	4.06±1.58 [1.1,11.4]	0.84±0.73 [0.0, 3.9] 278	0.64±0.60 [0.0, 4.5]
nPn_{1400}	12.2±1.8 [10.9,13.5]	18.7±6.2 [2.4,36.1]	37.2±7.6 [19.0,55.0]	37.8±8.1 [15.0,57.7]	23.6±5.0 [10.3,41.1]	17.2±4.8 [0.0,33.2]
nMn_{1400}	6.1±0.4 [5.8, 6.4]	8.1±3.7 [0.0,18.5]	16.3±6.4 [6.3,38.9]	17.1±3.5 [5.9,24.0]	12.1±3.3 [2.2,28.6]	6.1±3.1 [0.0,17.2]
$nPrMe_{1400}$	0.75±1.06 [0.0,1.5]	5.9±3.2 [0.0,19.0]	11.8±3.4 [3.1,19.2]	14.2±3.6 [5.3,22.6]	6.7±2.6 [0.0,14.0]	1.9±1.6 [0.0,7.8]
nPe_{1400}	2.45±1.77 [1.2,3.7]	4.8±1.7 [1.2,10.1]	7.4±1.9 [0.9,11.9]	8.1±1.7 [3.9,11.9]	5.1±1.6 [0.5,10.2] 278	3.8±1.8 [0.0,16.9]
$nHFex_{1400}$	0.0±0.0 [0.0,0.0]	0.7±1.0 [0.0,5.2]187	0.6±0.9 [0.0,4.0]	3.9±2.7 [0.0,11.8]	0.7±0.8 [0.0,5.1]	0.2±0.4 [0.0,2.4] 269
$nHFfl_{1400}$	7.3±0.3 [7.1,7.5]	6.9±2.1 [1.9,12.2]	9.5±2.4 [3.1,16.3]	12.8±3.5 [5.5,20.0]	6.9±1.6 [2.8,12.7]	3.3±1.6 [0.0,11.0]
nHT_{1400}	0.0±0.0 [0.0,0.0	1.5±1.6 [0.0,9.1]187	3.7±2.3 [0.0,10.9]	11.2±5.9 [1.3,30.5]	3.3±2.7 [0.0,21.1]	0.8±1.1 [0.0,8.3] 271
$RipD_{1400}$	**9.30**±0.71 [8.8,9.8]	**5.62**±0.41 [4.7,7.3]	4.27±0.29 [3.8,5.0]	4.28±0.34 [3.7,5.1]	4.24±0.31 [3.5, 5.2]	4.28±0.29 [3.5, 5.0] 271
$sqPDG_{1400}$	2.49±0.20 [2.35,2.63]	2.99±0.20 [2.53,3.53]	3.21±0.20 [2.80,3.78]	3.26±0.19 [2.88,3.67]	3.29±0.14 [2.91,3.70]	3.24±0.17 [2.71,3.70] 271
$PIGM_{1400}$	0.0±0.0 [0,0]	5.0±7.8 [0,59]	17.6±12.0 [0,54]	10.7±6.4 [0,30]	15.6±13.3 [0,72]	13.1±12.0 [0,67]
$CONT_{1400}$	0.00±0.00 [0.0,0.0]	0.03±0.06 [0.0,0.5]	0.24±0.22 [0.0,1.0]	0.10±0.07 [0.0,0.3]	0.15±0.12 [0.0,0.9]	0.17±0.17 [0.0,0.9]

petiole less dense. Whole head, mesosoma, coxae, all appendages and petiole light yellowish red, gaster dark brown.

Habitat and Biology. The two workers were collected at a road margin in a semidesert close to a creek lined by shrubs.

Taxonomic comments: The two specimens did not show phenotypic abnormalities. They are described here as new species because they represent a unique combination of high RipD, very low sqPDG, long scape, presence of rather many setae on flexor profile of hind femur and bright orange head and mesosoma. In the first impression they appear very similar to sympatric *Formica orangea* but can be separated alone by the much higher $nHFfl_{1400}$ and SL/CS_{1400}. *Formica iranica* n.sp. ist probably closely related to *F. subpilosa*.

7.3 *Formica kashmirica* Bolton 1995

***Formica kashmirica* Bolton 1995** [type investigation]
First available use of *Formica* (*Serviformica*) *rufibarbis rufibarbis var. kashmirica* Stärcke 1935

Stärcke (1935) described this ant from Kashmir and Jammu, India. Investigated were the holotype worker labelled: “Nubra Valley 3000 m 14-18 VII.1930”, “Nederlandsche Karakorum-Expeditie J.A.Sillem leg.”, “Holotype var. kashmirica” (handwritten by Stärcke) and “~~PARA~~TYPE Formica (Serviformica) rufibarbis rufibarbis var. kashmirica 1933 Stärcke”; two paratype workers labelled “Nubra Valley 3000 m 14-18 VII.1930”, “Nederlandsche Karakorum-Expeditie J.A.Sillem leg.”, and “PARATYPE Formica (Serviformica) rufibarbis rufibarbis var. kashmirica 1933 Stärcke”; all material in ZM Amsterdam. The holotype has the data CW 1256 µm, PeW 606 µm, GHL 145 µm.

All material examined. Only the type sample was available. For details see supplementary information SI1 and SI2.

Geographic range. *Formica kashmirica* is known to us only from the type locality which is situated at approximately 34.6°N, 77.6°E and 3100 m.

Description: --Worker (Tab. 6; key). Rather small, CS 1277 ± 103 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape rather short, CL/CW 1.128 ± 0.011, SL/CS 1.047 ± 0.003. Eye rather small, EYE/CS 0.276 ± 0.001. Ocellar distance large, OceD/CS 0.187 ± 0.005. Petiole scale in frontal view wide, reaching its largest width in upper third, with slightly convex sides, the dorsal crest only slightly convex, PeW/CS 0.446 ± 0.019. Setae on first gaster tergite rather short, GHL/CS 8.21 ± 2.86%. Dorsal plane of scape in the two larger workers with a single semierect seta, frontal edge of scape with 5-7 semierect setae (if repeated in other samples, a clear difference from all related species). Genae without setae, nGen 0.0 ± 0.0. Margin of hind vertex and underside of head with few standing setae, nCH 2.0 ± 1.9, nGu 2.3 ± 0.7. Pilosity on mesosoma in contrast to other members of the *subpilosa* group strongly reduced, nPn 4.0 ± 0.4, nMn 0.0 ± 0.0, nPrMe 1.3 ± 0.9. Petiole scale above stigma without or only single setae, nPe 0.7 ± 0.8. Extensor profile of hind femur without setae, nHFex 0.0 ± 0.0. Extensor profile of hind tibia with few standing setae, nHT 2.3 ± 2.7. Flexor profile of hind femur with many long setae, nHFfl 10.1 ± 1.8. Coxae ventrally and gaster tergites with long setae. Distance of transverse ripples on dorsum of first gaster tergite low, RipD 4.13 ± 0.25. Gaster covered by a dense silvery pubescence, sqPDG 3.22 ± 0.13. Pubescence on head, mesosoma and petiole less dense. Mesosoma, coxae, all appendages and petiole yellowish red; in the holotype whole head yellowish red, in the paratypes, frons and posterior vertex infuscated. Gaster medium brown with red tinge, frontal face of first tergite in two specimens yellowish red.

Habitat and Biology. There is no information on habitat and biology - the actual landscape picture of the type locality shows an unregulated, rather plane river valley with big areas of bare alluvial soil and shrubs.

Taxonomic comments: The remarkable reduction of setae on dorsal mesosomal sclerites compared to those on lower body parts, scape and legs is apparently not the result of secondary mechanical damage - the undisturbed, homogenous pubescence condition and the missing remnants of setae bases in the scattered microfoveolae on dorsal mesosoma support this view. If the type sample shows characters representative for the species, *Formica kashmirica* should be easily separable from any species of the *subpilosa* and *cinerea* group by the reduced pilosity on mesosoma and from any member of the *rufibarbis* group by the much higher nHFfl.

7.4 *Formica clarissima* Emery 1925

***Formica rufibarbis* var. *clarissima* Emery 1925** [Replacement name for *F. rufibarbis* ssp. *subpilosa* var. *clarior* Ruzsky, 1915 (junior homonym of *F. sanguinea* var. *clarior* Ruzsky 1905), type investigation]
***Formica subilosa ruzskyi* Dlussky 1965** [unnecessary replacement name for *F. rufibarbis* ssp. *subpilosa* var. *clarior* Ruzsky 1915]

Formica clarissima has been described from Eastern Tibet. Investigated was the lectotype worker labelled “V.Tsajdam, st. Barun-Tszazaka. Kozlov. nach. V. 1900.”, “Form. rufibarbis subpilosa Ruzsky v. clarior, n.var.”, “F.rufibarbis subpilosa v. clarior nov. M.Ruzsky det.” and

Table 6: RAV-corrected morphological data of workers of the *Formica subpilosa* group and *Formica lhasaensis*. Only specimens with available data on petiole width and eye size are included. Sequence of data: arithmetic mean ± standard deviation [minimum, maximum]. Numbers following the maximum indicate a reduced sample size for the given character.

	subpilosa morph 1 (n=99)	ANOVA	***subpilosa*** morph 2 (n=95)	***kashmirica*** (n=3)	***superpilosa*** (n=7)	***lhasaensis*** (n=20)
CS[µm]	1385±129 [1049,1699]	n.s.	1368±138 [1071,1676]	1277±103 [1158,1349]	1276±69 [1166,1384]	1122±79 [1002,1258]
CL/CW_{1400}	1.150±0.016 [1.112,1.204]	n.s.	1.153±0.016 [1.114,1.189]	1.128±0.011 [1.121,1.140]	1.121±0.016 [1.094,1.137]	1.111±0.017 [1.073,1.134]
SL/CS_{1400}	1.073±0.025 [0.998,1.122]	n.s.	1.078±0.022 [1.024,1.131]	1.047±0.003 [1.045,1.051]	1.076±0.018 [1.050,1.100]	0.960±0.026 [0.926,1.002]
EYE/CS_{1400}	0.275±0.005 [0.264,0.285]	62.79, 0.000	0.280±0.004 [0.267,0.292]	0.276±0.001 [0.275,0.277]	0.284±0.006 [0.275,0.294]	0.299±0.007 [0.288,0.313]
$OceD/CS_{1400}$	0.173±0.008 [0.158,0.192]	50.58 0.000	0.164±0.008 [0.135,0.183]	0.187±0.005 [0.181,0.191]	0.163±0.005 [0.157,0.172]	0.181±0.011 [0.162,0.206]
$MTST/CS_{1400}$	0.113±0.011 [0.091,0.141] 39	8.76 0.004	0.107±0.011 [0.082,0.140] 88	no data	0.108±0.008 [0.098,0.118]	0.158±0.015 [0.136,0.181]
$MTPPST/CS_{1400}$	0.351±0.011 [0.332,0.380] 39	n.s.	0.348±0.009 [0.327,0.376] 88	no data	0.355±0.007 [0.344,0.364]	0.312±0.009 [0.294,0.333]
$MTMTP/CS_{1400}$	0.650±0.015 [0.628,0.682] 39	n.s.	0.645±0.011 [0.617,0.670] 88	no data	0.651±0.010 [0.637,0.665]	0.597±0.008 [0.584,0.611]
PeW/CS_{1400}	0.402±0.020 [0.368,0.448]	12.47 0.001	0.389±0.023 [0.314,0.441]	0.446±0.013 [0.431,0.455]	0.377±0.011 [0.354,0.390]	0.425±0.018 [0.390,0.460]
GHL/CS_{1400}	11.61±1.06 [8.82,14.08]	7.31 0.007	11.09±1.34 [3.59,14.08]	8.21±2.86 [5.18,10.85]	13.10±1.07 [11.70,14.52]	8.14±1.14 [5.48, 9.76]
$nGen_{1400}$	0.02±0.12 [0.0,1.0]93	7.30 0.008	0.03±0.09 [0.0,0.4] 94	0.0±0.0 [0.0,0.0]	8.3±2.3 [5.4,12.0]52	0.22±0.36 [0.0,1.2] 52
nCH_{1400}	2.03±1.45 [0.0, 8.3]	73.60 0.000	0.69±0.73 [0.0, 3.8]	2.00±1.95 [0.0, 3.9]	32.6±2.3 [29.7,36.9]	12.8±5.2 [1.3,21.2]
nGU_{1400}	0.42±0.53 [0.0,2.0]	25.18 0.000	0.12±0.25 [0.0,1.4]	2.33±0.68 [1.8, 3.1]	9.5±2.8 [5.7,12.9]	9.8±2.1 [5.6,13.6]
nPn_{1400}	23.0±4.9 [10.4,36.1]	**214.66** 0.000	14.3±3.8 [2.4,24.4]	4.0±0.4 [3.7,4.5]	64.3±11.6 [48.1,85.5]	36.0±12.0 [10.7,62.9]
nMn_{1400}	10.6±2.9 [2.6,18.5]	**219.79** 0.000	5.4±2.3 [0.0,11.7]	0.0±0.0 [0.0,0.0]	32.0±6.0 [27.1,43.8]	17.6±7.1 [5.0,31.8]
$nPrMe_{1400}$	7.9±2.9 [1.6,19.0]	**163.48** 0.000	3.9±1.8 [0.0,9.0]	1.3±0.9 [0.5,2.2]	33.2±6.3 [26.1,40.6]	13.3±5.8 [3.5,25.3]
nPe_{1400}	5.6±1.7 [1.5,10.1]	67.88 0.000	3.9±1.1 [1.2,8.2]	0.7±0.8 [0.0,1.6]	11.7±2.0 [8.5,14.0]	8.5±3.2 [0.0,14.9]
$nHFex_{1400}$	0.5±0.9 [0.0,5.2] 93	9.63 0.002	0.9±1.0 [0.0,4.6] 94	0.0±0.0 [0.0,0.0]	17.7±1.5 [15.6,19.8]	0.11±0.49 [0.0,2.2]
$nHFfl_{1400}$	8.1±1.8 [4.2,12.2]	**138.07** 0.000	5.5±1.6 [1.9,9.7]	10.1±1.8 [8.1,11.7]	27.2±4.4 [19.9,33.8]	11.1±3.26 [3.7,17.3]
nHT_{1400}	1.7±1.9 [0.0,9.1] 85	n.s.	1.3±1.3 [0.0,6.9] 94	2.3±2.7 [0.0,5.3]	11.0±1.0 [9.2,12.2]	0.23±0.48 [0.0,1.5]
$RipD_{1400}$	5.60±0.50 [4.7,7.9]	n.s.	5.68±0.41 [4.8,7.3]	4.13±0.25 [3.1,4.4]	5.47±0.37 [4.9,5.9]	7.40±0.52 [6.4,8.4]
$sqPDG_{1400}$	2.95±0.21 [2.53,3.53]	16.18 0.000	3.04±0.17 [2.62,3.40]	3.22±0.13 [3.10,3.36]	3.00±0.22 [2.64,3.26]	3.45±0.19 [3.21,4.10]
$PIGM_{1400}$	9.3±7.4 [1,26]	n.s.	5.1±9.2 [0,59]	2.0±3.5 [0,6]	9.9±4.8 [3,7]	68.0±6.4 [58,80]
$CONT_{1400}$	0.14±0.09 [0.1,0.5]	8.09 0.005	0.01±0.04 [0.0,0.1]	0.0±0.0 [0.0,0.0]	0.06±0.05 [0,0.1]	0.02±0.07 [0.0,0.3]

"Lectoergatotype F. subpilosa ruzskyi (Ruzk) Dluss."; depository ZMLU Moscow. The lectotype is allocated to the *Formica clarissima* cluster with p=0.9813 in a wild-card run of a 3-class LDA considering the species *F. clarissima*, *F. litoralis* and a cluster collecting *F. pamirica* and *F. kirgisica* n.sp. (see supplementary information SI3, setting 7).

All material examined. Numeric phenotypical data were taken in 88 nest samples with 274 workers. The material came from China (22 samples), Mongolia (56), and Russia (10). For details see supplementary information SI1 and SI2.

Geographic range. The range of *Formica clarissima* is obviously divided into a southern and northern population. The southern population with 22 evaluated samples is distributed between 33°N and 37°N, 97°E and 104°E and was found at elevations of 2356 ± 625 [1500, 3900] m. The northern population with 70 evaluated samples is delimited by 43.9°N, 50.6°N, 88°E, 126.6°E and occurred at elevations of 1070 ± 346 [180,1850] m (Fig. 61). No other species of the *subpilosa* group were found within the range of *clarissima*.

Description: --Worker (Tab. 5; key). Rather small, CS 1276 ± 105 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape rather short, CL/CW 1.128 ± 0.021, SL/CS 1.036 ± 0.024. Eye medium-sized, EYE/CS 0.279 ± 0.006. Ocellar distance large, OceD/CS 0.182 ± 0.011. Distance between metathoracal spiracles moderate, MtSt/CS 0.134 ± 0.016. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt/CS 0.344 ± 0.009, MtMtp/CS 0.628 ± 0.012. Petiole wide, PeW/CS 0.442 ± 0.026. Setae on first gaster tergite shorter than in other members of the *subpilosa* group, GHL/CS 8.49 ± 1.19%. Genae, margin of hind vertex and underside of head usually without or only with few standing setae, nGen 0.07 ± 0.27, nCH 0.57 ± 0.70, nGu 0.64 ± 0.60. Pronotum with a subaverage seta number, nPn 17.2 ± 4.8. Mesonotum and propodeum-metapleuron with fewer setae than *litoralis*, nMn 6.1 ± 3.1, nPrMe 1.9 ± 1.6. 0.8, nHFfl 0.7 ± 0.2. Number of setae on petiole scale above the stigma very low, nPe 3.8 ± 1.8. Extensor profile of hind femur and extensor profile of hind tibia without or very few standing setae, nHFex 0.2 ± 0.4, nHT 0.8 ± 1.1. Flexor profile of hind femur with few setae, nHFfl 3.3 ± 1.6. Distance of transverse ripples on dorsum of first gaster tergite medium, RipD 4.28 ± 0.29. Gaster covered by a dense silvery pubescence, sqPDG 3.24 ± 0.27. Pubescence on head, mesosoma and petiole less dense. Colour variable: average case: vertex, dorsal mesosoma, coxae, petiole and appendages brown, genae and ventrolateral pronotum lighter reddish brown. Gaster always dark brown. Larger workers lighter, sometimes entirely reddish brown except for darker brown gaster and posterior vertex.

Habitat and Biology. The habitat selection of this species shows similarities to that of *F. litoralis*. B. Pisarski (cited in Dlussky 1967) found the nests on rubble soils or sand banks of flooding terraces along the river Kergulen / Mongolia. R. Schultz found this species in Mongolian steppe and semidesert habitats always in proximity to open water. Near lake Nar Us Nur a polydomous colony with at least seven nest fractions could be observed on the border between wetland and semidesert. Sometimes nests were found in the wet depressions between sand dunes or in salty semidesert soil. Higher shrubs or trees were frequently absent from these sites but the species was also found in light *Populus* or *Salix* stands. Nests are typically located under stones, deadwood, though the species also utilizes the base of street trees in urban areas. Alate gynes were found within the nests on August 6, 2003 (lakes Shine Us Nur and Nar Us Nur) and on August 15, 2003 (semidesert W of mount Chara Obo).

Taxonomic comments: Considering 19 characters (see SI3, setting 7), *Formica clarissima* and *F. litoralis* can be separated from the species aggregate *F. pamirica* & *kirgisica* n.sp. by the exploratory data analyses NC-Ward and NC-part.kmeans with a mean error rate of 2.9% in 204 nest samples (Fig.62). *Formica clarissima* is equal to *F. litoralis* in a majority of evaluated characters (Tab. 5). According to the GAGE species concept, clear allopatry (as it is given in this case) is no argument to separate two species – species must be clusterable with a minimum error rate. This condition is given by the exploratory data analyses NC-Ward, NC-part.kmeans and NC-NMDS. kmeans which separated the clusters with an error rate of 3.6, 1.2 and 1.2% relative to the controlling LDA (Fig. 63). The latter classified 97.6% of 547 worker individuals correctly and 97.0% of 167 nest samples with posterior probabilities of p > 0.90.

7.5 *Formica litoralis* Kuznetzov-Ugamsky 1926

***Formica subpilosa* ssp. *litoralis* Kuznetzov-Ugamsky 1926** [description of Dlussky (1967) and zoogeography]

Kuznetzov-Ugamsky (1926) reported in the original description the following localities:"... exclusively in the bassin of Issyk-Kul: settlement Rybyatchi, Chok Tal, Kok-Moynok, Jety-Ogus (Kashka Su), near to mouth of river Mal. Dshargylchak, divide Chubardshan (Kuznetzov)".

Dlussky (1967) fixed a lectotype worker, deposited in either the collection of St. Petersburg or Moscow, with the supposed labelling transliterated from Russian "neoergatotyp: s. Kurminty, severo-vostochnij bereg osera Issyk Kul, leg. Dlussky". This specimen was not available for investigation but the identity of *Formica litoralis* is clear by a very strong geographic argument: Among the 49 *Serviformica* samples collected by us in the whole Issyk-Kul bassin, as much as 30 belonged to *F. litoralis* and it was the only species of the *F. subpilosa* group found there. Furthermore, it can be excluded that the skilled determinator Dlussky (1967) did confuse members of the *F. subpilosa* group with those of the *F. rufibarbis* group of which we confirmed *F. clara* and *F. orangea* to be present in the Issyk-Kul bassin. A sample from the type locality Jety-Oguz was allocated to the *Formica litoralis* cluster with p=0.9921 in a wild-card run of a 3-class LDA considering the species *F. clarissima*, *F. litoralis* and a cluster collecting *F. pamirica* and *F. kirgisica* n.sp. (see supplementary information SI3, setting 7).

