

## A taxonomic revision of the *Formica subpilosa* RUSKY, 1902 group (Hymenoptera: Formicidae)

Bernhard SEIFERT & Roland SCHULTZ



### Abstract

The members of the West to Central Asian *Formica subpilosa* group were investigated by means of numeric morphology-based alpha-taxonomy (NUMOBAT). 18 phenotypic characters were described on the basis of 201 nest samples comprising 591 worker individuals. Five morphospecies were distinguished: *Formica subpilosa* RUSKY, 1902, *F. litoralis* KUZNETZOV-UGAMSKY, 1926, *F. clarissima* EMERY, 1925, *F. pamirica* DLUSSKY, 1965, and *F. kashmirica* STÄRCKE, 1935. A leave-one-out cross-validation discriminant analysis (LOOCV-DA) separated the first four species with an error indication of 0% and allocated all available type series near to the cluster centres with a-posteriori probabilities of  $p = 1.000$ . The heterospecificity of *Formica kashmirica*, represented only by the type sample and not reasonably testable by a DA, is justified by a character combination not found in any of the other species. *Formica clarissima*, *F. kashmirica*, *F. litoralis*, and *F. pamirica* are elevated to species rank. *Formica litoralis* and *F. pamirica* are parapatric sibling species – there seems to be no morphological convergence with falling geographic distance but the question of possible hybridisation in contact zones cannot be answered by the existing data. *Formica cinerea* var. *bipilosa* KARAVAJEV, 1926 was confirmed to be a junior synonym of *F. subpilosa*. The separation of the Palaearctic *Serviformica* species with reddish pigmentation into a *Formica cinerea* MAYR, 1853, a *F. rufibarbis* FABRICIUS, 1793, and a *F. subpilosa* group is confirmed by a discriminant analysis. All species are depicted and a simplified identification key is given. Species of this group prefer habitats with exposed alluvial, lacustrine or aeolian soils and sparse plant cover. The *F. subpilosa* group ecologically replaces the *F. cinerea* group in Central Asia.

**Key words:** Numeric morphology-based alpha-taxonomy, cryptic species, discriminant analysis, leave-one-out cross-validation, error estimate.

Myrmecol. News 12: 67-83 (online 21 December 2008)

ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 21 July 2008; revision received 18 September 2008; accepted 13 October 2008

Dr. Bernhard Seifert (contact author) & Dr. Roland Schultz, State Museum of Natural History, Am Museum 1, D-02826 Görlitz, Germany. E-mail: [bernhard.seifert@smng.smwk.sachsen.de](mailto:bernhard.seifert@smng.smwk.sachsen.de), [roland.schultz@smng.smwk.sachsen.de](mailto:roland.schultz@smng.smwk.sachsen.de)

### Introduction

Within the ant subgenus *Serviformica* FOREL, 1913, there are three species groups the members of which may show large reddish or orange cuticular surfaces in addition to the dark brown or blackish pigmentation:

- the *Formica* (*Serviformica*) *rufibarbis* group, distributed from Europe to East Asia, characterised by the reduction of setae on posterior vertex and underside of head, smaller eyes, and wider petioles;
- the West to Central Asian *F.* (*Serviformica*) *subpilosa* group, characterised by intermediate setae numbers on posterior vertex and underside of head, smaller eyes, and wider petioles; and
- the Eurocaucasian *F.* (*Serviformica*) *cinerea* group, characterised by large setae numbers on posterior vertex and underside of head, large eyes and narrow petioles.

As it will be shown below, the *F. rufibarbis* and *F. subpilosa* groups are morphologically more similar while the *F. cinerea* group is more distant from both these groups (SEIFERT 2003). The currently known geographic ranges of the *F. cinerea* and *F. subpilosa* group are almost fully separated. This is explained by the widely distant radiation centres and the most similar ecological niches which prevented that sympatry could secondarily develop. Both

groups avoid habitats with dense herbaceous plant cover such as xerothermic or meagre grasslands. Instead, they prefer open habitats with sparse vegetation on sand and gravel banks along rivers, on other alluvial soils, on sand dunes or anthropogenic habitats with similar physical surface structure. In both the *F. cinerea* and *F. subpilosa* group there are species with adaptation to flooding.

The taxonomy of the *F. subpilosa* group has been considered by DLUSSKY (1965, 1967). He recognised four entities which he named *F. subpilosa* RUSKY, 1902, *F. subpilosa litoralis* KUZNETZOV-UGAMSKY, 1926, *F. subpilosa ruzskyi* DLUSSKY, 1965 (valid name *F. clarissima* EMERY, 1925), and *F. subpilosa pamirica* DLUSSKY, 1965. As we will show in this paper, DLUSSKY's distinctions and zoogeographical data pointed into the right direction but he gave only a very sparse verbal argumentation using the widely overlapping characters of mesosomal pigmentation and cephalic pilosity.

Here we present an extensive numeric study of morphological characters and will show that all these forms deserve the rank of separate species. We also want to clarify the nomenclatural situation within this ecologically important ant group. A conclusive argumentation for hetero-

specificity of most similar entities is only possible if a sufficiently large sample is available for each considered species. This condition is only given in the worker caste. Rarity or lack of gynes and males in collections and inadequate knowledge of the diagnostic value of their characters do not allow one to use these castes reliably for determination. Hence, the scope of this revision is restricted to the worker caste.