All material examined. Numeric phenotypical data were taken in 83 nest samples with 284 workers. The material came from China (13 samples), Kazakhstan (1), Kyrgyzstan (68) and Pakistan (1). For details see supplementary information SI1 and SI2.

Geographic range. The Middle Asian main range of *F. litoralis* is delimited by 41.2°N, 44.7°N, 72.3°E and 81.5°E, with elevations of 1991 ± 400 [738, 2770] m (Fig. 61). The single sample from Pakistan (36.02°N, 74.53°E, 2800 m), 570 km south of the main range, appears to be a geographic outlier but Pakistan and Tajikistan are strongly under-recorded in our data set – only 0.4% of all 2460 *Serviformica* samples came from these regions.

Description: --Worker (Tab. 5; key). Rather small, CS 1291 ± 116 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape rather short, CL/CW 1.126 ± 0.014, SL/CS 1.040 ± 0.022. Eye medium-sized, EYE/CS 0.280 ± 0.006. Ocellar distance large, OceD/CS 0.182 ± 0.012. Distance between metathoracal spiracles moderate, MtSt/CS 0.138 ± 0.017. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt/CS 0.342 ± 0.010, MtMtp/CS 0.637 ± 0.011. Petiole wide, PeW/CS 0.440 ± 0.023. Setae on first gaster tergite longer than in *clarissima*, GHL/CS 10.49 ± 1.27%. Genae, margin of hind vertex and underside of head usually without or with only few standing setae, nGen 0.10 ± 0.25, nCH 1.56 ± 1.25, nGu 0.84 ± 0.73. Pronotum with lower seta number than in *pamirica* and *kirghisica* n.sp., nPn 23.6 ± 5.0. Mesonotum with moderate seta number, nMn 12.1 ± 3.3. Propodeum-metapleuron and flexor profile of hind femur with fewer setae than in *pamirica* and *kirghisica* n.sp., nPrMe 6.7 ± 2.6, nHFfl 6.9 ± 1.6. Number of setae on petiole scale above the stigma low, nPe 5.1 ± 1.6. Extensor profile of hind femur and extensor profile of hind tibia without or few standing setae, nHFex 0.7 ± 0.8, nHT 3.3 ± 2.7. Distance of transverse ripples on dorsum of first gaster tergite medium, RipD 4.24 ± 0.31. Gaster covered by a dense silvery pubescence, sqPDG 3.29 ± 0.14. Whole body covered by a silvery pubescence, somewhat more

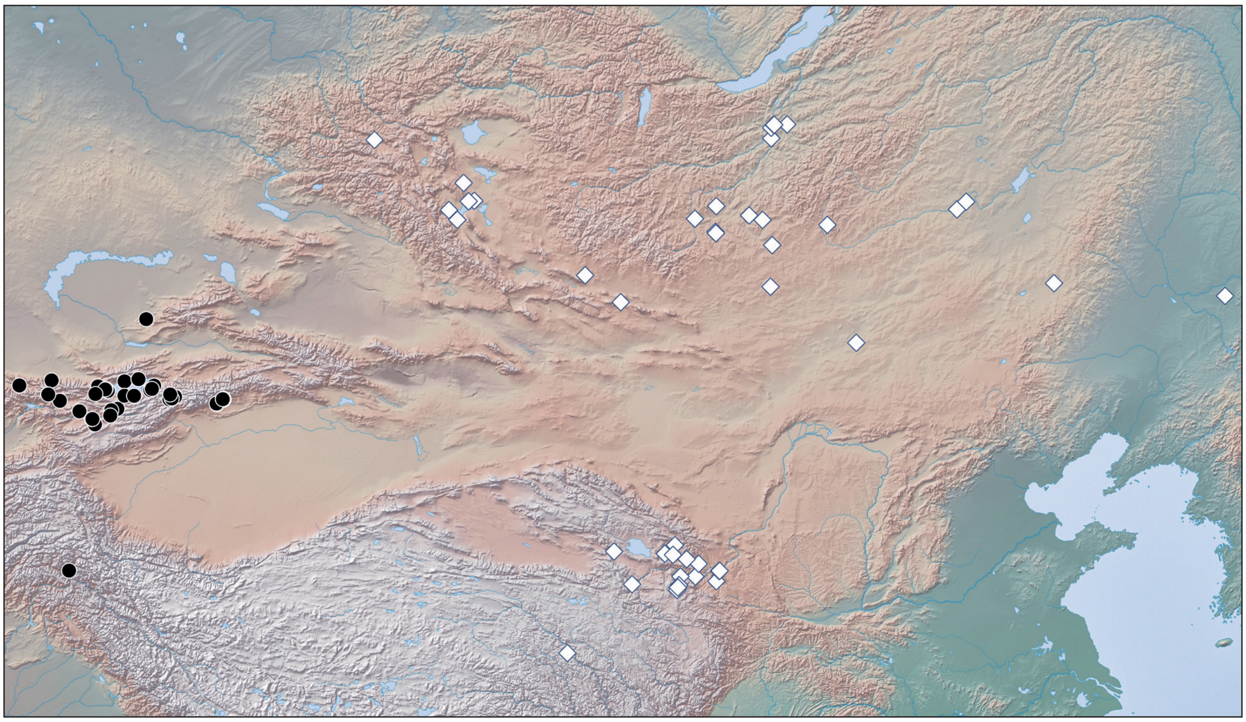


Figure 61. Geographic distribution of *Formica litoralis* (black dots) and *F. clarissima* (white rhombs).

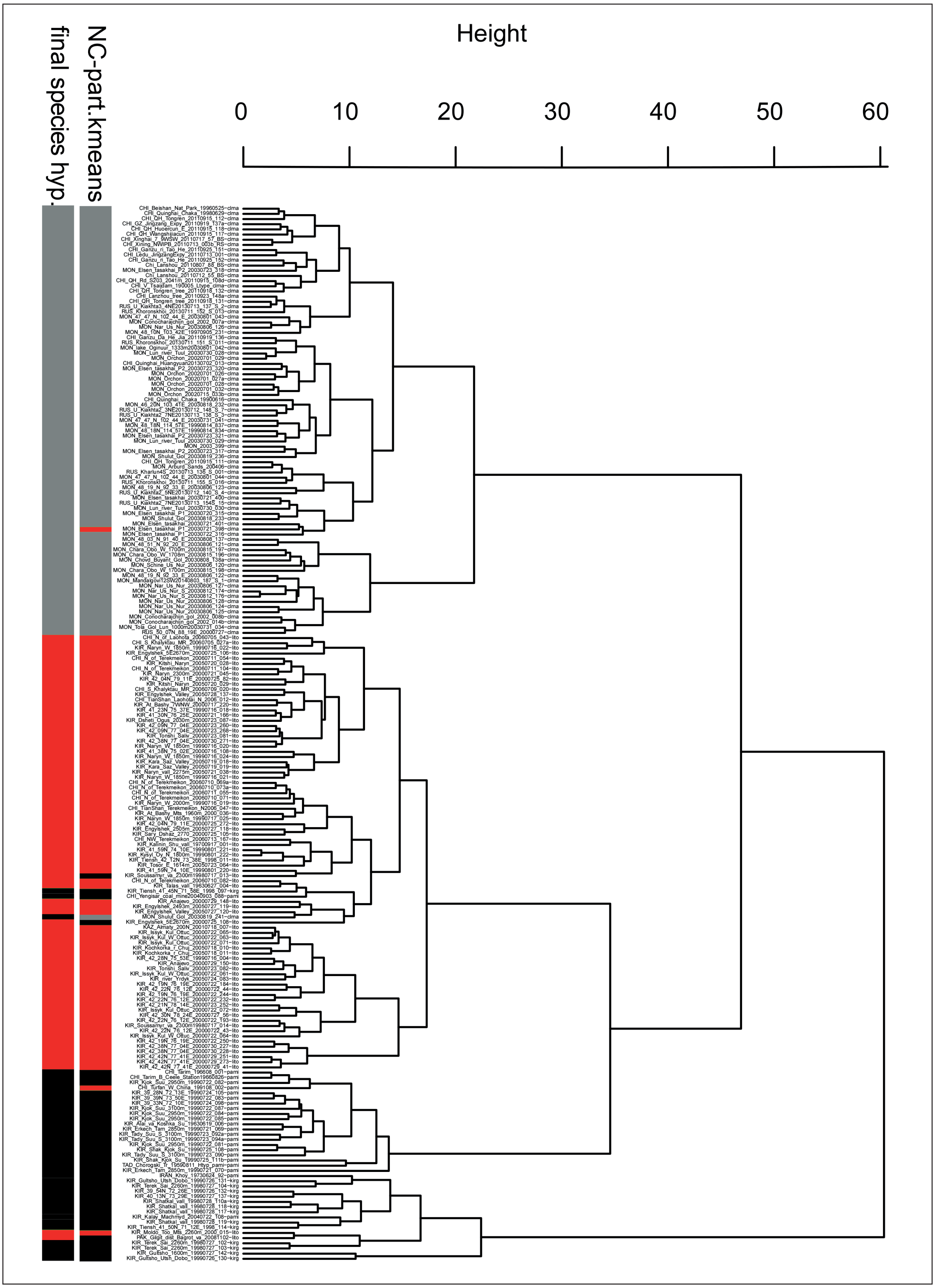


Figure 62. NC-Ward and NC-part.kmeans clustering of 204 nest samples of *Formica clarissima* (grey bars), *F. litoralis* (red bars) and *F. pamirica* et *kirgisica* (black bars). The mean error of both analyses for K=3 is 2.9%.

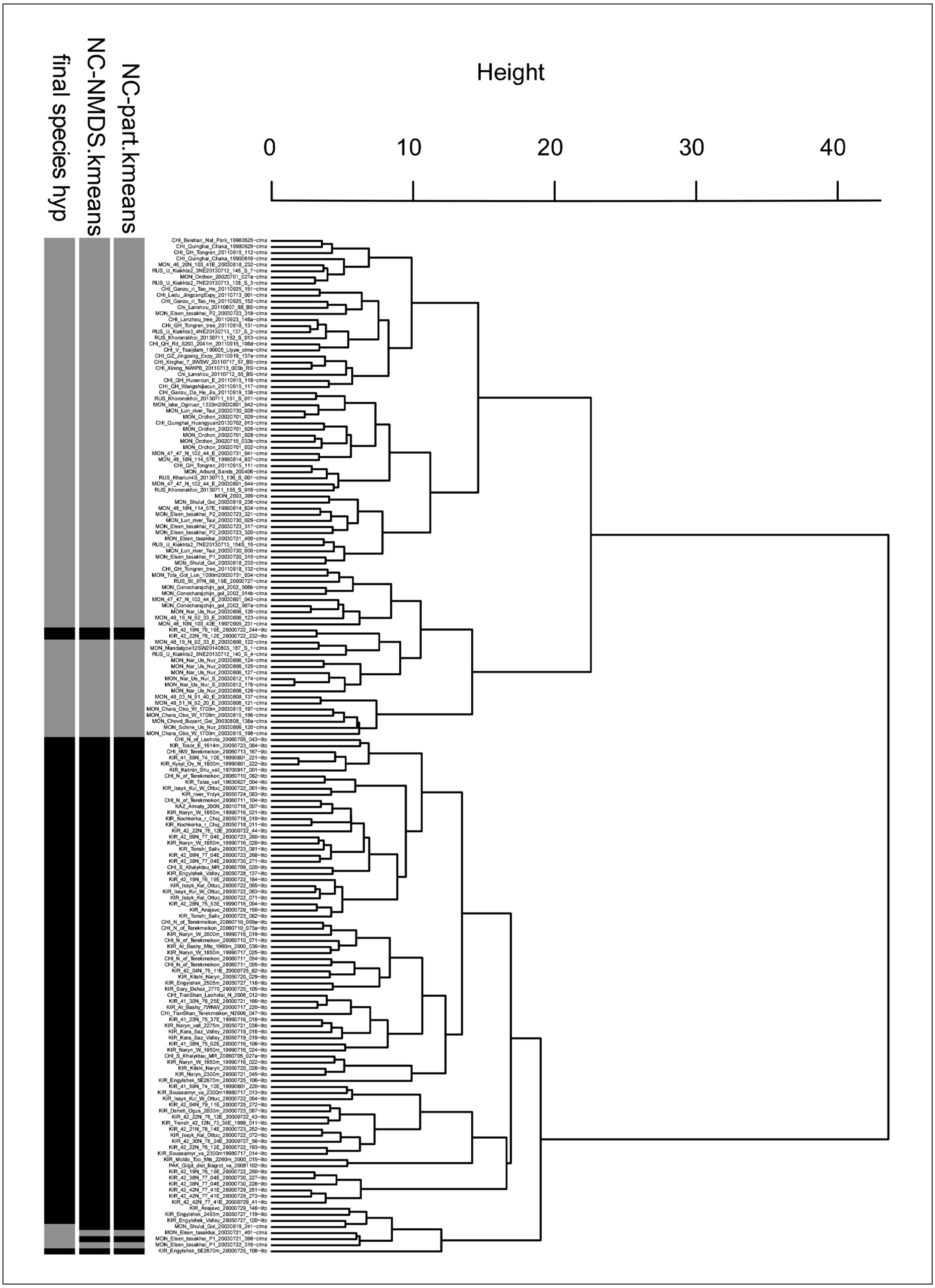


Figure 63. Separation of nest samples of *Formica clarissima* (gray bars) and *F. litoralis* (black bars) by by NC-Ward, NC-part. kmeans and NC-NMDS.kmeans with error rates of 3.6, 1.2 and 1.2%

dense on gaster (sqPDG 3.24). Colour similar to *F. clarissima* and *F. pamirica*: vertex, dorsal mesosoma, metapleuron, petiole, coxae and all appendices brown to dark brown, gaster always dark brown. Other surfaces lighter reddish brown.

Habitat and Biology. In the mountains, *F. litoralis* only occurs along rivers and creeks. Here it is typically found on stony, gravelly or sandy river banks with sparse vegetation. The nests are mainly placed above the level of the mean annual flooding line, but not rarely also below this line - indicating a good resistance against short-term inundation. This is directly confirmed by Dlussky (1967) who observed that flooded nests began to repair damaged nest galleries and resumed full foraging activity as soon as one day after the retreat of the flood. However, Dlussky did not state to which of the Middle Asian species his observations referred. According to our direct observations on fine-scale nest distribution, all three species (*litoralis*, *pamirica* and *kirghisica* n.sp.) should have this capability. In agreement with Dlussky (1967) and Tarbinsky (1976), we found *F. litoralis* as a mass species on moist sand and gravel banks at the margin of Lake Issyk-Kul where it can build up polydomous (and most certainly polygynous) colonies. Nests are typically found near to bushes or trees of *Hippophae*, *Salix*, *Populus*, *Ulmus* and other woody plants on which various trophobionts are attended.

The time of sexual development and nuptial flight cannot be answered by us because all our expeditions took place after June and it is unclear with the data of Dlussky (1967) and Tarbinsky (1976) to which of the three Middle Asian species their observations refer. We found alates July 17, 1998 (males within a nest in the Soussamyr valley), July 23, 2000 (alate gynes in a nest near Jety Oguz / Inner Tian Shan) and July 26, 2000 (one alate gyne in a yellow bowl).

Taxonomic comments: The clear separation from *F. clarissima* and the collective cluster *F. pamica* & *kirgisica* was reported in section 7.4 and is visualized in Figs 20 and 21.

7.6 *Formica pamirica* Dlussky 1965

***Formica subpilosa pamirica* Dlussky 1965** [type investigation]

This taxon has been described from Tajikistan. Investigated was 1 paratype worker from the holotype nest, labelled “Khorogski trakt, Darvazski Khrebet, 11.VIII. 59, A.Rasnizyn.” and “Paratype F. subpilosa pamirica Dlussky”; depository ZMLSU Moskva. The specimen from the holotype nest was allocated to the *Formica pamirica* cluster with p=0.9929 in a wild-card run of a 2-class LDA considering the species *F. pamirica* and *F. kirgisica* n.sp. (see supplementary information SI3, setting 8).

All material examined. Numeric phenotypical data were taken in 23 nest samples with 74 workers. The material came from China (4 samples), Kyrgyzstan (17) and Tajikistan (2). For details see supplementary information SI1 and SI2.

Geographic range. The Middle Asian range of *F. pamirica* is delimited by 41.2°N, 44.7°N, 72.3°E and 81.5°E, with elevations of 1991 ± 400 [738, 2770] m. It goes from Alay valley and the bordering Alay and Trans-Alay mountains to the southern foothills of the Kakshaal Too north of the Turpan Depression. There is an isolated finding in the Kunlun Mountains, but the description of this spot is not very clear. (Fig. 64).

Description: --Worker (Tab. 5; key). Rather small, CS 1297 ± 116 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head longer than in *kirgisica* n.sp., CL/CW 1.144 ± 0.018. Scape moderately long SL/CS 1.055 ± 0.022. Eye medium-sized, EYE/CS 0.284 ± 0.005. Ocellar distance large, OceD/CS 0.182 ± 0.008. Distance between metathoracal spiracles, between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron larger than in *kirgisica* n.sp., MtSt/CS 0.144 ± 0.013, MtPpSt/CS 0.354 ± 0.007, MtMtp/CS 0.656 ± 0.012. Petiole narrower than in *kirgisica* n.sp., PeW/CS 0.397 ± 0.018. Setae on first gaster tergite rather long, GHL/CS 11.70 ± 1.32%. Genae almost without setae, nGen 0.11 ± 0.30. Margin of hind vertex and underside of head with fewer setae than in *kirgisica* n.sp., nCH 4.0 ± 2.1, nGu 1.95 ± 0.88. Pronotum and mesonotum with many standing setae, nPn 37.2 ± 7.6, nMn 16.3 ± 6.4. Propodeum-metapleuron, petiole scale above stigma and flexor profile of hind femur always with setae, nPrMe 11.8 ± 3.4, nPe 7.4 ± 1.9. Extensor profile of hind femur and extensor profile of hind tibia with fewer setae than in *kirgisica* n.sp., nHFex 0.6 ± 0.9, nHT 3.7 ± 2.3. Flexor profile of hind femur always with setae, nHFfl 9.5 ± 2.4. Distance of transverse ripples on dorsum of first gaster tergite medium, RipD 4.27 ± 0.29. Gaster covered by a dense silvery pubescence, sqPDG 3.21 ± 0.20. Whole body covered by a silvery pubescence, on mesosoma and head less dense than on gaster. Colour similar to *F. clarissima* and *F. litoralis*: vertex, dorsal mesosoma, metapleuron, petiole, coxae and all appendices brown to dark brown, gaster always dark brown. Other surfaces lighter reddish brown.

Habitat and Biology. *F. pamirica* was mainly found on stony, gravelly or sandy river banks with sparse vegetation.

Taxonomic comments: *F. pamirica* it is safely separable from *F. kirgisica* n.sp. with 0% classification error by LDA and PCA already on worker individual level as it is on nest sample level by any variant of NC-clustering (not shown). The separation from *Formica clarissima* and *F. litoralis* was reported in section 7.4 and is visualized in Fig. 62.

7.7 *Formica kirgisica* n.sp.

Etymology: The name is given according to the terra typica.

Type material

Holotype and five paratype worker on two pins labelled "KIR: 41.8327°N, 71.1948°E Kolnysh Kya, Tschatkal-Tal, 1830 m R.Schultz 1998.07.28-119" and "Holotype (top) and paratypes *Formica kirgisica* Schultz & Seifert"; depository SMN Görlitz. The specimens from the holotype nest were allocated to the *Formica kirgisica* n.sp. cluster with p=0.9995 in a wild-card run of a 2-class LDA considering the species *F. pamirica* and *F. kirgisica* n.sp. (see supplementary information SI3, setting 8).

All material examined. Numeric phenotypical data were taken in 14 nest samples with 53 workers. All material came from Kyrgyzstan. For details see supplementary information SI1 and SI2.

Geographic range. The known range of *Formica kirgisica* n.sp. is small and restricted to mountain areas north (Talas Ala-Too) and south (Fergana Range) of the Fergana Valley within the limits 39.9°N, 41.8°N, 70.8°E and 73.5°E (Fig. 64 Map). The altitudinal range of the 14 samples is similar to that of *pamirica*: 1937 ± 360 [1100, 2300] m. Syntopic occurrence of both species has not been observed so far.

Description: --Worker (Tab. 5, Figs 44-46; key). Slightly larger than *pamirica*, CS 1326 ± 83 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head shorter than in *pamirica*, CL/CW 1.126 ± 0.014. Scape moderately long SL/CS 1.051 ± 0.019. Eye smaller than in *pamirica*, EYE/CS 0.276 ± 0.003. Ocellar distance large, OceD/CS 0.187 ± 0.008. Distance between metathoracal spiracles, between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron smaller than in *pamirica*, MtSt/CS 0.126 ± 0.013, MtPpSt/CS 0.335 ± 0.009, MtMtp/CS 0.630 ± 0.010. Petiole wider than in *pamirica*, PeW/CS 0.431 ± 0.022. Setae on first gaster tergite rather long, GHL/CS 10.64 ± 1.42%. Genae occasionally with setae, nGen 0.52 ± 0.87. Margin of hind vertex and underside of head with more setae than in *pamirica*, nCH 8.0 ± 3.6, nGu 4.1 ± 1.6. Pronotum and mesonotum with many standing setae, nPn 37.8 ± 8.1, nMn 17.1 ± 3.5. Propodeum-metapleuron, petiole scale above stigma and flexor profile of hind femur always

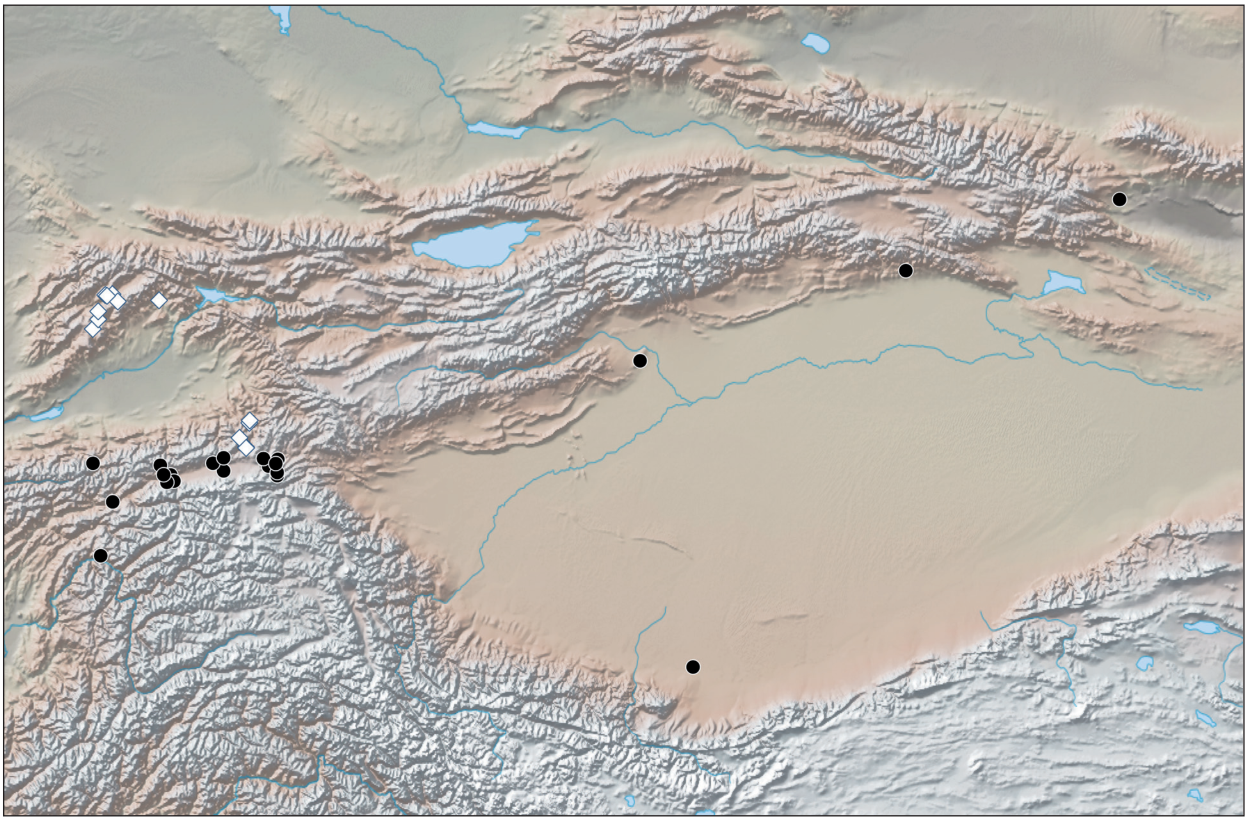


Figure 64. Geographic distribution of *Formica pamirica* (black dots) anf *F. kirgisica* (white rhombs).

with setae, nPrMe 14.2 ± 3.6, nPe 8.1 ± 1.7, nHFfl 12.8 ± 3.5. Extensor profile of hind femur and extensor profile of hind tibia with more setae than in *pamirica*, nHFex 3.9 ± 2.7, nHT 11.2 ± 5.9. Distance of transverse ripples on dorsum of first gaster tergite medium, RipD 4.28 ± 0.34. Gaster covered by a dense silvery pubescence, sqPDG 3.26 ± 0.19. Whole body covered by a silvery pubescence, on mesosoma and head less dense than on gaster. Colour similar to *F. clarissima* and *F. litoralis*: vertex, dorsal mesosoma, metapleuron, petiole, coxae and all appendices brown to dark brown, gaster always dark brown. Other surfaces lighter reddish brown.

Habitat and Biology. *F. kirgisica* n.sp. was mainly found on stony, gravelly or sandy river banks with sparse vegetation.

Taxonomic comments: Due to strong differences in many shape variables, *F. kirgisica* n.sp. is separable from *F. pamirica* with 0% classification error by LDA and PCA on worker individual level as it is on nest sample level by any variant of NC-clustering (not shown). The separation from *Formica clarissima* and *F. litoralis* was reported in section 7. 4 and is visualized in Fig. 62.

7.8 *Formica superpilosa* n.sp.

Etymology: The name is given according to the extremely developed pilosity.

Type material

This taxon was found in a single sample in Kyrgyzstan. Investigated were the holotype and six paratype worker on three pins labelled "KYR: Tian Shan, 1116 m, 41.6876°N, 72.8936°E S of pass Kok-Bel, edge of alluvion, in soil R.Schultz 2004.07.31-256" and "Holotype (bottom) and paratype *Formica superpilosa* Schultz & Seifert"; depository SMN Görlitz.

All material examined. Only the type sample was available. For details see supplementary information SI1 and SI2.

Geographic range. Only the type sample from a tributary to the lower Naryn-River was available.

Description: --Worker (Tab. 6; Figs 29-31; key). Medium-sized, CS 1276 ± 69 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head rather short, CL/CW 1.121 ± 0.016. Scape long SL/CS 1.076 ± 0.018. Eye medium-sized, EYE/CS 0.284 ± 0.006. Ocellar distance small, OceD/CS 0.163 ± 0.005. Distance between metathoracal spiracles small, MtSt/CS 0.108 ± 0.008, those between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron relatively large, MtPpSt/CS 0.355 ± 0.007, MtMtp/CS 0.651 ± 0.010. Petiole narrow, PeW/CS 0.377 ± 0.011. Setae on first gaster tergite long, GHL/CS 13.10 ± 1.07%. Almost all body parts with much more standing setae than in any other species of the *subpilosa* group, nGen 8.3 ± 2.3, nCH 32.6 ± 2.3, nGu 9.5 ± 2.8, nPn 64.3 ± 11.6, nMn 32.0 ± 6.0, nPrMe 33.2 ± 6.3, nPe 11.7 ± 2.0, nHFex 17.7 ± 1.5, nHFfl 27.2 ± 4.4, nHT 11.0 ± 1.0. In difference to any known Palaearctic *Serviformica*, dorsal profile of scape with many standing setae, nSC 11.0 ± 2.1 [8.5, 14.5]. Clypeus with a very sharp median keel. Microsculpture of frontal triangle not contrasting to adjacent surfaces of head, with fine transverse ripples and light appressed pubescence. Distance of transverse ripples on dorsum of first gaster tergite rather large, RipD 5.47 ± 0.37. Gaster covered by a dense silvery pubescence, sqPDG 3.00 ± 0.23; pubescence on mesosoma and head less dense. Color similar to *F. subpilosa*: dorsum of head reddish brown, mesosoma scape, coxae and legs light reddish brown, gaster blackish brown.

Habitat and Biology. The type nest was found in alluvial soil along a river.

Taxonomic comments: The species is not to be confused with any member of the *F. subpilosa* group and any other *Serviformica* due to its extremely developed pilosity. Despite the strong pilosity, the species does not fall into the *F. cinerea* group due to its structural characteristics (e.g. significantly smaller eye size). The geographical distribution of the species also lies well outside the *F. cinerea* group.

8 The species of the *Formica rufibarbis* group

8.1 *Formica rufibarbis* Fabricius 1793

***Formica rufibarbis* Fabricius 1793** [type investigation]

This taxon has been described from France ("Habitat in Gallia"). Investigated was the neotype worker (designated by Seifert & Schultz, 2009b) and six paratype workers from the neotype nest, labelled "FRA: 44.073°N, 7.295°E, St. Martin Vesubie, Cime de la Palu, 2058 m R. Schultz 2002.05.14 -108" and "Neotype Formica rufibarbis Fabricius 1793, des. Seifert & Schultz 2009"; depository SMN Görlitz. The neotype sample was allocated to the *Formica rufibarbis* cluster with p=0.9999 in a wild-card run of a 3-class LDA considering the species *F. rufibarbis*, *F. anatolica* and a cluster collecting the remaining nine species of the *F. rufibarbis* group (see supplementary information SI3, setting 9).

***Formica fusca* var. *cinereorufibarbis* Forel 1874** [type investigation]

This taxon has been described from Zurich, Switzerland. Investigated were two worker types (the specimen with CL = 1663 was labelled as lectotype by

B. Seifert in 1999) and 1 gyne paratype, all labelled "F.cinereo-rufibarbis Forel", "Z. hôpital" and "Type"; depository MNH Genève. The lectotype sample was allocated to the *Formica rufibarbis* cluster with p=0.9881 in a wild-card run of a 3-class LDA considering the species *F. rufibarbis*, *F. anatolica* and a cluster collecting the remaining nine species of the *F. rufibarbis* group (see supplementary information SI3, setting 9).

All material examined. Numeric phenotypical data were taken in 123 nest samples with 461 workers. The material came from Austria (13 samples), Bosnia (6), Bulgaria (1), Finland (4), France (6), Georgia (1), Germany (43), Greece (3), Hungary (1), Italy (2), Kazakhstan (20), Lebanon (1), Norway (5), Russia (1), Spain (1), Sweden (6), Switzerland (6) and Turkey (1). For details see supplementary information SI1 and SI2.

Geographic range. *Formica rufibarbis* is found throughout the temperate and submediterranean zones of the West Palaearctic from the Pyrenees to West Siberia (76° E) and the Southwest Siberian Saur Mountains (86° E). In Fennoscandia it goes north to 61° N, both in Sweden and Finland, and in the Alps and the Caucasus it ascends to 2100 m.

Description: --Worker (Tab. 8; key). Rather large, CS 1424 ± 171 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape longer than in *anatolica*, CL/CW 1.139 ± 0.020, SL/CS 1.065 ± 0.025. Eye smaller than in *anatolica*,EYE/CS 0.292 ± 0.005. Ocellar distance rather low, OceD/CS 0.168 ± 0.010. Distance between metathoracal spiracles smaller than in *anatolica*, MtSt/CS 0.132 ± 0.016. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron larger than in *anatolica*, MtPpSt/CS 0.369 ± 0.011, MtMtp/CS 0.666 ± 0.015. Petiole very wide, PeW/CS 0.471 ± 0.023. Setae on first gaster tergite moderately long, GHL/CS 8.40 ± 0.86%. Genae, margin of hind vertex and underside of head without setae, nGen 0.01 ± 0.07, nCH 0.06 ± 0.18, nGu 0.01 ± 0.10. Pronotum and mesonotum with more standing setae than in any other member of the *F. rufibarbis* group except for *anatolica* and *sinae*, nPn 10.6 ± 3.8, nMn 6.2 ± 2.9. Propodeum-metapleuron often with single setae, nPrMe 0.75 ± 1.0. Petiole scale above stigma and flexor profile of hind femur usually with few setae, nPe 3.1 ± 1.4, nHFfl 2.6 ± 1.5. Extensor profile of hind femur without setae, nHFex 0.07 ± 0.27, extensor profile of hind tibia without or occasionally few, small subdecumbent setae 0.55 ± 0.87. Distance of transverse ripples on dorsum of first gaster tergite medium, RipD 4.44 ± 0.34. Gaster covered by a dense silvery pubescence, sqPDG 3.16 ± 0.20. Pubescence on head, mesosoma and petiole dense. Posterior vertex, sometimes dorsal promesonotum, coxae and all appendages normally brown or dark brown, gaster always dark brown. All other body parts reddish. Dark morphs with pigmentation similar to that of *F. cunicularia* occasionally occurring.

Habitat and Biology. See Seifert 2018.

Taxonomic comments: With exception of the endemic *Formica anatolica* and allopatric *F. sinae*, *F. rufibarbis* is safely separable from any member of the *F. rufibarbis* group alone by its high setae numbers *a* (Tab. 7). The separation from *anatolica* is reported in section 8.2.

8.2 *Formica anatolica* Seifert & Schultz 2009

***Formica anatolica* Seifert & Schultz 2009** [type investigation]

This taxon has been described from Asia Minor. Ivestigated were the holotype worker plus 4 worker paratypes labelled "TUR: 37.348°N, 34.360°E Halkapinar-32 rkm SE, Aydos Dagi 1600-1800 m, A.Schulz 1997.05.08-115" and "Holotype Formica anatolica Seifert & Schultz" / "Paratype Formica anatolica Seifert & Schultz"; depository SMN Görlitz. The holotype sample was allocated to the *Formica antatolica* cluster with p=1.0000 in a wild-card run of a 3-class LDA considering the species *F. rufibarbis*, *F. anatolica* and a cluster collecting the remaining nine species of the *F. rufibarbis* group (see supplementary information SI3, setting 9).

All material examined. Numeric phenotypical data were taken in 15 nest samples with 68 workers. All material came from Turkey. For details see supplementary information SI1 and SI2.

Geographic range. *Formica anatolica* is an endemic of the region of the Taurus Mountains (Toros Daglari) in south-central Anatolia. It occurs there at elevations between 1300 and 1900 m.

Description: --Worker (Tab. 8; key). Rather large, CS 1422 ± 178 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape shorter than in *rufibarbis*, CL/CW 1.111 ± 0.018, SL/CS 1.032 ± 0.024. Eye larger than in *rufibarbis*, EYE/CS 0.303 ± 0.006. Ocellar distance rather low, OceD/CS 0.169 ± 0.009. Distance between metathoracal spiracles larger than in *rufibarbis*, MtSt/CS 0.143 ± 0.012. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron smaller than in *rufibarbis*, MtPpSt/CS 0.343 ± 0.011, MtMtp/CS 0.638 ± 0.016. Petiole very wide, PeW/CS 0.479 ± 0.031. Setae on first gaster tergite moderately long, GHL/CS 7.98 ± 0.70%. Genae and margin of hind vertex without setae, nGen 0.0 ± 0.0, nCH 0.05 ± 0.15. Underside of head in contrast o any member of the *F. rufibarbis* group with

Table 7. RAV-corrected morphological data of workers of the Formica rufibarbis group. Only specimens with available data on petiole width and eye size are included. Sequence of data: arithmetic mean ± standard deviation [minimum, maximum]. Numbers following the maximum indicate a reduced sample size for the given character.

	lusatica W (n=269)	***clara W*** (n=318)	***lusatica E*** (n=57)	***clara E*** (n=251)	***himalayensis*** (n=56)	***cunicularia*** (n=593)	***tianshanica*** (n=156)	***tianshanica*** Yunnan (n=4)
CS[µm]	1495±151 [1103,1846]	1400±149 [1031,1690]	1486±147 [1162,1808]	1423±152 [1080,1794]	1281±109 [990,1571]	1358±130 [1040,1.800]	1237±101 [1042,1489]	1374±64 [1313,1455]
CL /CW_{1400}	1.150±0.019 [1.100,1.205]	1.132±0.019 [1.077,1.183]	1.143±0.022 [1.088,1.191]	1.135±0.019 [1.076,1.187]	1.116±0.023 [1.040,1.148]	1.140±0.024 [1.071,1.215]	1.141±0.019 [1.081,1.190]	1.112±0.020 [1.085,1.134]
SL /CS_{1400}	1.084±0.026 [0.995,1.174]	1.075±0.026 [1.004,1.167]	1.090±0.030 [1.034,1.162]	1.084±0.029 [1.001,1.162]	1.069±0.031 [0.966,1.125]	1.087±0.029 [0.955,1.167]	1.057±0.025 [1.000,1.113]	1.090±0.025 [1.055,1.114]
EYE /CS_{1400}	0.290±0.006 [0.267,0.302]	0.290±0.007 [0.273,0.314]	0.290±0.009 [0.278,0.317]	0.291±0.006 [0.275,0.309]	0.292±0.006 [0.279,0.305]	0.299±0.007 [0.278,0.318]	0.297±0.006 [0.282,0.311]	0.291±0.004 [0.288,0.296]
OceD /CS_{1400}	0.162±0.008 [0.142,0.187]	0.163±0.011 [0.135,0.193]	0.164±0.008 [0.148,0.181]	0.159±0.009 [0.136,0.184] 238	0.168±0.012 [0.139,0.196]	0.164±0.010 [0.138,0.193] 592	0.168±0.009 [0.150,0.194] 154	0.159±0.007 [0.150,0.167]
MTST /CS_{1400}	0.128±0.015 [0.083,0.184] 215	0.125±0.017 [0.085,0.170] 243	0.116±0.014 [0.082,0.148]	0.131±0.016 [0.088,0.215] 215	0.126±0.016 [0.090,0.175] 45	0.130±0.019 [0.090,0.242] 413	0.145±0.015 [0.115,0.202] 152	0.118±0.014 [0.108,0.139]
MTPPST/CS_{1400}	0.383±0.012 [0.348,0.414] 215	0.357±0.012 [0.321,0.410] 243	0.379±0.013 [0.355,0.410]	0.373±0.013 [0.307,0.398] 219	0.347±0.010 [0.328,0.366] 45	0.371±0.013 [0.333,0.410] 413	0.348±0.010 [0.317,0.376] 152	0.342±0.013 [0.328,0.356]
MTMTP /CS_{1400}	0.682±0.014 [0.646,0.716]215	0.657±0.016 [0.598,0.700]243	0.682±0.013 [0.654,0.720]	0.671±0.013 [0.634,0.713]219	0.641±0.011 [0.617,0.658]45	0.670±0.014 [0.628,0.713]413	0.641±0.011 [0.608,0.669]152	0.638±0.014 [0.618,0.648]
PeW /CS_{1400}	0.472±0.023 [0.411,0.536]	0.454±0.028 [0.374,0.545]	0.474±0.020 [0.433,0.531]	0.474±0.021 [0.410,0.525]	0.454±0.021 [0.400,0.503]	0.460±0.028 [0.381,0.559]	0.436±0.020 [0.381,0.503]	0.456±0.021 [0.429,0.475]
GHL /CS_{1400}[%]	6.76±0.89 [0.00,10.16]	7.57±0.94 [0.00,10.36]	7.29±0.91 [5.52, 9.62]	7.33±1.02 [0.00, 9.56]	8.00±0.76 [6.36, 9.79]	6.77±0.84 [3.76,9.55]	7.23±0.80 [5.10, 9.58]	5.98±0.80 [5.03, 6.98]
nGU_{1400}	0.00±0.02 [0.0,0.3]	0.01±0.07 [0.0,0.6]	0.03±0.18 [0.0,1.0]	0.02±0.11 [0.0,1.1]	0.00±0.00 [0.0,0.0]	0.02±0.11 [0.0,1.5]	0.01±0.12 [0.0,1.1]	0.0±0.0 [0.0,0.0]
nPn_{1400}	3.76±2.27 [0.0,10.2]	4.07±2.62 [0.0,13.4]	3.36±2.06 [0.0,7.3]	1.46±1.27 [0.0,5.5]	0.63±0.70 [0.0,2.2]	1.15±1.69 [0.0,13.0]	1.77±1.40 [0.0,5.9]	0.22±0.45 [0.0,0.9]
nMn_{1400}	1.61±1.40 [0.0,7.3]	1.57±1.45 [0.0,6.2]	1.75±1.60 [0.0,6.9]	0.51±0.70 [0.0,3.3]	0.06±0.19 [0.0,0.8]	0.66±1.10 [0.0,9.5]	0.67±1.02 [0.0,4.4]	0.0±0.0 [0.0,0.0]
$nPrMe_{1400}$	0.03±0.13 [0.0,1.0]	0.04±0.14 [0.0,0.8]	0.03±0.13 [0.0,0.6]	0.02±0.12 [0.0,1.2]	0.01±0.04 [0.0,0.3]	0.02±0.10 [0.0,1.0]	0.00±0.00 [0.0,0.0]	0.0±0.0 [0.0,0.0]
nPe_{1400}	0.89±0.79 [0.0,3.5]	0.72±0.79 [0.0,3.4]	0.99±0.78 [0.0,2.7]	0.48±0.58 [0.0,2.7]	0.34±0.55 [0.0,2.2]	0.36±0.59 [0.0,3.0]	0.01±0.10 [0.0,1.1]	0.0±0.0 [0.0,0.0]
$nHFfl_{1400}$	0.52±0.65 [0.0,4.0]	0.65±0.86 [0.0,4.2]	0.73±0.80 [0.0,3.5]	0.53±0.75 [0.0,5.3]	0.31±0.55 [0.0,2.2]	0.21±0.40 [0.0,2.3]	0.64±0.79 [0.0,3.2]	1.28±0.99 [0.0,2.2]
$RipD_{1400}$	4.42±0.30 [3.4,5.3]	4.45±0.27 [3.5,5.3]	4.27±0.25 [3.9,4.8]	4.39±0.29 [3.7,5.3]	4.56±0.27 [4.1,5.6]	4.49±0.34 [3.4,5.7]	**6.07**±0.65 [4.5,8.0]	6.08±0.05 [6.0,6.1]
$sqPDG_{1400}$	3.17±0.18 [2.68,3.67]	3.14±0.18 [2.58,3.74]	3.15±0.18 [2.66,3.47]	3.14±0.20 [2.55,3.74]	3.27±0.15 [2.92,3.69]	3.09±0.20 [2.49,4.37] 592	3.22±0.22 [2.56,3.65]	3.11±0.13 [2.94,3.25]
$Pigm_{1400}$	10.9±13.4 [0,69]	10.4±14.5 [0, 82]	2.3±3.1 [0,12]	10.8±12.6 [0,82]	18.7±24.0 [0,86]	65.3±29.1 [0,99]	82.7±13.6 [17,99]	94.8±9.8 [86,106]
$CONT_{1400}$	0.21±0.27 [0.0,1.0]	0.15±0.20 [0.0,1.0]	0.43±0.24 [0.0,1.0]	0.18±0.20 [0.0,1.0]	0.20±0.19 [0.0,0.8]	0.54±0.30 [0.0,1.0]	0.35±0.29 [0.0,1.0]	0.01±0.02 [0.0,0.1]