## Methods

### Character recording

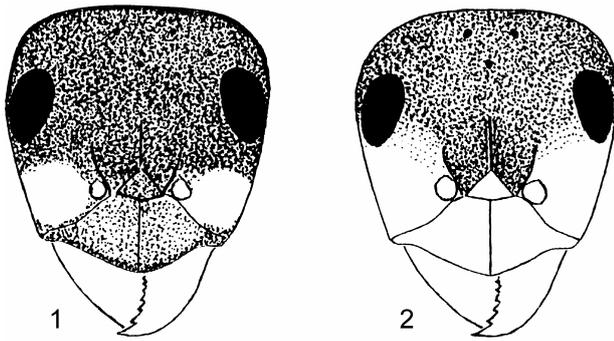
Eighteen numerically described morphological characters were used. All measurements were made on mounted and dried specimens using a pin-holding stage, permitting full rotations around X, Y, and Z axes. Two high-performance stereomicroscopes, a Leica Wild M10 and a Leica MZ 16A, each equipped with a  $1.6 \times$  planapochromatic front lens, were used at magnifications of 160 - 320  $\times$ . A Schott KL 1500 cold-light source equipped with two flexible, focally mounted light-cables, providing 30° inclined light from variable directions, allowed sufficient illumination over the full magnification range and a clear visualisation of silhouette lines. A Schott KL 2500 LCD cold-light source in combination with a Leica coaxial polarised-light illuminator provided optimum resolution of tiny structures and microsculpture at highest magnifications. Simultaneous or alternative use of the cold-light sources depending on the required illumination regime was quickly provided by regulating the voltage up and down. A Leica cross-scaled ocular micrometer with 120 graduation marks ranging over 65% of the visual field was used. To avoid parallax error, its measuring line was constantly kept vertical within the visual field. The measuring error in the Leica MZ 16A (which is less accurate than the Wild M10) achieved  $\pm 1.5 \mu\text{m}$  in small and well-defined structures such as setae length, but one of  $\pm 3.0 \mu\text{m}$  for larger structures that are difficult to position such as cephalic length. To avoid rounding errors, all measurements were recorded in  $\mu\text{m}$  even for characters for which a precision of  $\pm 1 \mu\text{m}$  is impossible.

Setae, also called pilosity or simply "hairs", are differentiated from pubescence hairs in having at least twice the basal diameter of neighbouring pubescence hairs. All seta counts (acronyms beginning with "n") are restricted to standing setae projecting  $> 10 \mu\text{m}$  from cuticular surface as they are seen in a specifically defined profile view.

### Definition of numeric characters and descriptive terms

- CL Maximum cephalic length in median line; head must be carefully tilted to position yielding true maximum; excavations of hind vertex and / or clypeus reduce CL.
- CONT Contrast between dark and light pigmentation on genae, subjectively interpolated between values 1.0 (Fig. 1) and 0 (Fig. 2). Do not use magnifications  $> 100 \times$  and test different angles of light incidence.
- CS Cephalic size; arithmetic mean of CL and CW, used as a less variable indicator of body size.
- CW Maximum cephalic width; maximum in *Formica* is found either behind (larger specimens) or across eyes (smaller specimens).
- EYE Eye-size index: arithmetic mean of large (EL) and small diameter (EW) of elliptic compound eye.
- Full face view Dorsal aspect of head with both maximum CL and maximum CW in visual plane.

- Gena 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 row of setae immediately anterior of the hind tergite margin.
- nGU Unilateral number of setae protruding more than  $10 \mu\text{m}$  from underside of head (= "gula") as visible in lateral view.
- nHFFL Arithmetic mean of number of setae protruding more than  $10 \mu\text{m}$  from cuticular surface of flexor profile of hind femora.
- nMN Unilateral number of setae on mesonotum protruding more than  $10 \mu\text{m}$  from cuticular surface.
- nOCC With head in full face view, unilateral number of setae protruding more than  $10 \mu\text{m}$  from posterior margin of vertex and head sides anterior to level of anterior eye margin.
- nPE Unilateral number of setae protruding more than  $10 \mu\text{m}$  from margin of petiole scale dorsal of spiracle in caudal or frontal viewing position.
- nPN Unilateral number of setae protruding more than  $10 \mu\text{m}$  from cuticular surface of pronotum.
- nPRME Unilateral number of setae protruding more than  $10 \mu\text{m}$  from cuticular surface on propodeum and lateral metapleuron (excluding setae fringing metapleural gland orifice and those on ventrolateral edge of metapleuron).
- OceD Distance between inner margins of posterior ocelli.
- PEW Maximum width of petiole.
- PIGM Percent ratio of blackish or brownish pigmented surface of mesosoma excluding 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  $> 100 \times$  and test different angles of light incidence.
- RipD Average distance of transverse microripples on dorsal plane of first gaster tergite. At least three counts along a  $90 \mu\text{m}$  distance on different surface spots are averaged. Counting is performed at a magnification of 320  $\times$ . Use clean surfaces and light inclined perpendicular to ripples.
- Setae All stronger hairs having at least twice the basal diameter of neighbouring pubescence hairs (typical of *Serviformica* are  $3.5 \mu\text{m}$  diameter for pubescence and  $> 8 \mu\text{m}$  for setae)
- SL Maximum straight line scape length excluding 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 320  $\times$ . In each specimen 4 - 6 measuring-lines of  $400 \mu\text{m}$  are averaged under exclusion of surface parts with apparently detached pubescence.



Figs. 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. lusatica* showing the lower extreme of pigmentation contrast on genae (CONT = 0).

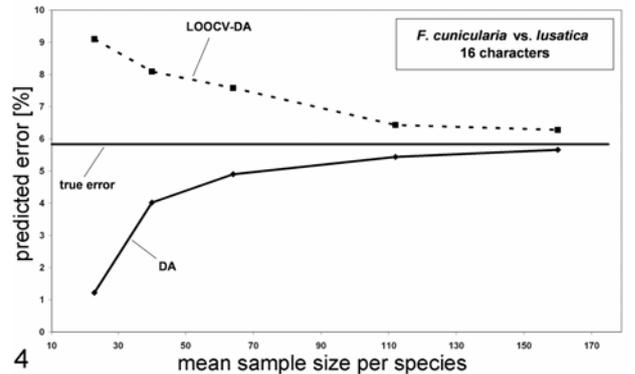
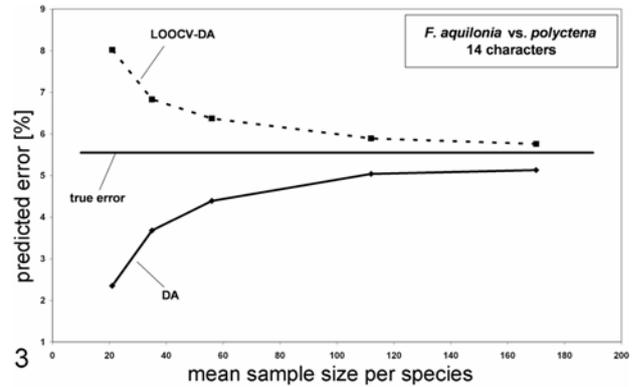
### Removal of allometric variance

In most species groups of *Formica*, body ratios are strongly influenced by allometric growth. In order to make body ratios such as CL / CW, SL / CS, EYE / CS or PEW / CS directly comparable in synoptic tables, a removal of allometric variance (RAV) was performed with the procedure described by SEIFERT (2008). RAV was calculated for the assumption of all individuals having an identical cephalic size of 1.4 mm. We applied group specific RAV functions the collective parameters of which were calculated as the arithmetic mean of the species-specific functions of *F. clarissima*, *F. litoralis*, *F. pamarica*, and *F. subpilosa*. Evaluation of scatter plots indicated the use of monophasic RAV functions. In order to avoid misindications in case of setae numbers close or equal to zero, all setae numbers were increased by 1. The RAV functions were

$$\begin{aligned} CL / CW_{1.4} &= CL / CW / (-0.0879 * CS + 1.2593) * 1.1363 \\ SL / CS_{1.4} &= SL / CS / (-0.1000 * CS + 1.1893) * 1.0493 \\ EYE / CS_{1.4} &= EYE / CS / (-0.0539 * CS + 0.3537) * 0.2783 \\ GH / CS_{1.4} &= GH / CS / (2.604 * CS + 7.036) * 10.681 \\ PEW / CS_{1.4} &= PEW / CS / (0.0935 * CS + 0.2946) * 0.4255 \\ Ocd / CS_{1.4} &= Ocd / CS / (0.0213 * CS + 0.1495) * 0.1793 \\ sqPDG_{1.4} &= sqPDG / (0.0323 * CS + 3.119) * 3.164 \\ RipD_{1.4} &= RipD / (0.630 * CS + 3.70) * 4.58 \\ nOCC_{1.4} &= (nOCC + 1) / (5.729 * CS - 4.29) * 2.73 \\ nGU_{1.4} &= (nGU + 1) / (1.57 * CS + 0.04) * 1.24 \\ nPN_{1.4} &= (nPN + 1) / (25.14 * CS - 10.78) * 23.42 \\ nMN_{1.4} &= (nMN + 1) / (16.33 * CS - 11.57) * 10.30 \\ nPRME_{1.4} &= (nPRME + 1) / (12.13 * CS - 8.83) * 7.16 \\ nPE_{1.4} &= (nPE + 1) / (7.70 * CS - 4.22) * 5.56 \\ nHFFL_{1.4} &= (nHFFL + 1) / (7.80 * CS - 2.75) * 7.16 \\ PIGM_{1.4} &= PIGM / (-22.32 * CS + 43.3) * 12.1 \\ CONT_{1.4} &= CONT / (-0.205 * CS + 0.37) * 0.087 \end{aligned}$$

### Discriminant analysis and error estimation

A canonical discriminant analysis (DA) was performed using the SPSS 10.0 statistical package based on sample means. All characters passed the tolerance test in a DA to the level of 0.01 as implemented by SPSS both when calculated as primary (crude) or as indexed data. The performance and reliability of a DA was assessed by the degree of coincidence of a-priori and a-posteriori-hypotheses (error rate) and by a statistics of a-posteriori-probabilities.



Figs. 3 - 4: Mean error indication of a discriminant analysis (DA) and a leave-one-out cross-validation discriminant analysis (LOOCV-DA) for worker individuals in (3) *Formica aquilonia* vs. *F. polyctena* and (4) *Formica cunicularia* vs. *F. lusatica*. Sets of smaller subsamples were generated by random combination with replacement in 50 runs for each subsample size. The true error was estimated from the source sample.