Table 8. RAV-corrected morphological data of workers of the *Formica rufibarbis* group. This table includes only specimens for which data on petiole width and eye size were available. Sequence of data: arithmetic mean ± standard deviation [minimum, maximum]. Numbers following the maximum indicate a reduced sample size for the given character.

	tarimica (n=126)	***orangea*** (n=81)	***persica*** (n=87)	***gebaueri*** (n=55)	***rufolucida*** (n=42)	***glabridorsis*** (n=38)	***sinae*** (n=6)	***rufibarbis*** (n=325)	***anatolica*** (n=68)
CS[µm]	1240±126 [912,1503]	1361±122 [0.981,1.672]	1335±137 [1.103,1.703]	1373±164 [1.016,1.613]	1522±88 [1381,1774]	1425±96 [1142,1579]	1328±68 [1229,1431]	1424±171 [1023,1811]	1422±178 [1083,1855]
CL /CW_{1400}	1.156±0.019 [1.111,1.238]	1.111±0.018 [1.068,1.149]	1.158±0.018 [1.116,1.209]	1.168±0.018 [1.128,1.202]	1.130±0.016 [1.131,1.191]	1.163±0.016 [1.131,1.191]	1.139±0.008 [1.132,1.152]	1.139±0.020 [1.022,1.186]	1.111±0.018 [1.070,1.143]
SL /CS_{1400}	1.072±0.021 [1.000,1.128]	1.015±0.025 [0.949,1.062]	1.152±0.027 [1.076,1.198]	1.132±0.030 [1.047,1.199]	1.235±0.030 [1.163,1.300]	1.188±0.028 [1.110,1.241]	1.063±0.011 [1.053,1.080]	1.065±0.025 [0.999,1.124]	1.032±0.024 [0.969,1.081]
EYE /CS_{1400}	0.280±0.005 [0.268,0.295]	0.288±0.007 [0.273,0.302]	0.295±0.006 [0.283,0.315]	0.294±0.005 [0.281,0.304]	0.278±0.005 [0.280,0.313]	0.299±0.007 [0.280,0.313]	0.283±0.004 [0.279,0.290]	0.292±0.005 [0.273,0.308]	0.303±0.006 [0.290,0.315]
OceD /CS_{1400}	0.165±0.008 [0.146,0.184]	0.170±0.010 [0.149,0.194]	0.165±0.009 [0.141,0.181]	0.161±0.012 [0.132,0.191]	0.161±0.009 [0.136,0.185]	0.158±0.013 [0.136,0.185]	0.169±0.011 [0.160,0.189]	0.168±0.010 [0.148,0.206]	0.169±0.009 [0.155,0.193]
MTST /CS_{1400}	0.118±0.013 [0.087,0.148] 106	0.134±0.015 [0.098,0.172] 64	0.127±0.014 [0.098,0.166] 86	0.114±0.014 [0.078,0.158]	0.114±0.010 [0.093,0.141] 19	0.101±0.010 [0.081,0.116] 19	0.116±0.010 [0.104,0.131]	0.132±0.016 [0.099,0.179] 84	0.143±0.012 [0.121,0.180] 44
MTPPST /CS_{1400}	0.338±0.010 [0.307,0.376] 106	0.334±0.009 [0.298,0.349] 64	0.360±0.012 [0.329,0.385] 86	0.361±0.010 [0.334,0.379]	0.368±0.014 [0.347,0.392] 19	0.397±0.009 [0.382,0.415] 19	0.356±0.011 [0.335,0.369]	0.369±0.011 [0.341,0.394] 84	0.343±0.011 [0.317,0.375] 44
MTMTP /CS_{1400}	0.638±0.011 [0.616,0.688] 106	0.630±0.014 [0.590,0.657] 64	0.663±0.015 [0.620,0.701] 86	0.654±0.011 [0.633,0.676]	0.639±0.021 [0.618,0.715] 19	0.711±0.010 [0.694,0.727] 19	0.650±0.015 [0.622,0.663]	0.666±0.015 [0.618,0.691] 84	0.638±0.016 [0.594,0.668] 44
PeW/CS_{1400}	0.393±0.019 [0.348,0.462]	0.422±0.018 [0.369,0.472]	0.454±0.024 [0.413,0.520]	0.416±0.028 [0.355,0.476]	0.371±0.014 [0.348,0.407]	0.431±0.027 [0.353,0.466]	0.428±0.008 [0.413,0.436]	0.471±0.023 [0.419,0.541]	0.479±0.031 [0.393,0.542]
GHL /CS_{1400}[%]	9.45±0.78 [7.02,11.28]	7.89±0.71 [6.33,9.82]	4.97±2.42 [0.00,7.82]	6.87±0.93 [4.96,9.33]	9.38±1.62 [1.02,11.73] 39	5.91±0.53 [4.96,7.67]	7.82±0.42 [7.20, 8.25]	8.40±0.86 [6.27,10.99] 324	7.98±0.70 [5.25,9.57]
nGU_{1400}	0.05±0.17 [0.0,1.1]	0.01±0.09 [0.0,0.6]	0.01±0.08 [0.0,0.6]	0.05±0.19 [0.0,1.0]	0.04±0.21 [0.0,1.3]	0.00±0.00 [0.0,0.00]	0.00±0.00 [0.0,0.0]	0.02±0.11 [0.0,1.1]	1.57±0.82 [0.0,3.5]
nPn_{1400}	11.91±2.98 [3.3,19.0]	1.10±1.50 [0.0, 8.1]	0.05±0.21 [0.0,1.3]	0.85±1.13 [0.0,5.4]	0.44±0.74 [0.0,3.7]41	0.09±0.25 [0.0,1.2]	11.5±3.2 [6.5,14.5]	10.62±3.77 [0.0,21.0]	8.61±5.39 [1.3,19.0]
nMn_{1400}	3.8±2.9 [0.0,15.3]	0.86±0.63 [0.0,3.0]	0.03±0.11 [0.0,0.5]	0.19±0.38 [0.0,1.7]	0.01±0.06 [0.0,0.4]	0.03±0.12 [0.0,0.6]	2.0±2.3 [0.0,6.3]	6.15±2.87 [0.0,17.2]	3.70±3.61 [0.0,14.7]
$nPrMe_{1400}$	0.52±0.79 [0.0,3.7]	0.08±0.33 [0.0,1.9]	0.00±0.00 [0.0,0.0]	0.00±0.00 [0.0,0.00]	0.01±0.05 [0.0,0.3]	0.02±0.06 [0.0,0.15]	0.60±0.80 [0.0,2.0]	0.75±1.02 [0.0,6.0]	0.14±0.42 [0.0,2.7]
nPe_{1400}	1.23±1.08 [0.0,4.1]	0.22±0.42 [0.0,1.9]	0.01±0.05 [0.0,0.5]	0.01±0.04 [0.0,0.2]	0.01±0.12 [0.0,0.8]	0.04±0.17 [0.0,0.9]	2.77±0.90 [1.1,3.5]	3.07±1.42 [0.0,7.9]	0.70±0.97 [0.0,4.1]
$nHFfl_{1400}$	0.86±0.98 [0.0,4.7]	0.31±0.58 [0.0,3.9]	0.05±0.16 [0.0,0.9]	0.65±0.86 [0.0,3.5]	0.47±0.64 [0.0,2.6]	0.07±0.20 [0.0,0.9]	0.27±0.29 [0.0,0.6]	2.57±1.53 [0.0,6.9]	1.21±1.17 [0.0,4.6]
$RipD_{1400}$	8.02±0.82 [6.0,11.0]	6.77±0.76 [5.3,9.5]79	5.74±0.49 [4.7,7.0]	6.46±0.68 [5.0,8.2]	9.32±0.53 [8.1,10.2] 39	4.24±0.31 [3.6,5.0]	4.12±0.23 [3.8,4.4]	4.44±0.34 [3.5,6.0]	4.54±0.27 [3.9,5.4]
$sqPDG_{1400}$	3.13±0.27 [2.30,3.61]	3.17±0.17 [2.63,3.61] 79	3.31±0.24 [2.66,4.54]	7.37±1.64 [3.98,11.15]	3.63±0.27 [3.09,4.30] 39	2.89±0.13 [2.53,3.17]	2.96±0.09 [2.86,3.11]	3.16±0.20 [2.59,3.65]	3.40±0.18 [3.04,4.18]
$Pigm_{1400}$	2.6±6.0 [0,39]	3.9±4.4 [0,17]	63.9±23.5 [75,139]	87.1±23.9 [23,134]	19.2±20.5 [0,82]	49.5±36.2 [0,116]	13.3±5.6 [8,22]	17.9±19.4 [0,86]	90.5±54.5 [4,344]
$CONT_{1400}$	0.03±0.05 [0.0,0.2]	0.04±0.07 [0.0,0.3]	0.59±0.26 [0.0,1.0]	0.30±0.30 [0.0,1.0]	0.43±0.42 [0.0,2.6]	0.21±0.17 [0.0,0.9]	0.40±0.15 [0.2,0.6]	0.39±0.30 [0.0,1.0]	0.33±0.24 [0.0,1.0]
$CONT_{1400}$	0.03 ±0.05 [0.0,0.2]	0.04 ±0.07 [0.0,0.3]	0.59 ±0.26 [0.0,1.0]	0.30 ±0.30 [0.0,1.0]	0.43 ±0.42 [0.0,2.6]	0.21 ±0.17 [0.0,0.9]	0.40 ±0.15 [0.2,0.6]	0.39 ±0.30 [0.0,1.0]	0.33 ±0.24 [0.0,1.0]

single setae which may be very long, nGu 1.57 ± 0.82. Pronotum and mesonotum with more standing setae than in any other member of the *F. rufibarbis* group except for *rufibarbis*, nPn 8.6 ± 5.4, nMn 3.7 ± 3.6. Propodeum-metapleuron usually without setae, nPrMe 0.14 ± 0.42. Petiole scale above stigma and flexor profile of hind femur occasionally with single setae, nPe 0.70 ± 0.97, nHFfl 1.26 ± 1.2. Extensor profile of hind femur and extensor profile of hind tibia without setae, nHFex 0.0 ± 0.0, nHT 0.0 ± 0.0. Distance of transverse ripples on dorsum of first gaster tergite medium, RipD 4.54 ± 0.27. Pubescence on head, mesosoma and gaster rather dense, sqPDG 3.40 ± 0.20. In overall impression, this species appears relatively dark with remarkable contrasts between brown and reddish parts on mesosoma and on genae but a weak overall brightness contrast between dorsal mesosoma and gaster.

Habitat and Biology. *Formica anatolica* is so far only found in woodland stands with *Abies*, *Juniperus*, *Quercus* and other deciduous tree species - occasionally interspersed with grassland patches.

Taxonomic comments: The 15 samples *Formica anatolica* are separated from 100 samples of *F. rufibarbis* with 0% classification error by any variant of NC-clustering even when excluding the diagnostic mesosomal shape variables MtSt/CS, MtPpSt/CS and MtMtp/CS which are not available in all samples. Worker individuals are separated with 0% classification error under inclusion of the mesosomal shape variables (see key). Overall, *rufibarbis* is more slender than *anatolica*.

8.3 *Formica sinae* Emery 1925 stat.nov.

***Formica rufibarbis* var. *sinae* Emery 1925** [type investigation]

[replacement name for *F. rufibarbis* var. *orientalis* Wheeler, 1923, a junior primary homonym of *F. fusca* ssp. *orientalis* Ruzsky, 1915]

This taxon has been described from "the sand-flats west of Nu Ku Kow, Kiachou Bay, Tsingtao, Shantung" (Wheeler 1923). Investigated were 6 syntype workers labelled "ShanTung', China Aug.24 1922 A.P.-Jacot" [integrated interpretation from both handwritten labels of Jacot], "A.P. Jacot No. 2287", "Gift of W.M. Wheeler", "M.C.Z. Type 1-3 21733", "var. orientalis Wheeler"; three further workers labelled "ShanTung', China Aug.24 1922 A.P.-Jacot" [integrated interpretation from both badly handwritten labels of Jacot], "Gift of W.M. Wheeler", "M.C.Z. Type 4-6 21733"; depository MCZ Cambridge.

All material examined. Only the type series from China consisting of 6 workers was available for investigation. For details see supplementary information SI1 and SI2.

Geographic range. The type locality is situated at 36.07°N, 120.13°E

Description: --Worker (Tab. 8; Figs 36, 37; key). Medium-sized, CS 1328 ± 68 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape as long as in *rufibarbis* but scape longer than in *clarissima*, CL/CW 1.139 ± 0.008, SL/CS 1.063 ± 0.011. Eye smaller than in *rufibarbis*, EYE/CS 0.283 ± 0.004. Ocellar distance smaller than in *clarissima*, OceD/CS 0.169 ± 0.010. Distance between metathoracal spiracles smaller than in *clarissima*, MtSt/CS 0.116 ± 0.010. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron slightly smaller than in *rufibarbis* but larger than in *clarissima*, MtPpSt/CS 0.356 ± 0.011, MtMtp/CS 0.650 ± 0.015. Petiole much narrower than in *F. rufibarbis*, PeW/CS 0.428 ± 0.008. Setae on first gaster tergite moderately long, GHL/CS 7.82 ± 0.42%. Genae, margin of hind vertex and underside of head without setae, nGen 0.0 ± 0.0, nCH 0.0 ± 0.0, nGu 0.0 ± 0.0. Pronotum and mesonotum with fewer standing setae than in *F. clarissima*, nPn 11.5 ± 3.2, nMn 2.0 ± 2.3. Propodeum-metapleuron often with single setae, nPrMe 0.6 ± 0.8. Petiole scale above stigma usually with few setae, nPe 2.8 ± 0.9. Flexor profile of hind femur in difference to *rufibarbis* and *clarissima* almost without setae, nHFfl 0.3 ± 0.3. Extensor profile of hind femur and extensor profile of hind tibia without setae, nHFex 0.0 ± 0.0, nHT 0.0 ± 0.0. Distance of transverse ripples on dorsum of first gaster tergite medium, RipD 4.12 ± 0.23. Gaster covered by a dense silvery pubescence, sqPDG 2.96 ± 0.09. Head, mesosoma, petiole and all appendages yellowish-red. Gaster, vertex, dorsal parts of pronotum and mesonotum distinctly darker but with reddish tinge.

Habitat and Biology. The type locality was in 1922 a natural sand dune but is today an urban area.

Taxonomic comments: The species most similar to *sinae* are *Formica rufibarbis* and *clarissima*. Plotting the LDA score against the first principal component and considering the characters CS, EYE/CS_{1400}, PeW/CS_{1400}, $MtSt/CS_{1400}$, $MtMtp/CS_{1400}$, nGu_{1400}, nPn_{1400}, $nHFfl_{1400}$, and $sqPDG_{1400}$ places the type series of *Formica sinae* separate from the clusters of *rufibarbis* and *clarissima* (Fig. 65). A synonymy of *F. sinae* with *rufibarbis* appears unlikely due to a zoogeographic argument. The easternmost site of *rufibarbis* and the type locality of *sinae* are separated by 2600 km and the most winter-cold area of the Palaearctic. It appears reasonable to suppose a long term isolation of the populations not only during the glacial maximum but also in the interglacial(s) and recently. Based on this zoogeographic argument and significant differences in PeW/CS_{1400}, EYE/CS_{1400} and

$nHFfl_{1400}$ with p<0.0005 in a one-tailed ANOVA, we raise *Formica rufibarbis sinae* to species rank. However, the zoogeographic argument is not applicable to argue against a synonymy with *F. clarissima* because the latter is found in very wintercold regions and has reached eastern China (Fig. 61). We stay here with provisionally assuming heterospecificity of *F. sinae* and *clarissima* because there are significant differences in $nHFfl_{1400}$ and $MtMtp/CS_{1400}$ with p<0.0005 and $MtPpSt/CS_{1400}$ (p<0.003). Further samples from east China are required to clear this issue.

8.4 *Formica orangea* Seifert & Schultz 2009

***Formica orangea* Seifert & Schultz 2009** [type investigation]

This taxon has been described from the Tshatkal valley in Kyrgyzstan. Investigated were the holotype worker plus 5 worker paratypes labelled "KIR:41.8327°N, 71.1948°E, Tshatkal valley, 1830 m R.Schultz 1998.07.28-115" and "Holotype Formica orangea Seifert & Schultz" / "Paratype Formica orangea Seifert & Schultz"; from the same nest series 19 paratype worker in ethanol; depository SMN Görlitz. The holotype sample is allocated to the *Formica orangea* cluster with p=0.9846 in a wild-card run of a 3-class LDA considering the species *F. orangea*, *F. tarimica* and a cluster collecting the remaining 11 species of the *F. rufibarbis* group (see supplementary information SI3, setting 9).

All material examined. Numeric phenotypical data were taken in 35 nest samples with 110 workers. The material came from Afghanistan (2 samples), China (1), Iran (2), Kazakhstan (4), Kyrgyzstan (11), Mongolia (14) and Uzbekistan (1). For details see supplementary information SI1 and SI2.

Geographic range. *Formica orangea* has a large range extending over 3800 km from NE Iran (37.4°N, 58.5°E) to E Mongolia (47.4°N, 103.7°E). The southernmost site is Kabul (34.4°N, 69.2°E, 1740 m) and the altitudinal range goes from 400 m in the Saizan Bassin (47.7°N, 84.6°E) up to 2200 m in the Mongolian Gobi Altai (44.5°N, 99.3°E).

Description: --Worker (Tab. 8; key). Larger than *tarimica*, CS 1335 ± 137 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape distinctly shorter than in *tarimica*, CL/CW 1.111 ± 0.018, SL/CS 1.015 ± 0.025. Eye rather small, EYE/CS 0.288 ± 0.007. Ocellar distance small, OceD/CS 0.170 ± 0.010. Distance between metathoracal spiracles higher than in *tarimica*, MtSt/CS 0.134 ± 0.015. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt/

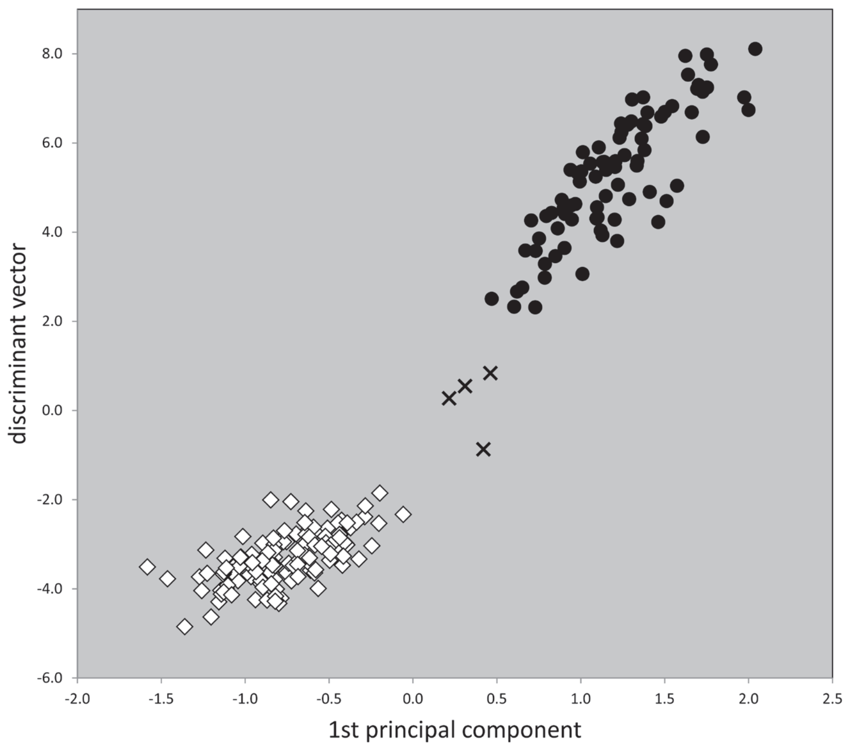


Figure 65. Plotting of discriminant analysis (LDA) scores of *F. rufibarbis* (white squares) and *F. clara* (black dots) against the first principal component. The type series of *Formica sinae* (black X) was run as wild-card in the LDA.

CS 0.334 ± 0.009, MtMtp/CS 0.630 ± 0.014. Petiole wider than in *tarimica*, PeW/CS 0.422 ± 0.018. Petiole scale in lateral aspect relatively low and thicker than in other species of the *F. rufibarbis* group, except *tarimica*, with convex anterior and straight to slightly convex posterior profile. Setae on first gaster tergite shorter than in *tarimica*, GHL/CS 7.89 ± 0.71%. Genae, margin of hind vertex and underside of head without setae, nGen 0.01 ± 0.10, nCH 0.01 ± 0.08, nGu 0.01 ± 0.09. Pronotum and mesonotum with much fewer setae than in *tarimica*, nPn 1.10 ± 1.50, nMn 0.86 ± 0.63. Setae on propodeum-metapleuron, petiole scale above stigma and on flexor profile of hind femur usually fully absent, nPrMe 0.08 ± 0.33, nPe 0.22 ± 0.42, nHFfl 0.31 ± 0.58. Extensor profile of hind femur and extensor profile of hind tibia almost always without standing setae, nHFex 0.07 ± 0.24, nHT 0.05 ± 0.18. Distance of transverse ripples on dorsum of first gaster tergite much larger than in any member of the *F. rufibarbis* group except *tarimica* and *tianshanica*, RipD 6.77 ± 0.76. Gaster covered by a dense silvery pubescence, sqPDG 3.17 ± 0.17. Pubescence on head, mesosoma and petiole less dense. Whole head, mesosoma, coxae, all appendages and petiole in typical cases reddish yellow; sometimes in smaller specimens brown spots may occur on posterior vertex and dorsal promesonotum, but always with low contrast between the pigmented and the light parts, gaster always brown.