However, when sample size is small compared to the number of evaluated characters, an ordinary DA without cross-validation is biased toward the taxonomist's prejudice resulting in an optimistic error indication and in possibly wrong conclusions. We found, that a parallel run of the pessimistic "leave-one-out cross-validation" DA (LOOCV-DA, LACHENBRUCH & MICKY 1968, LESAFFRE & al. 1989) compensates for this erroneous indication. We compared the error indication of DA and LOOCV-DA in simulations with safely determined worker individuals in the species pair *Formica aquilonia* YARROW, 1955 (233 workers from 74 nest samples from the whole Palaearctic) and *Formica polyctena* FOERSTER, 1850 (144 workers from 45 West Palaearctic nest samples) and in the species pair *Formica cunicularia* LATREILLE, 1798 (189 workers from 65 West Palaearctic nest samples) and *Formica lusatica* SEIFERT, 1997 (189 workers from 63 West Palaearctic nest samples). Because of the large sample size of these source samples the error values of the DA and LOOCV-DA were identical and they were taken as an estimate of the true error. Five sets of subsamples were then generated from the source samples by random combination with replacement in 50 runs for each subsample size. Subsample size was 21, 35, 56, 112, and 170 workers for each species in the first species pair and 23, 40, 64, 112, and 170 in the second species pair. The data show that the means of the pessimistic deviation in the LOOCV-DA and the means of the opti-

mistic deviation of the ordinary DA from the true error have similar absolute values but different signs – i.e., the true error rate can be approximated quite accurately as the mean from both analyses (Figs. 3, 4).

### Geographic analysis of morphological distance

The morphological distance was analysed on the basis of sample means of the fifteen characters CS, CL / CW<sub>1,4</sub>, SL / CS<sub>1,4</sub>, GH1 / CS<sub>1,4</sub>, PEW / CS<sub>1,4</sub>, Ocd / CS<sub>1,4</sub>, sqPDG<sub>1,4</sub>, RipD<sub>1,4</sub>, nOCC<sub>1,4</sub>, nGU<sub>1,4</sub>, nPN<sub>1,4</sub>, nMN<sub>1,4</sub>, nPRME<sub>1,4</sub>, nPE<sub>1,4</sub>, and nHFFL<sub>1,4</sub>. For each possible intraspecific and heterospecific pair of samples, the overall morphological distance (OMD) and the square root of geographic distance (sqrtGD) were calculated. The morphological distance for a character was calculated as the linear distance divided by the arithmetic mean of the character-specific standard deviations of the compared species. OMD was then calculated as arithmetic mean of the fifteen character-specific distances. A regression analysis of OMD against sqrtGD was performed to indicate a possible convergence of morphological characters with falling geographical distance. A positive regression slope of OMD against sqrtGD in heterospecific pairings would indicate a cline and a possible degradation to subspecies status.

### Material

69% of the samples available from the *F. subpilosa* group was collected during our own expeditions to Central Asia in the years 1998 - 2001, 2003 - 2005. The provenance and composition of the *F. cinerea* and *F. rufibarbis* group samples, which are only used here as comparative group collectives and not as species, are summarised at the end of this section. Detailed collecting data are given here only for the species of the *F. subpilosa* group and are arranged as follows: locality, date, geographical coordinates in decimal format [in square brackets]. In samples without exact dates available, names of collectors are given to allow an approximate estimation of the collecting period.

***Formica (Serviformica) subpilosa* RUSZKY, 1902:** Forty-seven samples with 186 workers were subject to a numeric character analysis. **Afghanistan:** Kandahar-Kunar (7 samples), 18.I.1953, 20.I.1953, 22.I.1953, 30.I.1953, 7.II.1953, 17.II.1953, 7.XI.1953 [34.633° N, 70.900° E, coordinates estimated]; Khanabad, 27.VI.1953 [36.683° N, 69.117° E]; Sham-Shir-Ror, 14.I.1953 [31.617° N, 65.717° E]. **Azerbaijan:** Vataga Khurshud near Salyany, 20.III.1907 (No.3306, Karavajev) [39.500° N, 48.917° E], syntypes of *F. bipilosa*; Gobustan, IV.2006 [40.208° N, 49.250° E]; Mingacevir-E, 8.VI.2006 [40.822° N, 47.201° E]. **China:** Fukuong, VIII.1990 [44.133° N, 87.967° E, coordinates estimated]. Iran: Khoy, 24.VI.1973 [38.683° N, 45.133° E]. **Kazakhstan:** Chielii, 5.VII.2006 [44.229° N, 66.637° E]; Lepsy River, 18.VII.2001 [45.999° N, 79.673° E]; Karachingil at Mouth of Syr Darya (lectotype of *F. subpilosa*), 29.VI.1900 [46.06° N, 61.32° E, coordinates estimated]. **Kyrgyzstan:** Kanibadam, 23.VI.1963 [40.0° N, 70.5° E, coordinates estimated]; Osh (No. 143) 27.VII.1999 [40.536° N, 72.835° E]; Osh (No. 156), 28.VII.1999 [40.495° N, 72.768° E]; Kara Suu, 28.VII.1999 [40.710° N, 72.893° E]; Batken, 23.VII.2004 [40.062° N, 70.822° E]; Burgöndy, 31.VII.2004 [41.083° N, 72.353° E]; Dshalalabad, 16.VII.2004 [40.921° N, 72.955° E]; Isfara riv., 26.VII.2004 [39.879° N, 70.519° E]; Karavshin riv., 23.VII.

2004 [39.818° N, 70.565° E]; Karavshin riv., 23.VII.2004 [39.817° N, 70.565° E]; Karavshin riv., 24.VII.2004 [39.817° N, 70.564° E]; Karavshin riv., 24.VII.2004 [39.815° N, 70.564° E]; Karavshin vall. (5 samples No. 166, 167, 168, 169, 172), 26.VII.2004 [39.795° N, 70.494° E]; Karavshin vall. (2 samples No. 170, 171), 26.VII.2004 [39.795° N, 70.495° E]; Kyzyl-Kyja-E, 17.VII.2004 [40.303° N, 72.694° E]; Kyzyl-Kyja, 17.VII.2004 [40.304° N, 72.693° E]; Kyzyl-Kyja-E, 28.VII.2004 [40.243° N, 72.057° E]; Shamaldy-Say, 31.VII.2004 [41.119° N, 72.189° E]; Utsh-Korgon, 30.VII.2004 [40.243° N, 72.040° E]. **Tajikistan:** Pamir (coll. Forel) [38° N, 70° E, coordinates assumed]. **Turkey:** Kagizman, 18.VI.1996 [40.162° N, 43.115° E]. **Turkmenistan:** Imam Baba (3 samples pre 1909) [36.750° N, 62.467° E, coordinates estimated]. **Uzbekistan:** Kara Suu, 28.VII.1999 [40.780° N, 73.001° E].

***Formica (Serviformica) clarissima* EMERY, 1925:** Fifty-nine samples with 190 workers were subject to a numeric character analysis. China: Beishan NP, 25.V.1996 [36.978° N, 101.839° E]; Chaka (2 samples), 16.VI.1990, 29.VI.1998 [36.750° N, 99.100° E]. **Mongolia:** Shulut-Gol riv. (No. 232), 18.VIII.2003 [47.344° N, 103.684° E]; Shulut-Gol riv. (No. 233) 18.VIII.2003 [47.344° N, 103.683° E], Shulut-Gol (No. 236), 19.VIII.2003 [47.347° N, 103.684° E]; Shulut-Gol riv. (No. 241), 19.VIII.2003 [47.347° N, 103.685° E]; Oginuur lake (4 samples), 31.VII.2003 (No. 041), 01.VIII.2003 (No. 042, 043, 044) [47.786° N, 102.739° E]; Chovd (2 samples: No. 137, 138a), 08.VIII.2003 [48.048° N, 91.667° E]; sample No. 855, 15.VIII.1999 [48.067° N, 114.533° E]; sample No. 231, 05.IX.1997 [48.167° N, 103.700° E], samples No. 832, 834, 837, 14.VIII.1999 [48.300° N, 114.950° E]; Nar-Us-Nur lake, 06.VIII.2003, (3 samples: No. 124, 125, 126) [48.310° N, 92.556° E]; Nar-Us-Nur lake (2 samples: No. 127, 128), 06.VIII.2003 [48.311° N, 92.554° E]; Nar-Us-Nur lake S (2 samples: No. 174, 176), 12.VIII.2003 [47.753° N, 92.044° E]; Shine-Us-Nur lake (No. 120), 06.VIII.2003 [48.857° N, 92.329° E]; Shine-Us-Nur lake (121), 06.VIII.2003 [48.857° N, 92.330° E]; Arburd Sands, VI.2004 [46.983° N, 106.217° E]; Chara Obo (No. 197), 15.VIII.2003 [46.050° N, 46.798° E]; Chara Obo (2 samples: No. 196, 198), 15.VIII.2003 [46.050° N, 46.798° E]; Conocharajchijn-Gol (3 samples: No. 007a, 008b, 014b), 27.VIII.2002 [48.326° N, 92.807° E]; Elsen tasakhai, 20.VII.2003 (No. 315), 21.VII.2003 (4 samples: No. 398, 400, 401 and one without number), 22.VII.2003 (No. 316), 23.VII.2003 (4 samples: No. 317, 318, 320, 321) [47.389° N, 103.661° E]; Tuul riv. (2 samples: No. 028, 029), 30.VII.2003 [47.885° N, 105.179° E]; Tuul riv. (No. 030) 30.VII.2003 [47.885° N, 105.178° E]; Molt-sog els, 03.VII.2003 [47.750° N, 105.783° E]; Orchon (No. 026), 01.VII.2002 [50° N, 106° E, coordinates estimated]; Orchon (No. 027a), 01.VII.2002 [50.162° N, 106.173° E]; Orchon (No. 028), 01.VII.2002 [50.164° N, 106.176° E]; Orchon (No. 029), 01.VII.2002 [50.165° N, 106.175° E]; Orchon (No. 032), 01.VII.2002 [50.163° N, 106.174° E]; Orchon (No. 033b); 15.VII.2003 [50.161° N, 106.173° E]; Tola-Gol, 31.VII.2003 [47.886° N, 105.179° E]; Russia: Ortolky-NW, 27.VII.2000 [50.117° N, 88.317° E].

***Formica (Serviformica) litoralis* KUZNETZOV-UGAMSKY, 1926:** Eighty-two samples with 276 workers were subject to a numeric character analysis. **China:** Laohotai-N (No. 043), 05.VII.2006 [41.900° N, 81.218° E]; Laohotai-N (2 samples), 05.VII.2006 (No. 027a), 09.VII.2006 (No.