Habitat and Biology. *Formica orange*a prefers dry steppe and semi-desert habitats, typically situated in proximity to rivers or lakes. It also invades rural areas and gardens. Nests are found in moderately dry sand, often with characteristic slant gateways leading to the underground. It forages on available trees and bushes, tending trophobionts.

Taxonomic comments: *Formica orangea* differs from *F. tarimica* by much lower seta numbers on pro- and mesonotum as well as by shorter scape and head (Tab. 8) and is unmistakable. All 101 samples of the three *Formica rufibarbis* group species with increased RipD – *orangea*, *tarimica* and *tianshanica* – are separated with 0% error by any variant of NC-clustering.

8.5 *Formica tarimica* Seifert & Schultz 2009

***Formica tarimica* Seifert & Schultz 2009** [type investigation]

This taxon has been described from the Eastern Tian Shan near to the northern margin of the Tarim Basin. Investigated were the holotype worker plus 7 worker paratypes labelled “CHI: 42.1251°N, 84.4323°E, Yengisar, 1515 m R.Schultz 2004.09.03-086” and “Holotype Formica tarimica Seifert & Schultz” / “Paratype Formica tarimica Seifert & Schultz”; 48 unmounted paratype worker in ethanol; depository SMN Görlitz. The holotype sample is allocated to the *Formica tarimica* cluster with p=1.0000 in a wild-card run of a 3-class LDA considering the species *F. orangea*, *F. tarimica* and a cluster collecting the remaining 11 species of the *F. rufibarbis* group (see supplementary information SI3, setting 9). In another analysis, the holotype sample is allocated to the *Formica tarimica* cluster with p=0.9999 in a wild-card run of a 3-class LDA considering the species *F. subpilosa*, *F. tarimica* and a cluster collecting *F. clarissima, F. litoralis, F. pamirica* and *F. kirgisica* n.sp. (see supplementary information SI3, setting 6).

All material examined. Numeric phenotypical data were taken in 34 nest samples with 126 workers. All material came from China. For details see supplementary information SI1 and SI2.

Geographic range. *Formica tarimica* is known from a narrow, only 140 km wide band extending from 82°E to 87° E along the northern margin of the Tarim Basin and lower mountain ranges of the Eastern Tian Shan (Fig. 59). The altitudinal range extends between 849 and 1528 m.

Description: --Worker (Tab. 8, key). Rather small, CS 1240 ± 126 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape distinctly longer than in *orangea*, CL/CW 1.156 ± 0.019, SL/CS 1.072 ± 0.023. Eye rather small, EYE/CS 0.280 ± 0.005. Ocellar distance small, OceD/CS 0.168 ± 0.009. Distance between metathoracal spiracles lower than in *orangea*, MtSt/CS 0.118 ± 0.013. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt/CS 0.338 ± 0.010, MtMtp/CS 0.638 ± 0.011. Petiole rather narrower than in *orangea*, PeW/CS 0.393 ± 0.019. Setae on first gaster tergite longer than in *orangea*, GHL/CS 9.45 ± 0.78%. Genae, margin of hind vertex and underside of head usually without or only exceptionally with single standing setae, nGen 0.07 ± 0.27, nCH 0.28 ± 0.38, nGu 0.05 ± 0.17. Pronotum and mesonotum with much more setae than in *orangea*, nPn 11.9 ± 3.0, nMn 3.8 ± 2.9. Setae numbers on propodeum-metapleuron and on flexor profile of hind femur strongly reduced, nPrMe 0.5 ± 0.8, nHFfl 0.7 ± 0.2. Number of setae on petiole scale above the stigma very low, nPe 1.2 ± 1.1. Extensor profile of hind femur and extensor profile of hind tibia without or single standing setae, nHFex 0.7 ± 0.3, nHT 1.2 ± 1.1. Distance of transverse ripples on dorsum of first gaster tergite much larger than in any member of the *F. rufibarbis* group except *F. orangea* and *tianshanica*, RipD 8.02 ± 0.82. Gaster covered by a dense silvery pubescence, sqPDG 3.13 ± 0.27. Pubescence on head, mesosoma and petiole less dense. Whole head, mesosoma, coxae, all appendages and petiole in typical case light yellowish red, gaster always dark brown.

Habitat and Biology. Perhaps due to rarity of competing *Formica* species in its range it occupies a diversity of habitats including semidesert, pastures, irrigated crop plantations, gardens, open alluvial sand banks and poplar or tamarisk stands. As a rule, the habitats are found on water-influenced ground, frequently near the Tarim River. Nests are found in moderately dry sand, often with characteristic slant gateways leading to the underground. A change of nest sites after inundation was once observed. Foraging on poplars, probably tending trophobionts.

Taxonomic comments: As a combination of extremely high distance of ripples and small pubescence distance on gaster tergite and bright reddish color, *Formica tarimica* is not to be confused with exception of *F. orangea* which differs by much lower seta numbers on pro- and mesonotum as well as shorter scape and head (Tab. 8).

8.6 *Formica clara* Forel 1886

***Formica rufibarbis* var. *clara* Forel 1886** [type investigation]

This taxon has been described from Damascus, Syria. Investigated were 9 syntype workers labelled

"F. rufibarbis v. clara Forel, Damas (Lortet)"; depository MHN Genéve. The syntype sample was allocated to the *Formica clara* cluster with p=0.9771 in a wild-card run of a 3-class LDA considering *F. cunicularia* and the western populations of *F. clara* and *F. lusatica* (see supplementary information SI3, setting 11) and was allocated to the *Formica clara* cluster with p=0.9874 in a wild-card run of a 2-class LDA considering *F. himalayensis* n.sp. and the eastern populations of *F. clara* (see supplementary information SI3, setting 12).

***Formica rufibarbis* var. *glauca* Ruzsky 1896** [type investigation] [first available use of *Formica fusca* subsp. *rufibarbis* var. *glauca* Ruzsky 1895]

This taxon has been described from the gouvernements Perm and Orenburg, Russia. Investigated were 2 syntype workers labelled "F. rufibarbis Fabr. var. glauca Ruszky "Perm (Ruszky)", "Cotypus", "Coll. A. Forel.", "ANTWEB CASENT 0911078", depository MHN Genéve. The syntype sample was allocated to the Formica clara cluster with p=0.8992 in a wild-card run of a 3-class LDA considering *F. cunicularia* and the western populations of *F. clara* and *F. lusatica* (see supplementary information SI3, setting 11). Ruzsky (1896) gives a bibliographic reference to Ruzsky (1895). Hence the sites given in the latter source can be considered as type localities: "Gouvernement Perm und Orenburg. Auf dem Salzgrunde in der Umgebung des Ssarykul-See, südlich von Tscheljabinsk."

All material examined. Numeric phenotypical data were taken in 188 nest samples with 707 workers. The material came from Azerbaijan (1 sample), Bulgaria (1), China (18), Cyprus (1), France (3), Georgia (1), Greece (4), Hungary (1), Iran (49), Israel (1), Kazakhstan (28), Kyrgyzstan (39), Portugal (2), Russia (7), Spain (8), Syria (2), Turkey (18) and Ukraine (2). This account includes 10 samples with uncertain determination in which the mesosomal measurements were not available. For details see supplementary information SI1 and SI2.

Geographic range. *Formica clara* has a large range extending over 7,600 km from Portugal east to the Chinese Bogda Shan Mountains (44.0°N, 88.2°E). The Westpalaearctic population (west of 60°E) has a much more southern distribution than that of the sister species *F. lusatica* in this region (Fig. 66). Corresponding to this and as adaptation to climate, the altitudinal ranges of the Westpalaearctic population of both species differ also strikingly with 1140 ± 857 [-21, 3160] m in *F. clara* and 260 ± 310 [1, 1700] m in *F. lusatica*.

Considering the whole range (Figs 66, 67), both species are sympatric in the Balkans, Ukraine, Asia Minor, Caucasus and the Tarbagatai and Saur moutains in Middle Asia. *F. lusatica* is allopatric in Central Europe and goes north to south Fennoscandia and seems to be alone in the Baikal region. *Formica clara* is alone in the Middle East and the whole Tian Shan east to the Bogda Shan Mountains. Regarding data points in the maps, we cannot exclude some misclassifications. Suspicious is the northernmost site of *F. clara* found on a sandy terrace of the Ob river, but the species identity was confirmed with p=0.9999 in a wild-card run of the LDA.

Description: --Worker (Tab. 7, Figs 23-25; key). Rather large, but clearly smaller than *lusatica*, CS 1415 ± 150 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. For differences between the eastern and western populations see Tab. 7. Head distinctly shorter than in *lusatica*, CL/CW 1.134 ± 0.020. Scape rather long SL/CS 1.079 ± 0.028. Eye moderately large, EYE/CS 0.291 ± 0.006. Ocellar distance small, OceD/CS 0.161 ± 0.010. Distance between metathoracal spiracles rather low, MtSt/CS 0.128 ± 0.016. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron in the western populations much smaller than in *lusatica*, MtPpSt/CS 0.357 ± 0.012, MtMtp/CS 0.657 ± 0.016. This interspecific difference is mitigated in the eastern populations. Petiole in the western populations distinctly narrower than in *lusatica*, PeW/CS 0.454 ± 0.028; between the eastern populations there is no difference. Setae on first gaster tergite in the western populations longer than in *lusatica*, GHL/CS 7.55 ± 0.94%. This difference is almost lost in the

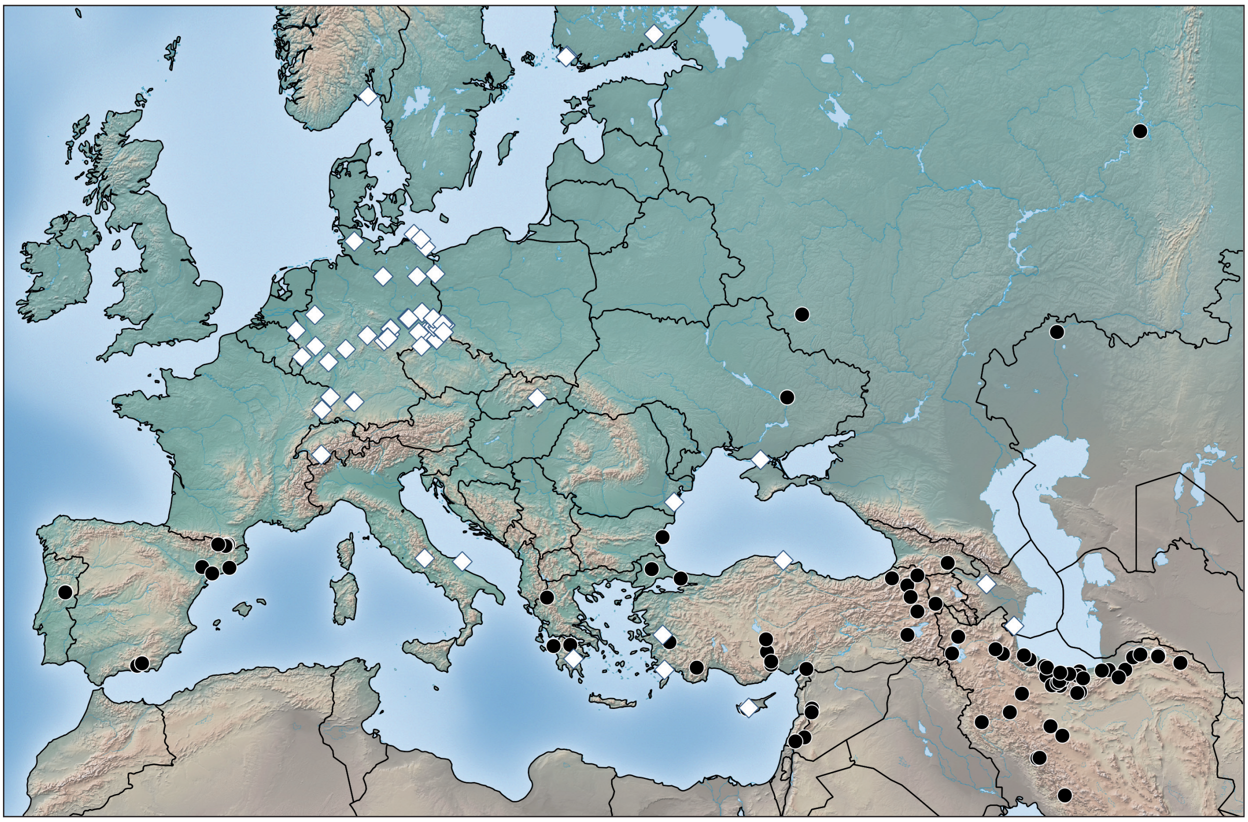


Figure 66. Geographic distribution of the western populations of *Formica clara* (black dots) and *F. lusatica* (white rhombs).

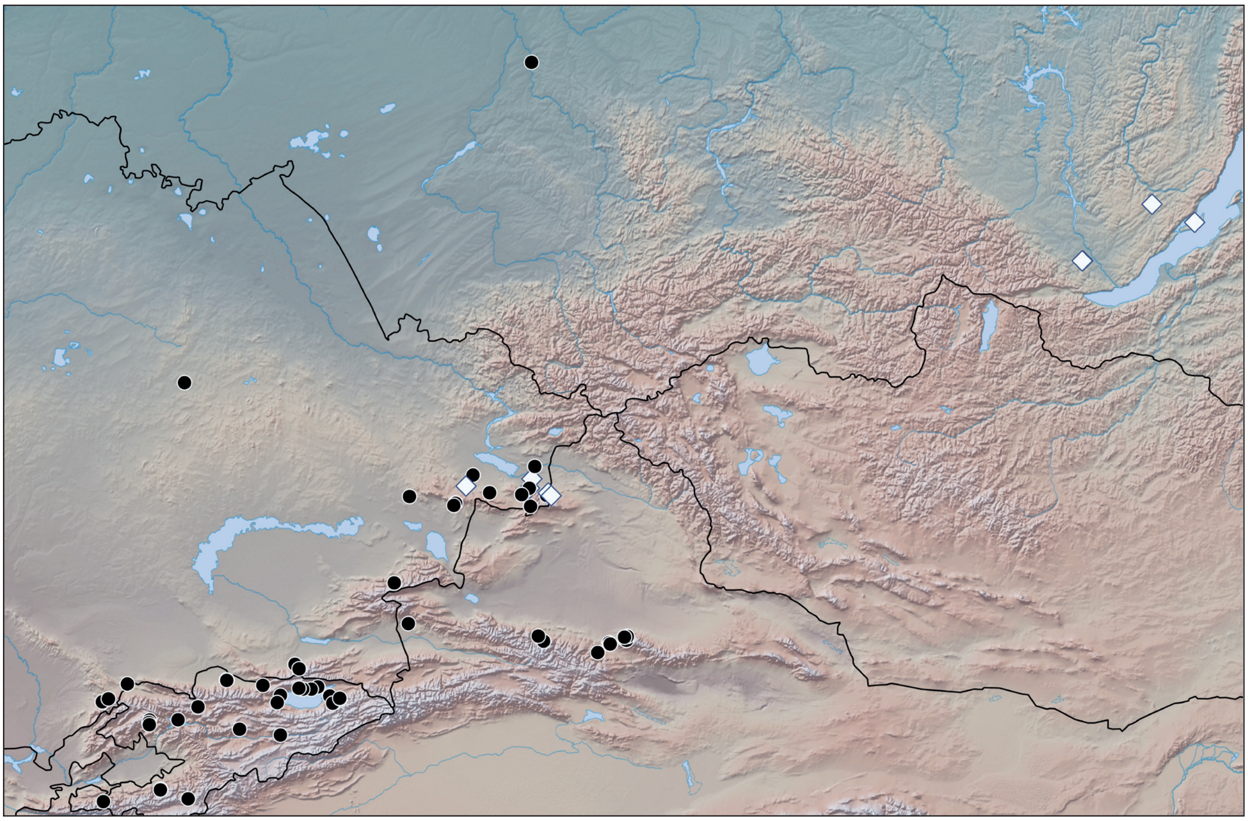


Figure 67. Geographic distribution of the eastern populations of *Formica clara* (black dots) and *F. lusatica* (white rhombs).

eastern populations. Genae, margin of hind vertex and underside of head as a rule without standing setae, nGen 0.00 ± 0.05, nCH 0.01 ± 0.09, nGu 0.01 ± 0.09. Setae number on pronotum and mesonotum low, nPn 2.83 ± 2.43, nMn 1.08 ± 1.28; in the eastern populations lower than in *lusatica*, in the western populations not differing. Setae on propodeum-metapleuron almost always fully absent nPrMe 0.03 ± 0.12. Petiole scale and on flexor profile of hind femur with occasional setae, nPe 0.60 ± 0.70, nHFfl 0.59 ± 0.81. Extensor profile of hind femur and extensor profile of hind tibia almost always without setae, nHFex 0.02 ± 0.17, nHT 0.07 ± 0.27. Distance of transverse ripples on dorsum of first gaster tergite low, RipD 4.42 ± 0.28. Gaster covered by a dense silvery pubescence, sqPDG 3.14 ± 0.19. Pubescence on head, mesosoma and petiole less dense. Genae, mesosoma, and petiole in typical case light yellowish red (dark specimens do occur), vertex and gaster usually dark brown.

Habitat and Biology. *Formica clara* shows some ecological differentiation between its western and eastern populations, reflecting adaptation to different biogeographic regions.

Eastern Population. This population is found in Central Asia at altitudes of 1566 ± 569 [390, 2650] m. The species occupies diverse habitats including steppes, alpine meadows, and high plateaus in open landscapes, as well as forested areas with walnut (*Juglans*), conifers (*Picea*, *Juniperus*), and deciduous trees (*Ulmus*). It frequently colonizes riparian habitats such as river terraces and floodplains, and shows notable synanthropic tendencies, occurring in urban parks, roadside plantings, and gardens. Nests are typically constructed in soil or under stones, sometimes with earth mounds in grass tufts. The eastern population demonstrates considerable habitat breadth, occurring from dry artemisia steppes to overgrazed meadows with tall herbs and shrubs, and tolerates both natural and anthropogenically modified environments. In several localities, nests were found parasitized by *Polyergus rufescens*. Fourteen observations of alates in the nests or during swarming were made between June 27 and August 23 with populations in higher mountain areas swarming mainly in August.

Western Population. This population occupies a vast geographic range from the Iberian Peninsula through the Mediterranean Basin to Iran and the Caspian region, occurring from -21 m (Gilan, Iran) to 3160 m (Elburz, Iran). The western population shows strong association with Mediterranean climatic zones and warm temperate steppe habitats, including cold Mediterranean steppes in Iran. It inhabits diverse environments ranging from coastal areas near sea level (including both Mediterranean and Caspian coasts) to high mountain elevations, occurring in Mediterranean vegetation types, forests at various elevations, and old gardens in cultivated areas. The population demonstrates considerable ecological plasticity, persisting in both xeric and mesic conditions. In the Caspian region of northern Iran, the species occurs in humid lowland areas with higher precipitation than typical for the species elsewhere. Two observations of alates in the nests or during swarming were made June 22 and July 17.

Taxonomic comments: The separation of the triple *Formica clara*, *F. lusatica* and *F. cunicularia* is the most difficult classification problem in this revision because geographic variation over the large range of the species complicates the picture. There is also suspicion for regional hybridization, but the high similarity of the species did not allow identifying particular hybrid samples, as it was possible in the *F. cinerea x selys*i or *F. balcanina x cinerea* scenarios. As a result, exploratory analyses considering the populations from the whole Palaearctic range did not reveal a sufficiently clear pattern. Better results were achieved by analyzing the populations west and east of 60° E separately and when all 24 characters were available. The analysis of the western populations was done with 870 workers from 290 nest samples. The characters nGen, nGu, nCH, nPrMe, nHFex and nHT, with zero or near to zero values, provided no information and were removed from analysis which included the 18 remaining characters. NC-part.kmeans recognized four clusters which were used as species hypothesis of the controlling LDA. NC-Part.kmeans proposed to split *Formica cunicularia* in two clusters A and B, but the LDA confirmed this subdivision in only 83.6% of the 134 *F. cunicularia* samples (Fig. 68). As a consequence, we accepted only a single *F. cunicularia* cluster and the controlling LDA (Fig. 69) confirmed 95.5% of the classifications for K=3.

The analysis of the populations east of 60°E excluded *Formica cunicularia* that was represented in the eastern material by only one sample (see section 8.8). The separation of the eastern populations of *Formica clara* and *F. lusatica* was much more difficult than in the west because the species converge here in MtPpSt/CS_{1400}, MtMtp/CS_{1400} and PeW/CS_{1400} (Tab. 7) whereas these characters are strongly separating in the western populations. This suggests increased hybridisation in the east. Using the same 18 characters considered in the western analysis, no exploratory data analysis provided a reasonably clear hypothesis except for the PCA. Separation of two clusters within 77 nest samples was given by the 2nd principal component with only one *Formica clara* sample (Sample No 1085) misplaced in the *F. lusatica* cluster. This sample from Bogda Shan Mountains in NW China was classified in a wild-card run of the LDA with p=0.732 as *Formica clara* (Fig. 70). This rectification is confirmed by a geographic argument: only *F. clara* was identified in all 18 samples from NW China (Fig. 67). The separation on individual level was sufficient: 95.2% of 269 workers were classified correctly.

8.7 *Formica lusatica* Seifert 1997

***Formica lusatica* Seifert 1997** [type investigation]
This taxon has been described from near Förstgen, Germany. Investigated were the holotype plus 4 paratype workers labelled "Kr.Niesky Förstgen-1.5W 1994.06.19-88» and «Formica lusatica Seifert Holotyp» / «Formica lusatica Seifert Paratyp»; 15 paratype workers from nest samples «-12», «-59», «-94», «-127» and «-A1» from the type locality with the same collecting date; depository SMN Görlitz.