020) [41.879° N, 81.220° E]; Laohotai-N (No. 012), 06.VII.2006 [41.896° N, 81.208° E]; Terekmeikon-N (No.069), 10.VII.2006 [42.060° N, 81.513° E]; Terekmeikon-N (2 samples: No. 071, 082), 10.VII.2006 [42.055° N, 81.514° E]; Terekmeikon-N (No. 073), 10.VII.2006 [42.032° N, 81.529° E]; Terekmeikon-N (No. 047), 11.VII.2006 [42.043° N, 81.488° E]; Terekmeikon-N (No. 054), 11.VII.2006 [42.040° N, 81.490° E]; Terekmeikon-N (No. 055), 11.VII.2006 [42.039° N, 81.485° E]; Terekmeikon-N (No. 104), 11.VII.2006 [42.041° N, 81.481° E]; Terekmeikon-NW, 13.VII.2006 [42.010° N, 81.484° E]. **Kazakhstan:** Byshy riv., 18.VII.2001 [44.661° N, 78.041° E]. **Kyrgyzstan:** Talas vall., 27.VI.1963 [42.500° N, 72.333° E, coordinates estimated]; Kalinin, 17.IX.1970 [42.667° N, 73.783° E]; Naryn-W (2 samples: No. 018, 020), 16.VII.1999 [41.375° N, 75.622° E]; Naryn-W (No. 021), 16.VII.1999 [41.372° N, 75.601° E]; Naryn-W (No. 022), 16.VII.1999 [41.372° N, 75.600° E]; Naryn-W (No. 024), 16.VII.1999 [41.372° N, 75.599° E]; Naryn-W (No. 025); 17.VII.1999 [41.372° N, 75.602° E]; Naryn, 21.VII.2000 [41.496° N, 76.425° E]; Tash Bahat, 21.VII.2000 [41.500° N, 76.417° E]; Dshanatalab riv. (No. 108), 16.VII.2000 [41.633° N, 75.033° E]; Dshanatalab riv. (No. 015), 16.VII.2000 [41.636° N, 75.036° E]; Kysyl-Oyn (3 samples: No. 463, 464, 963), 01.VIII.1999 [41.987° N, 74.159° E]; Engylshek vall. (2 samples: No. 82, 272), 25.VII.2000 [42.067° N, 79.183° E]; Engylshek vall. (No. 108), 25.VII.2000 [42.067° N, 79.191° E]; Engylshek vall. (No. 106), 25.VII.2000 [42.066° N, 79.187° E]; Engylshek vall. (No. 118), 27.VII.2005 [42.039° N, 79.088° E]; Engylshek vall. (No. 119), 27.VII.2005 [42.040° N, 79.088° E]; Engylshek vall. (No. 120), 27.VII.2005 [42.039° N, 79.087° E]; Engylshek vall. (No. 137), 28.VII.2005 [42.123° N, 79.340° E]; Tonshi Saliv (2 samples: No. 081, 082), 23.VII.2000 [42.157° N, 77.063° E]; Tonshi Saliv (2 samples: No. 260, 268), 23.VII.2000 [42.150° N, 77.067° E]; Ottuk (4 samples: No. 43, 44, 193, 232), 22.VII.2000 [42.250° N, 76.200° E]; Ottuk (3 samples: No. 184, 244, 250), 22.VII.2000 [42.317° N, 76.317° E]; Ottuk (No. 065), 22.VII.2000 [42.317° N, 76.312° E]; Ottuk (No. 071), 22.VII.2000 [42.315° N, 76.313° E]; Ottuk (No. 072), 22.VII.2000 [42.318° N, 76.312° E]; Ottuk W (No. 061), 22.VII.2000 [42.384° N, 76.215° E]; Ottuk W (No. 063), 22.VII.2000 [42.384° N, 76.216° E]; Ottuk W (No. 064), 22.VII.2000 [42.367° N, 76.196° E]; Shety-Oguz (No. 087), 23.VII.2000 [42.347° N, 78.228° E]; Shety-Oguz (No. 252), 23.VII.2000 [42.350° N, 78.233° E]; Shu riv.; 15.VII.1999 [42.468° N, 75.878° E]; Karakol, 27.VII.2000 [42.500° N, 78.400° E]; Sholpon Ata (3 samples: No. 227, 228, 271), 30.VII.2000 [42.633° N, 77.067° E]; Ananevo (3 samples: No. 41, 251, 273), 29.VII.2000 [42.700° N, 77.683° E]; Ananevo (2 samples: No. 148, 150), 29.VII.2000 [42.710° N, 77.698° E]; At Bashy (2 samples: No. 036, 220), 17.VII.2000 [41.195° N, 75.735° E]; Kara Saz vall. (2 samples: No. 018, 019), 19.VII.2005 [41.718° N, 76.746° E]; Kitshy Naryn (2 samples: No. 028, 029), 20.VII.2005 [41.672° N, 76.469° E]; Kochkorka (2 samples: No. 010, 011), 18.VII.2005 [42.216° N, 76.755° E]; Yrдыk riv. 24.VII.2005 [42.385° N, 78.299° E]; Sary-Shaz, 25.VII.2000 [42.199° N, 79.119° E]; Soussamyrvall. (No. 011), 17.VII.1998 [42.200° N, 73.633° E]; Soussamyrvall. (2 samples: No. 013, 014), 17.VII.1998 [42.207° N, 73.625° E]; Chodsha-Ata, 26.VII.1998 [41.757° N, 71.973° E]; Tosor-E, 23.VII.2005 [42.155° N, 77.495° E].

***Formica (Serviformica) pamirica* DLUSSKY, 1965:** Thirty-six samples with 119 workers were subject to a numeric character analysis. China: Yengisar-N, 03.IX.2004 [42.125° N, 84.433° E]; Qisa (Cele), 26.VIII.1966 [37.033° N, 80.883° E]; Tarim, VIII.1966 [41.0° N, 80.0° E, coordinates estimated]; Turfan, VIII.1991 [43.0° N, 88.0° E, coordinates estimated]. Kyrgyzstan: Koshka-Su, 19.VI.1963 [39.550° N, 72.050° E, coordinates estimated]; Daroot Korgon S, 24.VII.1999 [39.468° N, 72.222° E]; Daroot Korgon, 24.VII.1999 [39.547° N, 72.168° E]; Kok-Suu (5 samples: No. 081 - 085), 22.VII.1999 [39.658° N, 73.835° E]; Kok-Suu (No. 087), 22.VII.1999 [39.662° N, 73.800° E]; Shak (2 samples: No. 108, 111b), 25.VII.1999 [39.552° N, 72.084° E]; Gyltshoe (2 samples: No. 130, 131), 26.VII.1999 [39.904° N, 73.426° E]; Gyltshoe (No. 132), 26.VII.1999 [39.904° N, 73.425° E]; Gyltshoe (No. 137), 27.VII.1999 [40.214° N, 73.479° E]; Gyltshoe (No. 142), 27.VII.1999 [40.245° N, 73.487° E]; Erkech-Tam (2 samples: No. 069, 070), 21.VII.1999 [39.694° N, 73.921° E]; Kalay-Machmyd, 22.VII.2004 [39.697° N, 70.871° E]; Shatkal vall. (5 samples: No. 110a, 114, 117 - 119), 28.VII.1998 [41.833° N, 71.195° E]; Tady-Suu S (No. 090), 23.VII.1999 [39.679° N, 72.961° E]; Tady-Suu S (2 samples: No. 092a, 094a), 23.VII.1999 [39.678° N, 72.961° E]; Terek Say (3 samples: No. 102 - 104), 27.VII.1998 [41.500° N, 70.878° E]. **Tajikistan:** Chorogski Tr. (paratype from holotype nest of *F. pamirica*), 11.VIII.1959 [38.5° N, 71.0° E, coordinates estimated]; Dshirga vall. (paratype of *F. pamirica*), 08.VIII.1939 [39.2° N, 71.2° E, coordinates estimated].

***Formica (Serviformica) kashmirica* STÄRCKE, 1935:** Only the type worker sample consisting of the holotype and two paratypes was available for investigation: **India:** Nubra Valley, 3000 m, 14. - 18.VII.1930 [34.73° N, 77.57° E].

#### **The pooled sample of the *Formica (Serviformica) cinerea* group**

The pooled sample of the *Formica cinerea* group consisted of 96 samples and eight forms / species. It was composed of three samples of *Formica corsica* SEIFERT, 2002 from Corsica; 37 samples of *Formica cinerea* MAYR, 1853, form 1 from Austria, Finland, Germany, Italy, Spain, Sweden, and Switzerland; 8 samples of *Formica cinerea*, form 2 from Poland, Romania, Russia, Slovakia, and Ukraine; 4 samples of *Formica cinerea*, form 3 from Bulgaria, Romania, and Ukraine; 37 samples of *Formica fuscocinerea* FOREL, 1874, form 1 from Austria, France, Germany, and Switzerland; 3 samples of *Formica fuscocinerea*, form 2 from Italy; 37 samples of *Formica georgica* SEIFERT, 2002 from Georgia; 4 samples of *Formica selysi* BONDROIT, 1918 from Austria, France, and Switzerland.

#### **The pooled sample of the *Formica (Serviformica) rufibarbis* group**

The pooled sample of the *Formica rufibarbis* group consisted of 430 samples and eight species. Species still undescribed are designated with code strings. The pooled sample was composed of 15 samples of *Formica clara* FOREL, 1886 from Azerbaijan, Cyprus, India, Iran, Lebanon, Pakistan, and Turkey; 65 samples of *Formica cunicularia* LATREILLE, 1798 from England, France, Georgia, Germany, Hungary, Italy, Kazakhstan, Russia, Turkey, and Ukraine; 34 samples of *Formica* sp. cun2 from China, Kazakhstan,