The holotype sample was allocated to the *Formica lusatica* cluster with p=0.7769 in a wild-card run of a 3-class LDA considering *F. cunicularia* and the western populations of *F. clara* and *F. lusatica* (see supplementary information SI3, setting 11). This rather weak signal just in the holotype sample is considered accidental since the other five paratype nest samples from the type locality all showed posterior probabilities of p > 0.954.

All material examined. Numeric phenotypical data were taken in 124 nest samples with 517 workers. The material came from Austria (1 sample), Azerbaijan (1), Cyprus (1), Czechia (1), Finland (8), France (2), Germany (88), Greece (1), Italy (2), Kazakhstan (5), Netherlands (1), Norway (1), Romania (1), Russia (5), Slovakia (1), Switzerland (1), Turkey (3) and Ukraine (1). For details see supplementary information SI1 and SI2.

Geographic range. The huge range of *F. lusatica* extends over 7,200 km from S France east to the Baikal region within largely the temperate and mediterranean zones (Figs 66, 67). The Westpalaearctic population occurs in significantly higher latitudes and significantly lower altitudes than the sister species *F. clara* (see section 8.6). This trend is repeated in Middle Asia and Siberia but less clearly expressed.

Description: --Worker (Tab. 7, Figs 26-28; key). Largest species of the subgenus *Serviformica*, distincly larger than *F. clara*, CS 1499 ± 146 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. For differences between the eastern and western populations see Tab. 7. Head distinctly longer than in *clara*, CL/CW 1.150 ± 0.021. Scape long SL/CS 1.086 ± 0.029. Eye moderately large, EYE/CS 0.290 ± 0.006. Ocellar distance small, OceD/CS 0.162 ± 0.008. Distance between metathoracal spiracles rather low, MtSt/CS 0.126 ± 0.015. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron in the western populations much larger than in *clara*, MtPpSt/CS 0.383 ± 0.012, MtMtp/CS 0.682 ± 0.014. This interspecific difference is mitigated in the eastern populations. Petiole in the western populations distinctly wider than in *clara*, PeW/CS 0.472 ± 0.023; between the eastern populations there is no difference. Setae on first gaster tergite in the western populations shorter than in *clara*, GHL/CS 6.78 ± 0.91%. This difference is lost in the eastern populations. Genae, margin of hind vertex and underside of head without standing setae, nGen 0.00 ± 0.06, nCH 0.00 ± 0.04, nGu 0.00 ± 0.06. Setae number on pronotum and mesonotum low, nPn 3.60 ± 2.24, nMn 1.64 ± 1.49; in the eastern populations larger than in *clara*, in the western populations not differing. Setae on propodeum-metapleuron almost always fully absent nPrMe 0.03 ± 0.13. Petiole scale and flexor profile of hind femur with occasional setae, nPe 0.91 ± 0.78, nHFfl 0.56 ± 0.67. Extensor profile of hind femur and extensor profile of hind tibia almost always without setae, nHFex 0.03 ± 0.23, nHT 0.11 ± 0.59. Distance of transverse ripples on dorsum of first gaster tergite low, RipD 4.39 ± 0.30. Gaster covered by a dense silvery pubescence, sqPDG 3.17 ± 0.17. Pubescence on head, mesosoma and petiole less dense. Genae, mesosoma, and petiole in typical case light yellowish red (dark specimens do occur), vertex and gaster usually dark brown.

Habitat and Biology. Primarily a species of dry grassland. Most thermophilic of the Central European species of the *F. rufibarbis* group and in Central Europe the rarest of these species, with only regional occurrence in warm regions below 700 m, occurring here mainly on very xerothermic sandy and limestone grasslands, also on ruderal grassland, generally preferring open land with patchy herb layer. In sandy areas of the Lausitz (Germany) outcompeting *F. rufibarbis.* Presence and mean density on 81 potentially suitable Central European test plots 15% and 0.21 nests /100 m²; mean and maximum density on 16 positive Central European test plots 1.4 and 3.7 nests /100 m² (Seifert 2017, named there *Formica clara*). Nests in soil or under stones. The largest nests have a diameter of 80 cm and may show very flat mounds of mineralic soil particles. Nests often rather populous, monogynous to weakly polygynous, with aggressive workers which are notably larger than those of sympatric *F. cunicularia* and *F. rufibarbis.* In the planar and colline zone of Central Europe, alates occur July, 5 ± 9 d [June, 22; July, 20] n=11. The only direct observation of swarming was at 7:30 h solar time on a bright and hot day. Zoophagous, nectarivorous and trophobiotic. Seen to consume *Pinus* pollen. Large nests defend territories. Resistance against social parasites such as *Formica sanguinea* or *Polyergus rufescens* certainly stronger than in *F. cunicularia.*

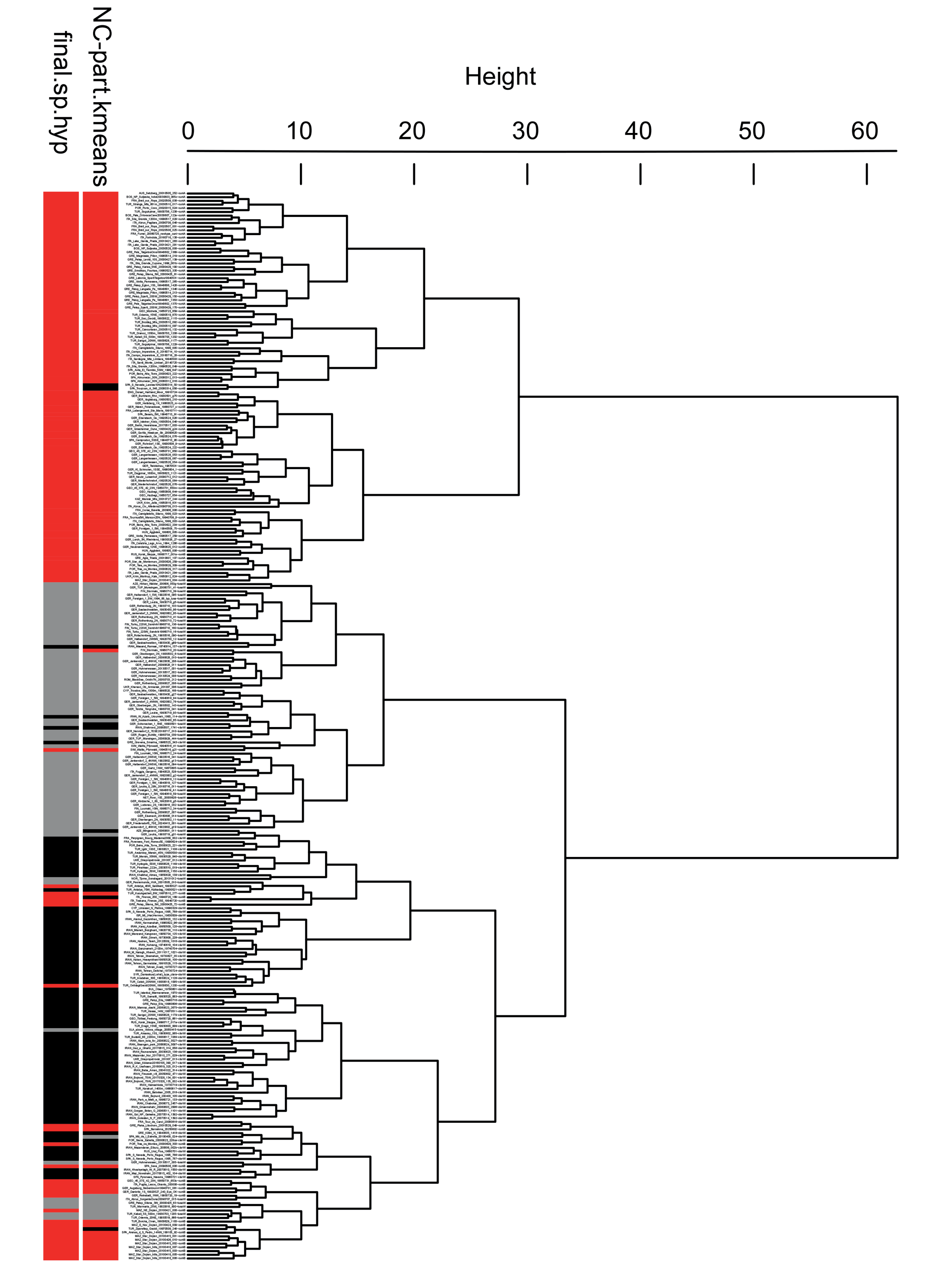


Figure 68. NC-clustering of the western populations of *Formica cunicularia* (red bars, n=119), *F. clara* (black bars, n=97) and *F. lusatica* (grey bars, n=74). The classifaction error of NC-part.kmeans is 4.5% in 290 nest samples.

There seems to exist a gyne size polymorphism: gynes from a polygynous nest were significantly smaller than those from putatively monogynous nests**.**

Taxonomic comments: The separation from *Formica clara* and *F. cunicularia* has been shown in section 8.6.

8.8 *Formica himalayensis* n.sp.

Etymology: The name is given according to the terra typica.

Type material

Holotype and three paratype worker on two pins labelled "01_Indien, Himachal Pradesh, 3km E Fagu, 20 km E Shimla, 29.09.1996, *389* Leg. A. Schulz, K. Vock"; four paratype workers on two pins from another nest sample labelled "01_Indien, Himachal Pradesh, 3km E Fagu, 20 km E Shimla, 29.09.1996, *385* Leg. A. Schulz, K. Vock"; depository; depository SMN Görlitz. The holotype sample was allocated to the *Formica himalayensis* n.sp. cluster with p=0.9976 in a wild-card run of a 2-class LDA considering *F. himalayensis* n.sp. and the eastern population of *F. clara* (see supplementary information SI3, setting 12).

All material examined. Numeric phenotypical data were taken in 21 nest samples with 56 workers. The material came from Afghanistan (1 sample), India (16) and Pakistan (4). For details see supplementary information SI1 and SI2.

Geographic range. The 21 samples were found in the West Himalayas from 70.9°E to 78.1°E at elevations of 2102 ± 677 [950, 3695] m.

Description: --Worker (Tab. 7, Figs 33-35; key). Smaller than eastern *F. clara*, CS 1281 ± 109 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head and scape shorter than in eastern *clara*, CL/CW 1.116 ± 0.023, SL/CS 1.069 ± 0.031. Eye medium-sized, EYE/CS 0.292 ± 0.006. Ocellar distance small, OceD/CS 0.168 ± 0.012. Distance between metathoracal spiracles medium, MtSt/CS 0.126 ± 0.016. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron much smaller than in eastern *clara*, MtPpSt/CS 0.347 ± 0.010, MtMtp/CS 0.641 ± 0.011. Petiole narrower than in eastern *clara*, PeW/CS 0.454 ± 0.021. Setae on first gaster tergite moderately long, GHL/CS 8.00 ± 0.76%. Genae, margin of hind vertex and underside of head without setae, nGen 0.0 ± 0.0, nCH 0.01 ± 0.07, nGu 0.0 ± 0.0. Pronotum without or with only single setae, nPn 0.63 ± 0.70. Mesonotum without setae, nMn 0.06 ± 0.19. Setae on propodeum-metapleuron, extensor and flexor profile of hind femur and extensor profile of hind tibia usually absent, nPrMe 0.01 ± 0.04, nhFex 0.0 ± 0.0, nHFfl 0.31 ± 0.55, nHT 0.0 ± 0.0. Setae on petiole scale above the stigma usually absent, nPe 0.34 ± 0.55. Distance of transverse ripples on dorsum of first gaster tergite low, RipD 4.56 ± 0.27. Gaster covered by a dense silvery pubescence, sqPDG 3.27 ± 0.15. Pubescence on head, mesosoma and petiole less dense. Mandibles, clypeus, genae, mesosoma and petiole light reddish brown. Antennae and legs reddish brown. Vertex, coxae and femora medium brown with reddish tinge. Gaster dark brown.

Habitat and Biology. Nearly unknown because precise site information is lacking. It seems to follow river valleys with more open habitats and sparse vegetation cover.

Taxonomic comments: The most similar species found in adjacent regions of Asia is eastern *Formica clara*. *Formica himalayensis* and eastern *F. clara* are clearly separable on nest sample level by NC-NMDS. kmeans and a PCA both considering the 11 characters CS, CL/CW_{1400}, GHL/CS_{1400}, nPn_{1400}, nMn_{1400}, $RipD_{1400}$, $sqPDG_{1400}$, $OceD/CS_{1400}$, $MtPpSt/CS_{1400}$, $MtMtp/CS_{1400}$, and $PIGM_{1400}$ (Fig. 71).

8.9 *Formica cunicularia* Latreille 1798

***Formica cunicularia* Latreille 1798** [type investigation]

This taxon has been described from France. Investigated was the neotype worker labelled "FRA: 44.4947°N, 0.9597°E, Fumel, 120 m, in a garden, leg. Galkowski 2008.07.25" and "Neotype Formica cunicularia Latreille 1798, des. B. Seifert 2009" plus three workers from the neotype nest with same collection data label; depository SMN Görlitz. The neotype sample was allocated to the *Formica cunicularia* cluster with p=1.000 in a wild-card run of a 3-class LDA considering *F. cunicularia* and the western populations of *F. clara and F. lusatica* (see supplementary information SI3, setting 11). Furthermore it was allocated to the *Formica cunicularia* cluster with p=1.000 in a wild-card run of a 3-class LDA considering *F. clara* west of 60°E, *F. cunicularia* and *F. persica* (see supplementary information SI3, setting 14).

***Formica fusca* var. *rubescens* Forel 1904** [type investigation]

This taxon has been described from Vaux, Switzerland. Investigated were 4 syntype workers labelled by Forel himself "Vaux", "Cotypus" and "F. fusca r. glebaria v. rubescens For"; depository MZ Lausanne. The syntype sample was allocated to the *Formica cunicularia* cluster with p=0.9975 in a wild-card run of a 3-class LDA considering *F. cunicularia* and the western populations of *F. clara and F. lusatica* (see supplementary information SI3, setting 13).

***Formica cunicularia fuscoides* Dlussky 1967** [type investigation]

This taxon has been described from Byurakan in Armenia. Investigated were five workers from the holotype sample labeled "1103", "Byurakan 1800 m Armen. Dlussky 13.VI. 1960" [in cyrillic letters], "Formica cunicularia kajastanica Dlussky paratypes"; depository ZMLU Moskow. The serial No. 1103 explicitly refers to the holotype (Dlussky 1967, p.74) but there is no holotype label attached to any specimen. A *"F. c. kajastanica"* has never been validly published. The five workers from the holotype nest were allocated to the *Formica cunicularia* cluster with p=0.9970 in a wild-card run of a 3-class LDA considering *F. cunicularia* and the western populations of *F. clara and F. lusatica* (see supplementary information SI3, setting 13).

All material examined. Numeric phenotypical data were taken in 204 nest samples with 842 workers. The material came from Armenia (2 samples), Austria (10), Bosnia (3), Czechia (3), England (2), France (13), Georgia (8), Germany (51), Greece (25), Hungary (3), Italy (22), Kazakhstan (1), North Macedonia (9), Netherlands (2), Portugal (7), Russia (1), Slovakia (1), Spain (10), Switzerland (8), Turkey (19) and Ukraine (3). For details see supplementary information SI1 and SI2.

Geographic range. *Formica cunicularia* is a mainly Westpalaearctic species found in the temperate and submediterranean zone with a main range extending from Portugal (8.8°W) east to the Caucasus (49°E). In the Atlantic climate of England it goes north to 53.8°N, in Norway to 58.8°N, in Sweden to 58°N, but it has not reached southern Finland so far. Having a planar to colline distribution in the northern parts of its range, it ascends to 1800 m in the Alps (at 46.5°N), to 2500 m in both Anatolia and Caucasus (at 42.7°N). The existence of a population in temperate southwest Siberia is indicated by a safely determined sample from the Manrak Mountains, E Kazakstan (47.322°N, 84.622°E, 1200 m). If this really represents an isolated population or if it is connected with the European population in steppes or woodland steppes remains unclear due to the very low sampling intensity within the temperate zone of W Siberia. It appears possible that the species is present there.

Description: --Worker (Tab. 7, Figs 20-22; key). Medium-sized, CS 1358 ± 128 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head rather long, CL/CW 1.140 ± 0.024. Scape longer than in *tianshanica*, SL/CS 1.087 ± 0.029. Eye rather large, EYE/CS 0.299 ± 0.007. Ocellar distance small, OceD/CS 0.164 ± 0.010. Distance between metathoracal spiracles smaller than in *tianshanica*, MtSt/CS 0.130 ± 0.019. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron larger than in *tianshanica*, MtPpSt/CS 0.371 ± 0.013, MtMtp/CS 0.670 ± 0.014. Petiole wider

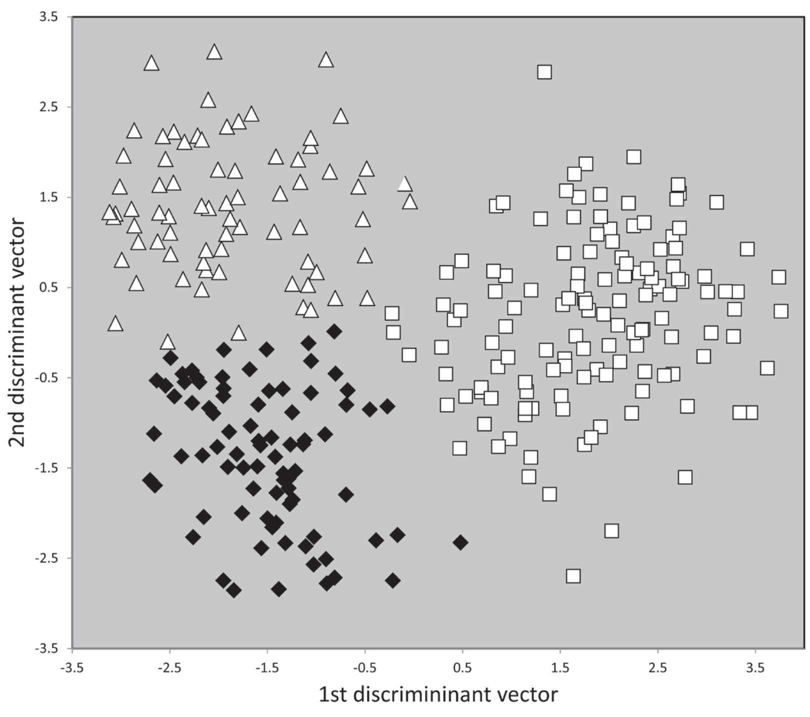


Figure 69. Nest sample means of a linear discriminant analysis of the western populations of *Formica cunicularia* (white squares, n=119), *F. clara* (black rhombs, n=97) and *F. lusatica* (white triangles, n=74).

than in *tianshanica*, PeW/CS 0.460 ± 0.028. Setae on first gaster tergite rather short, GHL/CS 6.77 ± 0.84%. Genae, margin of hind vertex and underside of head without setae, nGen 0.00 ± 0.03, nCH 0.00 ± 0.01, nGu 0.02 ± 0.10. Pronotum and mesonotum without or with few setae, nPn 1.15 ± 1.69, nMn 0.66 ± 1.10. Propodeum-

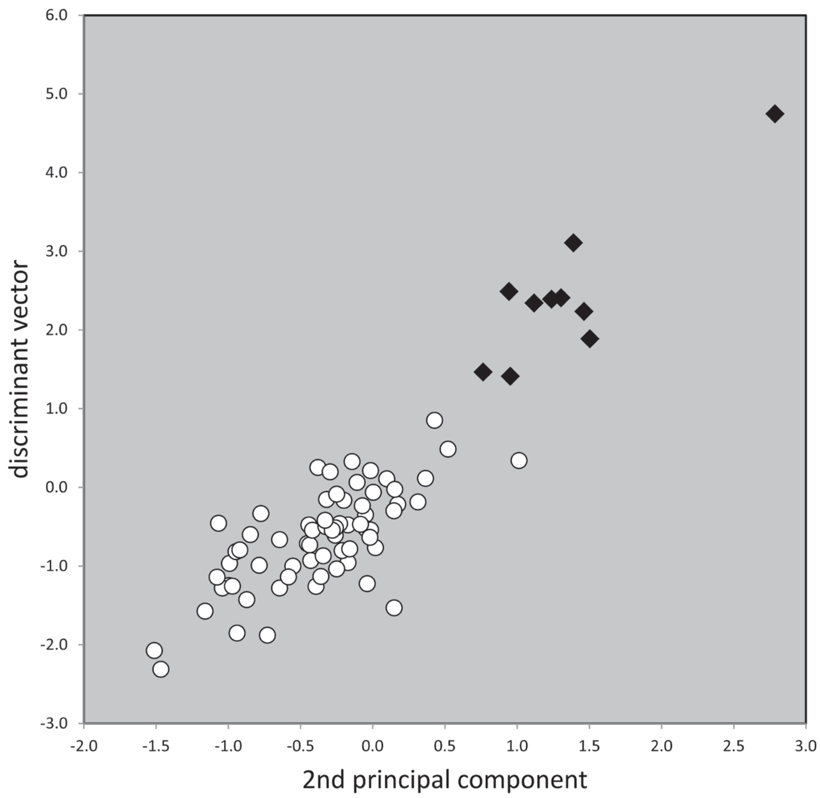


Figure 70. Nest sample means of a linear discriminant analysis and principal component analysis for the eastern populations of *Formica clara* (white dots, n=67) and *F. lusatica* (black rhombs, n=10)

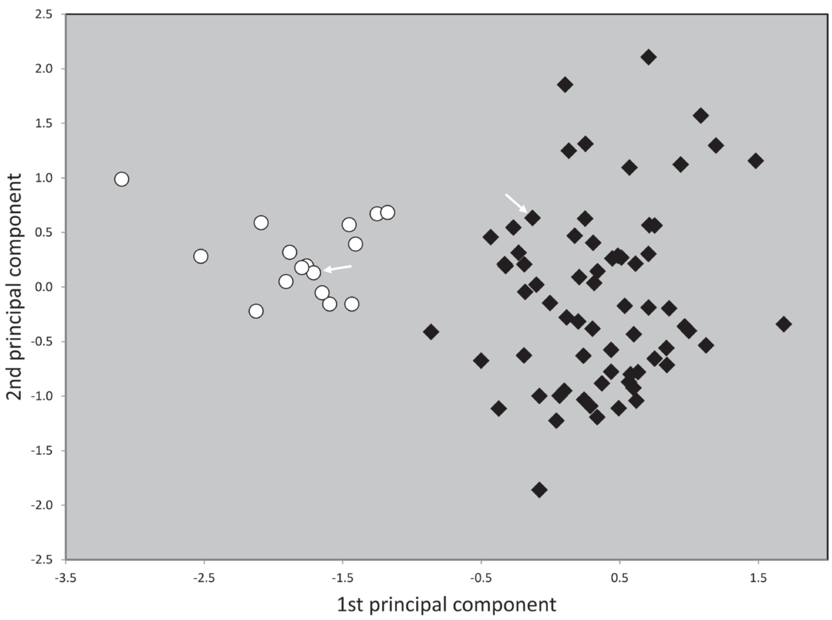


Figure 71. Nest sample means of a principal component analysis of *Formica himalayensis* n.sp. (white dots n=16) and eastern *F. clara* (black rhombs, n=68). The arrows point to the type samples.

metapleuron, petiole scale above the stigma and flexor profile of hind femur only exceptionally with single weak setae, nPrMe 0.02 ± 0.10, nPe 0.36 ± 0.59, nHFfl 0.21 ± 0.40. Extensor profile of hind femur and extensor profile of hind without setae, nHFex 0.00 ± 0.04, nHT 0.03 ± 0.18. Distance of transverse ripples on dorsum of first gaster tergite smaller than in *tianshanica*, RipD 4.49 ± 0.34. Gaster covered by a dense silvery pubescence, sqPDG 3.09 ± 0.20. Pubescence on head, mesosoma and petiole less dense. Typical colour pattern: Head with the exception of round reddish-yellowish spots on anterior genae, dorsal promesonotum, coxae and all appendages dark brown, gaster blackish brown. Other body parts more or less reddish-yellowish. Nests with much lighter specimens having whole mesosoma, coxae and petiole uniformly reddish occur with a frequency < 4 %. The other extreme is formed by very dark specimens having the reddish pigmentation reduced to a very small spot on frontal margin of ventrolateral mesonotum.

Habitat and Biology. See Seifert (2018).

Taxonomic comments: The introduction of the mesosomal shape variables MtSt, MtPpSt and MtMtp, which were not investigated by Seifert & Schultz (2009b), provided an extraordinary strong separation from *Formica tianshanica.* The two species are separated on the nest sample level with error rates of 0% in a PCA and NC-part. kmeans, 1.1% in NC-NMDS.kmeans and 1.7% in NC-Ward (Fig. 72) and the classification error by the LDA was 0.4% in 561 worker individuals. These results were achieved using 18 characters after exclusion of 6 uninformative characters with zero or close-to zero values in both species. All exploratory data analyses run in this study provided a signal for subdivision of the *F. cunicularia* cluster into a cluster A and B (e.g. – Figs 68, 72). However, analyzing the *F. cunicularia* samples alone (i.e., without outgroup species) led to strong disagreements of the final species hypothesis with the clustering proposal of any exploratory data analysis. Furthermore, the geographic distribution of the supposed entities is more compatible with intraspecific polymorphism rather than indicating different species (Fig. 73). Morph A seems to differ from morph B by a much more developed dark mesosomal pigmentation, a longer scape and lower setae numbers. This issue requires a more thorough investigation including informative nuDNA markers.

8.10 *Formica tianshanica* Seifert & Schultz 2009

***Formica tianshanica* Seifert & Schultz 2009** [type investigation]

This taxon has been described from Kyrgyzstan. Investigated was the holotype and four paratype workers labelled “KIR: 42.4079°N, 73.7893°E, Kap Tshigai valley, R.Schultz 1998.07.16-004” and “Holotype Formica tianshanica Seifert & Schultz” / “Paratype Formica tianshanica Seifert & Schultz”; additionally three mounted workers and 10 workers in ethanol from the holotype sample, depository SMN Görlitz. The holotype sample was allocated to the *Formica tianshanica* cluster with p=0.9998 in a wild-card run of a 3-class LDA considering *F. cunicularia*, *F. persica* and *F. tianshanica* (see supplementary information SI3, setting 15).

All material examined. Numeric phenotypical data were taken in 41 nest samples with 158 workers. The material came from China (31 samples), Kazakhstan (7) and Kyrgyzstan (3). For details see supplementary information SI1 and SI2.

Geographic range. The Central Asian population of *Formica tianshanica* is restricted to mountain areas of the Tian Shan, Tarbagatai, Saur, Bogda Shan. The westernmost sites are in the W Tian Shan (42.2°N, 71.5°E), the northernmost in the Tarbagatai Mountains (47.8°N, 81.8°E) and the most eastern site in Bogda Shan (43.8°N, 88.2°E). The altitudinal range of 41 samples is 2089 ± 410 [1005, 3010] m. A disjunct population, documented by a single sample, exists in the mountains of N Yunnan (27.05°N, 100.24°E, 2950 m) 2100 km SSE from the next site of the Central Asian population. The two populations are obviously isolated by the Tibetan Plateau.

Description: --Worker (Tab. 7, Figs 41-43; key). Rather small-sized, CS 1237 ± 101 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head rather long, CL/CW 1.141 ± 0.019. Scape shorter than in *cunicularia*, SL/CS 1.057 ± 0.0250. Eye rather large, EYE/CS 0.297 ± 0.006. Ocellar distance small, OceD/CS 0.168 ± 0.009. Distance between metathoracal spiracles larger than in *cunicularia*, MtSt/CS 0.145 ± 0.015. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron smaller than in *cunicularia*, MtPpSt/CS 0.348 ± 0.010, MtMtp/CS 0.641 ± 0.011. Petiole narrower than in *cunicularia*, PeW/CS 0.436 ± 0.020. Setae on first gaster tergite rather short, GHL/CS 7.23 ± 0.80%. Genae, margin of hind vertex and underside of head without setae, nGen 0.0 ± 0.0, nCH 0.0 ± 0.0, nGu 0.01 ± 0.12. Pronotum and mesonotum with few setae, nPn 1.77 ± 1.40, nMn 0.67 ± 1.02. Propodeum-metapleuron, petiole scale above the stigma and flexor profile of hind femur only exceptionally with single weak setae, nPrMe 0.0 ± 0.0, nPe 0.01 ± 0.10, nHFfl 0.64 ± 0.79. Extensor profile of hind femur and extensor profile of hind tibia without setae, nHFex 0.01 ± 0.06, nHT 0.07 ± 0.32. Distance of transverse ripples on dorsum of first gaster tergite larger than in *cunicularia*, RipD 6.07 ±

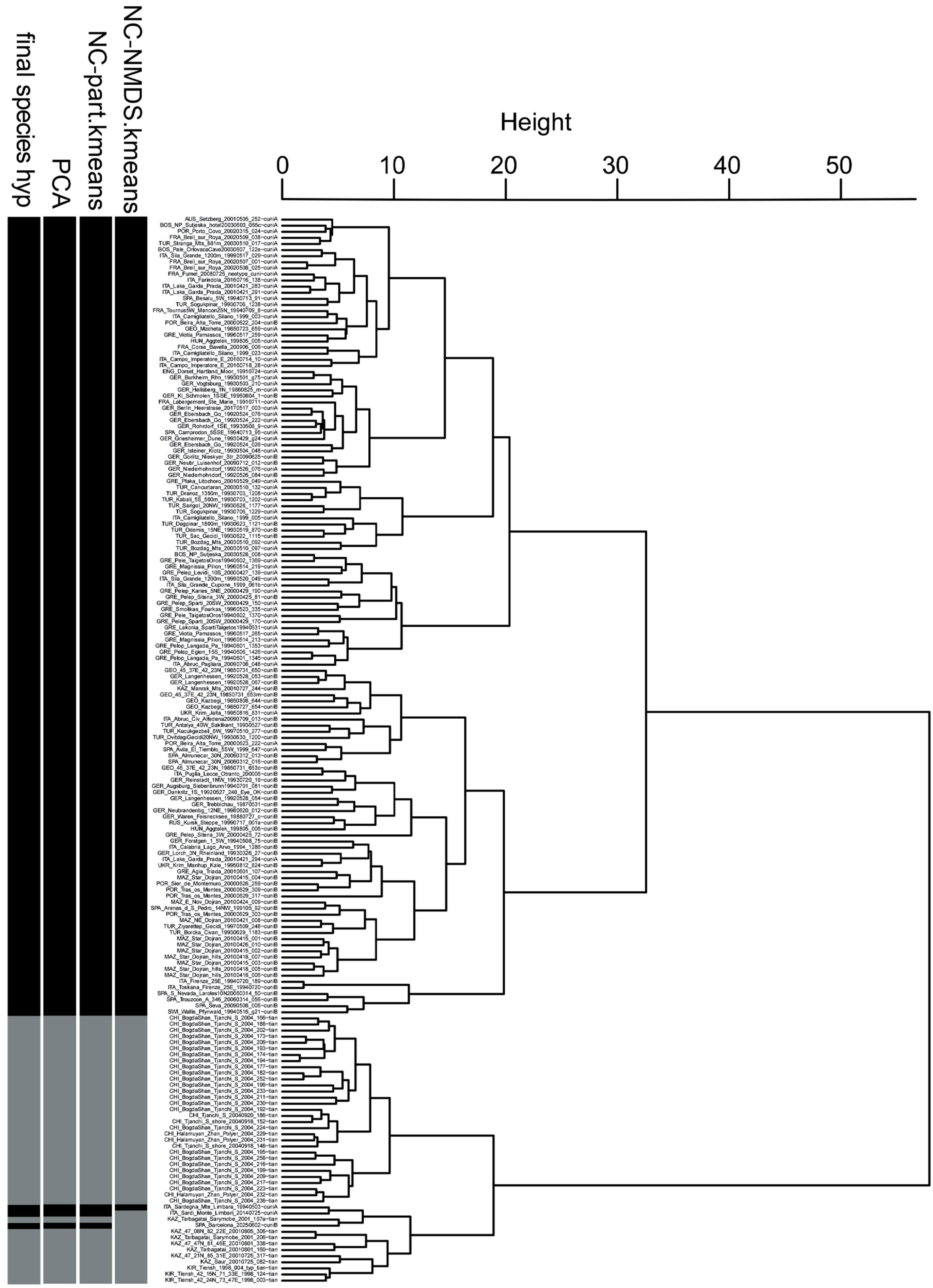


Figure 72. Exploratory data analyses of nest samples of *Formica cunicularia* (black bars, n=134) and of *F. tianshanica* (grey bars, n=41). The mean error of the four analyses is 0.7%.

0.65. Gaster covered by a dense silvery pubescence, sqPDG 3.22 ± 0.22. Pubescence on head, mesosoma and petiole less dense, ants appear mildly shiny. Posterior vertex, sometimes dorsal promesonotum, coxae and all appendages brown, gaster always dark brown. Other body parts more or less reddish, in the Bogda Shan population more yellowish-brown.

Habitat and Biology. *Formica tianshanica* is rare in regions with competing montane and subalpine *Serviformica* species as it was observed in the Tian Shan, Tarbagatai and Quin Ling Shan. In contrast, it is very abundant in the Bogda Shan where these competitors are missing. This correlates with variable habitat selection in Bogda Shan: it was found here in pastures of any kind above and below the tree line, in open rural areas, in clear-cuttings of former *Picea* forest, in habitat mosaics of grass, *Picea* and *Juniperus* and in light *Picea* forests.

Taxonomic comments: *Formica tianshanica* is similar to *cunicularia* in pigmentation pattern but is safely separable on individual level by a combination of mesosomal shape variables, scape length and RipD (Fig. 72). The sample of the disjunct *F. tianshanica* population from Yunnan is by morphology unseparable from samples of the Central Asian *F. tianshanica* population. Following the GAGE species concept, we do not consider it as heterospecific because allopatry alone is no argument for species separation. We suppose that the Yunnan population is really isolated because we had no sample of *F. tianshanica* within 355 *Serviformica* samples from the Tibetan Plateau.

8.11 *Formica persica* Seifert & Schultz 2009

***Formica persica* Seifert & Schultz 2009** [type investigation]

This taxon has been described from the Iran. Investigated was the holotype worker plus 6 worker paratypes (4 stored in ethanol) labelled "IRAN: 36.767°N, 54.567°E, Tuskestan forest, 900 m Juniperus forest O.Paknia 2005.09.23-517" and "Holotype Formica persica Seifert & Schultz" / "Paratype Formica persica Seifert & Schultz"; depository SMN Görlitz. The holotype sample was allocated to the *Formica persica* cluster with p=1.000 in a wild-card run of a 3-class LDA considering *F. clara*, *F. cunicularia* and *F. persica* (see supplementary information SI3, setting 15). Furthermore, the holotype sample was allocated to the *Formica persica* cluster with p=1.000 in a wild-card run of a 3-class LDA considering *F. gebaueri* n.sp., *F. glabridorsis* and *F. persica* (see supplementary information SI3, setting 16).

All material examined. Numeric phenotypical data were taken in 32 nest samples with 87 workers. The material came from Iran (31 samples) and Turkey (1). For details see supplementary information SI1 and SI2.

Geographic range.The main population of *Formica persica* is found in the North Iranian region of the Elburs Mountains between 48.5°E to 56°E and 36.2°N and 38.4°N – a region with much precipitation (600-1500 mm per year). The finding near Islambey (41.171°N, 36.894°E, 10 m) at the Turkish Black Sea coast is 1000 km west of the main population but is found in a very

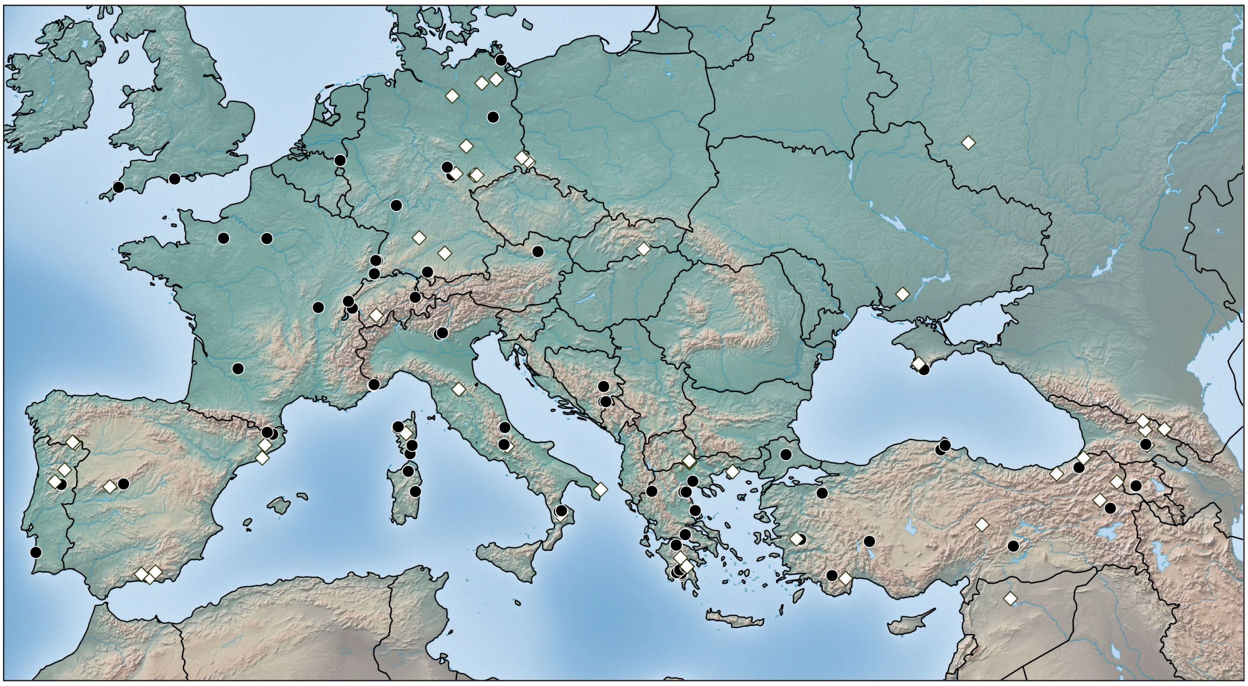


Figure 73. Geographic distribution of the A morph (black dots) and the B morphs (white rhombs) of *Formica cunicularia*.

similar climatic context with 900-1350 mm precipitation per year. The altitudinal range of 32 samples is 776 ± 574 [10, 2300] m.

Description: --Worker (Tab. 8, key). Medium-sized, CS 1335 ± 137 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head very long, CL/CW 1.158 ± 0.018. Scape much longer than in *cunicularia* and *clara*, SL/CS 1.152 ± 0.027. Eye medium-sized, EYE/CS 0.295 ± 0.006. Ocellar distance small, OceD/CS 0.165 ± 0.009. Distance between metathoracal spiracles medium, MtSt/CS 0.127 ± 0.014. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron smaller than in *cunicularia*, MtPpSt/CS 0.360 ± 0.012, MtMtp/CS 0.663 ± 0.015. Petiole rather wide, PeW/CS 0.454 ± 0.025. Setae on first gaster tergite very short, GHL/CS 4.97 ± 2.42%. Genae, margin of hind vertex, underside of head, pronotum, mesonotum, propodeum-metapleuron, hind femora and tibiae without setae. Distance of transverse ripples on dorsum of first gaster tergite larger than in *cunicularia* and *clara*, RipD 5.74 ± 0.49. Gaster covered by a dense silvery pubescence, sqPDG 3.31 ± 0.24. Pubescence on head, mesosoma and petiole less dense, all surfaces appear more shiny than in *cunicularia*. It frequently has a pied mesosoma pigmentation that is very similar to *cunicularia*. Posterior vertex, often dorsal promesonotum, coxae and all appendages brown, gaster always dark brown. Other body parts yellowish-reddish.

Habitat and Biology. The main habitat is woodland and includes deciduous and *Juniperus* forests. It also occurs in steppes, human settlements, rural areas and at river sides.

Taxonomic comments: *Formica persica* is clearly separable from *F. cunicularia* and the western population of *F. clara* which are the most similar species occurring within its geographic range. The same applies in respect to the allopatric species *F. gebaueri* n.sp. and *F. glabridorsis* (see Tab. 8).

8.12 *Formica glabridorsis* Santschi 1925

***F. rufibarbis var. glabridorsis Santschi*, 1925** [type investigation]

This taxon has been described from Peking / China. Investigated were two syntype workers labelled "Pechino S. Folchini 1905", "Formica (Servif.) rufibarbis Nyl v glabridorsis Sants SANTSCHI det 19.." MCZ CoType 28817"; depository MCZ Cambridge. The syntype sample was allocated to the *Formica glabridorsis* cluster with p=1.000 in a wild-card run of a 3-class LDA considering *F. gebaueri* n.sp., *F. glabridorsis* and *F. persica* (see supplementary information SI3, setting 16).

All material examined. Numeric phenotypical data were taken in 10 nest samples with 38 workers. All material came from east China. For details see supplementary information SI1 and SI2.

Geographic range. The species was found in E China between 99 and 118°E, 27 and 40°N and at elevations between 50 and 2680 m.

Description: --Worker (Tab. 8, key). Rather large, CS 1425 ± 96 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head very long, CL/CW 1.163 ± 0.016. Scape very long, much longer than in *sinae*, SL/CS 1.188 ± 0.016. Eye rather large, EYE/CS 0.299 ± 0.006. Ocellar distance small, OceD/CS 0.158 ± 0.013. Distance between metathoracal spiracles very small, MtSt/CS 0.101 ± 0.010. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron much larger than in any species delt with here, MtPpSt/CS 0.397 ± 0.009, MtMtp/CS 0.711 ± 0.010. Petiole moderately wide, PeW/CS 0.431 ± 0.027. Setae on first gaster tergite short, GHL/CS 5.91 ± 0.53%. Genae, margin of hind vertex, underside of head, pronotum, mesonotum, propodeum-metapleuron, hind femora and tibiae without or only occasional weak setae. Distance of transverse ripples on dorsum of first gaster tergite relatively small, RipD 4.24 ± 0.31._Gaster covered by a very dense silvery pubescence, sqPDG 2.89 ± 0.13. Vertex and gaster dark brown. Genae, mesosoma, petiole, coxae and appendages light to medium reddish brown.

Habitat and Biology. Based on current landscape conditions at known collection sites across its range, *Formica glabridorsis* appears to occupy a variety of habitats including urban and suburban areas, agricultural landscapes, open country, forest edges, and riverbanks, and it is also frequent in urban parks and stands of *Phragmites australis*. The substantial altitudinal and ecological range suggests a high degree of adaptability to various climatic and environmental conditions from lowland temperate to montane zones.

Taxonomic comments: *Formica glabridorsis* is not to be confused by its extraordinarily large SL/CS_{1400}, $MtPpSt/CS_{1400}$ and $MtMtp/CS_{1400}$.

8.13 *Formica gebaueri* n.sp.

Etymology: The name is given in honour of the naturalist and excellent wildlife film-maker Axel Gebauer who collected the first sample of this species.

Type material

Holotype and four paratype worker on two pins labelled "CHI: 36.82°N, 102.53°E, 2600 m, Beishan Nat. Park, Picea-Pinus-Wald, Geröllhang. A. Gebauer

1996.05.30"; depository SMN Görlitz. The holotype sample was allocated to the *Formica gebaueri* n.sp. cluster with p=1.000 in a wild-card run of a 3-class LDA considering *F. gebaueri* n.sp., *F. glabridorsis* and *F. persica* (see supplementary information SI3, setting 16).

All material examined. Numeric phenotypical data were taken in 17 nest samples with 55 workers. All material came from China. For details see supplementary information SI1 and SI2.

Geographic range. *Formica gebaueri* was found in the Chinese provinces Quinghai, Gansu, Shaanxi and Sichuan at elevations between 1520 and 3167 m.

Description: --Worker (Tab. 8, Figs 38-40; key). Rather large, CS 1373 ± 164 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head index very large, CL/CW 1.168 ± 0.018. Scape long, SL/CS 1.132 ± 0.030. Eye medium-sized, EYE/CS 0.294 ± 0.005. Ocellar distance small, OceD/CS 0.161 ± 0.012. Distance between metathoracal spiracles small, MtSt/CS 0.114 ± 0.014. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron rather large, MtPpSt/CS 0.361 ± 0.010, MtMtp/CS 0.653 ± 0.011. Petiole narrow, PeW/CS 0.416 ± 0.028. Setae on first gaster tergite rather short, GHL/CS 6.87 ± 0.93%. Genae, margin of hind vertex and underside of head without setae, nGen 0.0 ± 0.0, nCH 0.02 ± 0.09, nGu 0.05 ± 0.19. Pronotum without or with only few setae, nPn 0.85 ± 1.13. Mesonotum without or only single setae, nMn 0.19 ± 0.38. Setae on propodeum-metapleuron, extensor and flexor profile of hind femur and extensor profile of hind tibia usually absent, nPrMe 0.0 ± 0.0, nhFex 0.0 ± 0.0, nHFfl 0.65 ± 0.86, nHT 0.03 ± 0.19. Setae on petiole scale above the stigma usually absent, nPe 0.01 ± 0.04. Distance of transverse ripples and of pubescence hairs on dorsum of first gaster tergite high, RipD 6.46 ± 0.68, sqPDG 7.37 ± 1.64 – as result the surface is ususally very shiny. Lighter coloured specimens have a blackish brown vertex, reddish brown genae and appendages, the mesosoma reddish brown with diffuse darker patches, a yellowish petiole and a dark reddish brown gaster. Dark specimens have a blackish vertex, dark brown genae with a reddish tinge, a blackish brown mesosoma, a dark brown petiole, a blackish brown gaster and yellowish brown appendages.

Habitat and Biology. Almost all samples were taken in woodland - either inside the forest, at forest margins or in small clearings of woodland. Only one sample was collected in open heathland. *Formica gebaueri* n.sp. was found to be a slave species of *F. sanguinea* Latreille 1798. The holotype nest hosted the inquiline *Formicoxenus gebaueri* Seifert 2023.

Taxonomic comments: As a combination of elongated head and large RipD and sqPDG, *Formica gebaueri* n.sp. is not to be confused. There is some geographic variability in the distance of transverse microsculpture and pubescence hairs on gaster tergites, the strength of microsculpture on all body surfaces and in pigmentation. However, all attempts to verify a separation of clusters failed in any exploratory data analysis.

8.14 *Incertae sedis* of taxa attributed to the *Formica rufibarbis* group

The species identity of the following taxa deemed to belong to the *F. rufibarbis* group cannot be concluded because of insufficient descriptions and missing type material. According to information by the keepers of the entomological collections of St. Petersburg (letter of A. Zinovjev, May 1995, search of P. Krasilnikov in 2006), Moscow (letter of G. Dlussky, May 1996, letter of A. Antropov, September 2008), and Tucuman / Argentina (letter of E. Willink, February 1992) type material of these taxa is no longer available. According to our own search in German collections type material of Foerster is completely destroyed (Seifert 1992).

Formica ***nicaeensis*** Leach 1825

Formica ***stenoptera*** Foerster 1850
Described from Aachen, Germany

Formica ***defensor*** Smith 1878
Described from Kashmir (aproximately 33°N,77°E)

Formica ***fraterna*** Smith 1878
Described from Kashmir (aproximately 33°N,77°E)

Formica rufibarbis var. ***caucasica*** Wheeler 1913
First available use of *Formica rufibarbis* ssp. *clara* var. *caucasica* Ruzsky 1905
This taxon has been described from the Caucasus. The worker lectotype labelled "Form. rufib. clara, var. caucasica, Kavkaz Ruzsky" and "Lectotype des."; depository ZMLSU Moskva was investigated. The specimen is badly damaged: pilosity and pubescence of dorsal body surfaces is almost completely torn-off and both scapes are lacking.

Formica rufibarbis ***volgensis*** Ruzsky, 1914
Described from Volga river

Formica rufibarbis st. ***montivaga*** Santschi 1928;
[replacement name for *Formica rufibarbis* natio ***montana*** Kuznetzov-Ugamsky 1923, junior primary homonym of *F. subpolita* var. *montana* Wheeler 1910]
Described from Turkestan

Formica rufibarbis var. ***montaniformis*** Kuznetzov-Ugamsky 1929
Described from Dagestan

9 *Formica lhasaensis* n.sp.

Etymology: The name refers to Lhasa, the capital of Tibet, in the vicinity of which the species was found.

Type material

Holotype plus 4 paratype workers on two pins labelled “CHI: 29.7227°N, 91.1235°E, Lhasa N, Tar, S slope, pasture, 4209 m, M.Ritz 2012.08.29, Chi 2012-074”; “Holotype (top) and paratypes *Formica lhasaensis* Schultz & Seifert”; depository SMN Görlitz. 4 workers and 4 gynes in ethanol; depository SMN Görlitz.

All material examined. Numeric phenotypical data were taken in 6 nest samples with 18 workers. All material came from Tibet. For details see supplementary information SI1 and SI2.

Geographic range. *F. lhasaensis* was found at three sites in the surroundings of Lhasa and Southwest Tibet at elevations between 3884 and 4735 m.

Description: --Worker (Tab. 6, Figs 47-49; key). Very small, CS 1122 ± 79 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Because body size is unusually small in this species, the corrected setae numbers may deviate strongly from the raw data. Head index small, CL/CW 1.109 ± 0.017. Scape extremely short, SL/CS 0.960 ± 0.026. Eye medium-sized, EYE/CS 0.299 ± 0.007. Ocellar distance large, OceD/CS 0.181 ± 0.011. Distance between metathoracal spiracles large, MtSt/CS 0.158 ± 0.015. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron very small, MtPpSt/CS 0.312 ± 0.009, MtMtp/CS 0.597 ± 0.008. Petiole relatively narrow, PeW/CS 0.425 ± 0.018. Setae on first gaster tergite moderately long, GHL/CS 8.14 ± 1.14%. Genae usually without setae, nGen 0.22 ± 0.36. Hind margin of vertex and underside of head with many setae, nCH 12.8 ± 5.2, nGu 9.8 ± 2.1. Mesosoma with numerous setae, nPn 36.0 ± 12.0, nMn 17.6 ± 7.1. nPrMe 13.3 ± 5.8. Extensor profile of hind femur and of hind tibia without or only occasional setae, nHFex 0.11 ± 0.49, nHT 0.23 ± 0.48. Flexor profile of hind femur with rather numerous setae nHFfl 11.1 ± 3.3. Petiole scale above the stigma usually with a moderate number of setae, nPe 8.5 ± 3.2. Distance of transverse ripples on dorsum of first gaster tergite high, RipD 7.40 ± 0.52, but pubescence distance low, sqPDG 3.45 ± 0.19. Whole body dark brown with exception of the light brown coxae and appendages.

Habitat and Biology. As habitat were reported an alpine grassland in a treeline ecotone, an alpine grassland with *Juniperus* and an alpine pasture with scattered bushes. All sites were on south-facing slopes. The late development of alates (29 September 2012) is a consequence of extreme height above sea level with delayed development in spring.

Taxonomic comments: As a combination of short scape, large MtSt, small MtPpSt and MtMtp, presence of setae on gula and hind vertex and large RipD, *Formica lhasaensis* n.sp. is not to be confused. This deviating species cannot be allocated to one of the three species groups considered here and should represent an own clade. It is similar to *F. cinerea* in its pilosity condition but strongly different in absolute size, SL/CS, EYE/CS, the three mesosomal measurements and RipD.

10 *Formica rufolucida* Collingwood 1962

***Formica rufolucida* Collingwood 1962** [type investigation]

This taxon has been described from Myanmar. Investigated were 5 syntype workers labelled “N. E. BURMA, Kambaiti 7000 ft., 4/4 1934 R. MALAISE” and “FORMICA rufolucida S.N. det Collingwood Type”; 2 syntype workers labelled “”N. E. BURMA, Kambaiti 2000 m, 23/4. 1934 Malaise”, “FORMICA rufolucida S.N. det. C.A.Collingwood”, “478 63”; depository NRM Stockholm. Further four samples with 11 workers from the same locality were not labelled as types but could be considered as syntypes.

All material examined. Numeric phenotypical data were taken in 14 samples with 42 workers. The material came from east China (7 samples) and Myanmar (7). For details see supplementary information SI1 and SI2.

Geographic range. The eight known sites are situated in Myanmar and the adjacent part of the Chinese province Yunnan within a range demarcated by 20.8 and 27.0°N and 92.4 and 100.0°E. Their altitudinal range is 1721 ± 790 [300, 2370] m.

Description: --Worker (Tab. 8, Fig. 32, key). Very large CS 1522 ± 88 µm. All numeric data given below are RAV-corrected for the assumption of all specimens having CS = 1400 µm. Head long, CL/CW 1.130 ± 0.016. Scape extremely long, SL/CS 1.235 ± 0.0306. Eye small, EYE/CS 0.278 ± 0.005. Ocellar distance small, OceD/CS 0.161 ± 0.009. Anteromedian margin of clypeus in dorsofrontal view slightly excavated. Distance between metathoracal spiracles small, MtSt/CS 0.114 ± 0.010. Distance between metathoracal and propodeal stigma and between metathoracal stigma and caudalmost point of metapleuron moderate, MtPpSt/CS 0.368 ± 0.014, MtMtp/CS 0.639 ± 0.021. Petiole narrow, PeW/CS 0.371 ± 0.014. Setae on first gaster tergite rather long, GHL/CS 9.38 ± 1.62%. Genae, margin of hind vertex, underside of head, pronotum, mesonotum, propodeum-metapleuron, hind femora and tibiae without or only with occasional weak setae. Dorsum of first gaster tergite with a delicate network with large mesh width, RipD 9.32 ± 0.53. Gaster covered by a dense silvery pubescence, sqPDG 3.63 ± 0.27. Vertex and gaster dark brown. Genae, mesosoma, petiole, coxae and appendages light yellowish reddish. Mesosoma in some specimens with isolated dark patches, thus giving a pied appearance.

Habitat and Biology. This is one of the few *Formica* species that live in a zone with subtropical monsoon climate showing mild winters, warm summers and annual preciptiations of 1400–1800 mm. *Formica rufolucida* was reported by Collingwood (1962) from several localities in Burma (now Myanmar), including the Kambaiti Mountains (1700–2000 m), Malvedaung (now Maungdaw, 300 m), Inle Lake (900 m). Although Collingwood provided no details on habitat, these sites suggest that the species occurs across a broad elevational range from hill country to montane areas. Material from Yunnan indicates that *F. rufolucida* inhabits a variety of environments, including open landscapes with scrub vegetation, forest edges, agricultural areas, and semi-urban settings. This ecological breadth suggests a degree of tolerance to habitat disturbance and an ability to persist in both natural and modified environments.

Taxonomic comments: *Formica rufolucida* cannot be confused by its extraordinarily long scape, the large RipD and the slight excavation of anteromedian clypeus (Fig. 32). The latter is a rare structure, known in the Palaearctic so far only in *Formica sanguinea* Latreille and the two species of the *Formica sentschuensis* Ruzsky group. This indicates that *Formica rufolucida* is no member of the *F. rufibarbis* group and belongs to a separate clade.

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Online Supplementary Material

Table SI1.xlsx, SI2.xlsx and Tables SI3.pdf.

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References

Agosti, D. (1989). Versuch einer phylogenetischen Wertung der Merkmale der Formicini (Hymenoptera, Formicidae), Revision der *Formica exsecta*-Gruppe und Liste der Formicidae Europas. *Dissertation ETH Zürich No. 8774*, 278 pp. https://doi.org/10.3929/ethz-a-000510347

Borowiec, M. L., Cover, S. P. & Rabeling, C. (2021): The evolution of social parasitism in *Formica* ants revealed by a global phylogeny, *PNAS 118* (38) e2026029118. https://doi.org/10.1073/pnas.2026029118

Bračko, G. (2023). Atlas of the ants of Slovenia, *Biotechnical Faculty Ljubljana*, 251 pp.

Catharineu, C., Lorenzo, L., Aranega, B., Ferrandez, T., Espadaler, X., Perez Hidalgo, N. & Barbera, G.G. (2021). *Formica decipiens* Bondroit 1918, una especie dominante y territorial que modifica la comunidad local de hormigas en la Sierra de las Cabras (Albacete). Available at: https://www.researchgate.net/publication/357164946 (Accessed: 18 October 2025).

Collingwood, C.A. (1962). Some ants (Hymenoptera, Formicidae) from north-east Asia, *Entomologisk Tidskrift 83*, 215–230.

Csősz, S. & Fisher, B. L. (2016). Toward objective, morphology-based taxonomy: a case study on the Malagasy *Nesomyrmex sikorai* species group (Hymenoptera: Formicidae), *PLoS ONE 11* (4):31 pp. https://doi.org/10.1371/journal.pone.0152454

Dlussky, G.M. (1967). Muravi roda *Formica* (Ants of the genus Formica), *Izdatel'stvo Nauka*, Moskva, 236 pp.

Fontaine, M.C., Pease, J.B., Steele, A., Waterhouse, R.M., Neafsey, D.E., Sharakhov, I.V., Jiang, X., Hall, A.B., Catteruccia, F., Kakani, E., Mitchell, S.N., Wu, Y.-C., Smith, H.A., Love, R.R., Lawniczak, M.K., Slotman, M.A., Emrich, S.J., Hahn, M.W. & Besansky, N.J. (2015). Extensive introgression in a malaria vector species complex revealed by phylogenomics, *Science 347*, 1258524. https://doi.org/10.1126/science.1258524

Mallet, J., Besansky, N. & Hahn, M.W. (2016). How reticulated are species? *BioEssays 38*,140–149. https://doi.org/10.1002/bies.201500149

Muñoz-López, M., Palomeque, T., Carrillo, J. A., Pons, J., Tinaut, A. & Lorite, P. (2012). A new taxonomic status for Iberoformica (Hymenoptera, Formicidae) based on the use of molecular markers, *Journal of Zoological Systematics and Evolutionary Research1 50*, 30–37. https://doi.org/10.1111/j.1439-0469.2011.00649.x

Purcell, J., Zahnd, S., Athanasiades, A., Turler, R., Chapuisat, M. & Brelsford, A. (2016). Ants exhibit asymmetric hybridization in a mosaic hybrid zone, *Molecular Ecology 25*, 4866–4874. https://doi.org/10.1111/mec.13799

Ruzsky, M. (1895): Faunistichekye Izledovaniya v vostochnoi Rossii. K faune murav'ev vostoka Rossii, *Trudy Obshchestva Estestvoispytatelei pri Imperatorskom Kazanskom Universitete 28*(5), 1-32.

Schultz, R. & Seifert, B. (2005). *Lasius neglectus* (Hymenoptera: Formicidae) - a widely distributed tramp species in Central Asia, *Myrmecologische Nachrichten 7*, 47–50.

Schultz, R. & Seifert, B. (2025). *Formica sentschuensis* Ruzsky 1915 and *Formica tibetana* n.sp.– two unique and little known *Formica* species from Tibet (Hymenoptera: Formicidae), *Soil Organisms 97* (1), 85–95. https://doi.org/10.25674/452

Seifert, B. (1992). *Formica nigricans* Emery, 1909 - an ecomorph of *Formica pratensis* Retzius, 1783 (Hymenoptera, Formicidae), *Entomologica Fennica 2*, 217–226. https://doi.org/10.33338/ef.83554

Seifert, B. (2002). A taxonomic revision of the *Formica cinerea* group (Hymenoptera: Formicidae), *Abhandlungen und Berichte des Naturkundemuseums Görlitz 74* (2), 245–272.

Seifert, B. (2008). Removal of allometric variance improves species separation in multi-character discriminant functions when species are strongly allometric and exposes diagnostic characters, *Myrmecological News 11*, 91–105. https://doi.org/10.25849/myrmecol.news_011:091

Seifert, B. (2009). Cryptic species in ants (Hymenoptera: Formicidae) revisited: we need a change in the alpha-taxonomic approach, *Myrmecological News 12*, 149–166. https://doi.org/10.25849/myrmecol.news_012:149

Seifert, B. (2016). Analyzing large-scale and intranidal phenotype distributions in eusocial Hymenoptera – a taxonomic tool to distinguish intraspecific dimorphism from heterospecificity, *Myrmecological News 23*, 41–59. https://doi.org/10.25849/myrmecol.news_023:041

Seifert, B. (2017). The ecology of Central European non-arboreal ants – 37 years of a broad-spectrum analysis under permanent taxonomic control, *Soil Organisms 89* (1), 1–67.2

Seifert, B. (2018). The Ants of Central and North Europe, *Lutra Verlags- und Vertriebsgesellschaft*, Tauer, 408 pp.34

Seifert, B. (2020). The Gene and Gene Expression (GAGE) Species Concept: An Universal Approach for All Eukaryotic Organisms, *Systematic Biology 69* (5), 1033–10368. https://doi.org/10.1093/sysbio/syaa032

Seifert, B. (2021). A taxonomic revision of the Palaearctic members of the *Formica rufa* group (Hymenoptera: Formicidae) – the famous mound-building red wood ants. *Myrmecological News 31*, 133–179. https://doi.org/10.25849/myrmecol.news_031:133.

Seifert, B. (2023). Hybridisierung bei Waldameisen und anderen Ameisen – retikuläre Evolution als Anpassungsstrategie, *Ameisenschutz aktuell 23* (4), 85–99.

Seifert, B. (2024). Pleistocene population differentiation in the ant *Myrmica scabrinodis* (Hymenoptera: Formicidae) – a taxonomic borderline case, *Soil Organisms 96* (1), 11–21. https://doi.org/10.25674/357

Seifert, B. (2025). The *Monomorium carbonarium* species group in the Nearctic and Europe (Hymenoptera: Formicidae), *Soil Organisms 98* (5), 55–84. https://doi.org/10.25674/441

Seifert, B. & Schultz, R. (2009a). A taxonomic revision of the *Formica subpilosa* Ruzsky, 1902 group (Hymenoptera: Formicidae). Myrmecological News 12:67–83.

Seifert, B. & Schultz, R. (2009b). A taxonomic revision of the *Formica rufibarbis* Fabricius, 1793 group (Hymenoptera: Formicidae), *Myrmecological News 12*, 255–272.

Seifert, B., Ritz, M. & Csősz, S. (2013). Application of Exploratory Data Analyses opens a new perspective in morphology-based alpha-taxonomy of eusocial organisms, *Myrmecological News 19*, 1–15.

Seifert, B., Buschinger, A., Aldawood, A., Antonova, V., Bharti, H., Borowiec, L., Dekoninck, W., Dubovikoff, D., Espadaler, X., Flegr, J., Georgiadis, C., Heinze, J., Neumeyer, R., Ødegaard, F., Oettler, J., Radchenko, A., Schultz, R., Sharaf, M., Trager, J., Vesnić, A., Wiezik, M. & Zettel, H. (2016). Banning paraphylies and executing Linnaean taxonomy is discordant and reduces the evolutionary and semantic information content of biological nomenclature, *Insectes Sociaux 63* (2), 237–242. https://doi.org/10.1007/s00040-016-0467-1

Tarbinsky, J.S. (1976). Muravi Kirgisii (Ants of Kirgizia). Izdatelstvo Ilim, Frunse / Kirgisia, 217 pp.

Wagner, H.C. (2014). Die Ameisen Kärntens. Verbreitung, Biologie, Ökologie und Gefährdung, *Naturwissenschaftlicher Verein für Kärnten*, Klagenfurt, 464 pp.

Wagner H.C., Wiesmair B., Paill W., Degasperi G., Komposch C., Schattanek, P., Schneider M., Aurenhammer S., Gunczy L.W., Rabitsch W., Heimburg H., Zweidick O., Volkmer J., Frei B., Kerschbaumsteiner H., Huber E., Netzberger, R., Borovsky R., Kunz G., Zechmeister T., Ockermüller E., Preiml S., Papenberg, E., Kirchmair G., Fröhlich D., Allspach A., Zittra C., Svetnik I., Bodner, M., Vogtenhuber P., Körner A., Thieme T., Christian E., Seeber J., Baumann J., Gross H., Hittorf M., Rausch H., Burckhardt D., Graf W. & Baumgartner C. (2019): Bericht über das fünfte ÖEG-Insektencamp: Biodiversitätsforschung im Nationalpark Donau-Auen (Wien, Niederösterreich), *Entomologica Austriaca 26*, 25–113.

Ward, P. S., Brady, S. G., Fisher, B. L. & Schultz, T. R. (2015). The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae), *Systematic Entomology 40*, 61–81. https://doi.org/10.1111/syen.12090

Weyna, A., Bourouina, L., Galtier, N. & Romiguier, J. (2022). Detection of F1 hybrids from single-genome data reveals frequent hybridization in Hymenoptera and particularly ants, *Molecular Biology and Evolution 39* (4), msa9c071. https://doi.org/10.1093/molbev/msac071