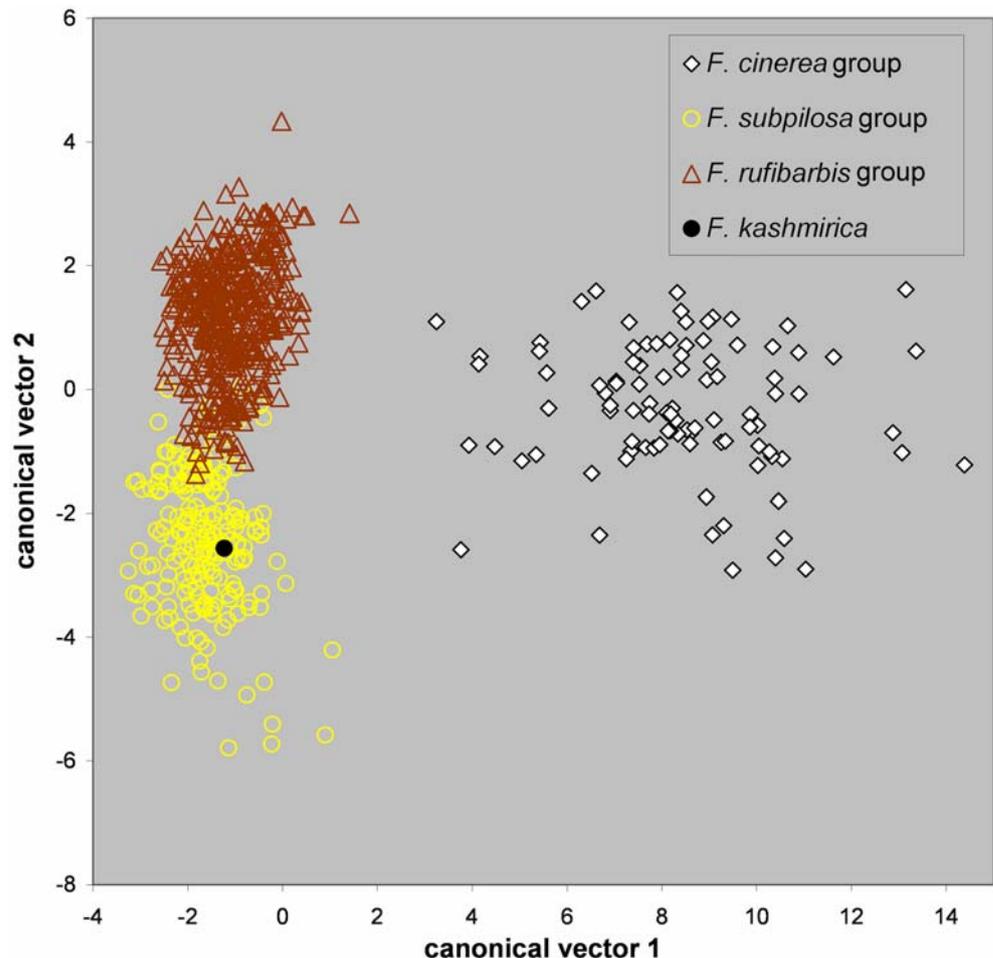


Fig. 5: Separation of pooled samples of the *F. cinerea* group (8 species / forms, 96 samples, white rhombs), the *F. rufibarbis* group (8 species / forms, 430 samples, empty, brown triangles) and *F. subpilosa* group (4 species, 200 samples, empty, yellow circles) in a discriminant analysis. Position of *F. kashmirica* black circle.

and Kyrgyzstan; 5 samples of *Formica* sp. cun3 from Iran; 181 samples of *Formica lusatica* SEIFERT 1997 from Bulgaria, China, Czech Republic, Finland, Georgia, Germany, Greece, Hungary, India, Iran, Italy, Kazakhstan, Kyrgyzstan, Netherlands, Pakistan, Russia, Slovakia, Slovenia, Switzerland, and Turkey; 25 samples of *Formica* sp. ORAN from Afghanistan, Iran, Kazakhstan, Kyrgyzstan, Mongolia, Switzerland, and Turkey; 34 samples of *Formica* sp. ORA2 from China; 181 samples of *Formica rufibarbis* FABRICIUS, 1793 from Austria, Bosnia, Bulgaria, Finland, France, Germany, Hungary, Kazakhstan, Sweden, and Switzerland; 13 samples of *Formica* sp. ruf2 from Turkey.

#### Acronyms of source collections of investigated material

coll.A.Schulz: collection of Andreas Schulz, Leverkusen, Germany  
 coll.R.Schultz: collection of Roland Schultz, Görlitz, Germany  
 MHN Genève: Muséum d'Histoire Naturelle Genève, Switzerland  
 NHM Basel: Naturhistorisches Museum Basel, Switzerland  
 SMN Görlitz: Staatliches Museum für Naturkunde Görlitz, Germany

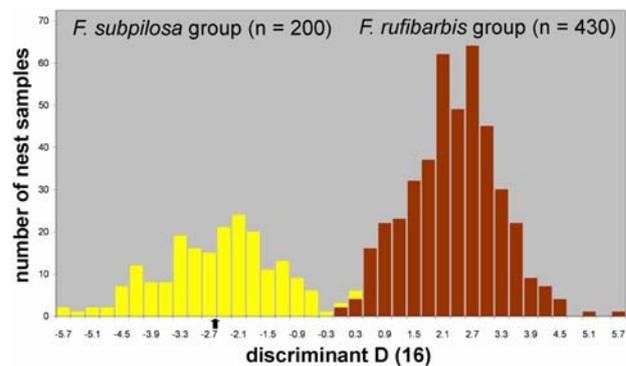


Fig. 6: Separation of pooled samples of the *F. subpilosa* group (4 species, 200 samples, yellow bars) and *F. rufibarbis* group (8 species / forms, 430 samples, brown bars). Position of *F. kashmirica* black arrow.

ZMLSU Moskva: Zoological Museum of the Lomonosov State University Moskva, Moscow, Russia  
 ZM Amsterdam: Zoological Museum Amsterdam, The Netherlands  
 ZMU Kiev: Zoological Museum of the University of Kiev, Ukraine

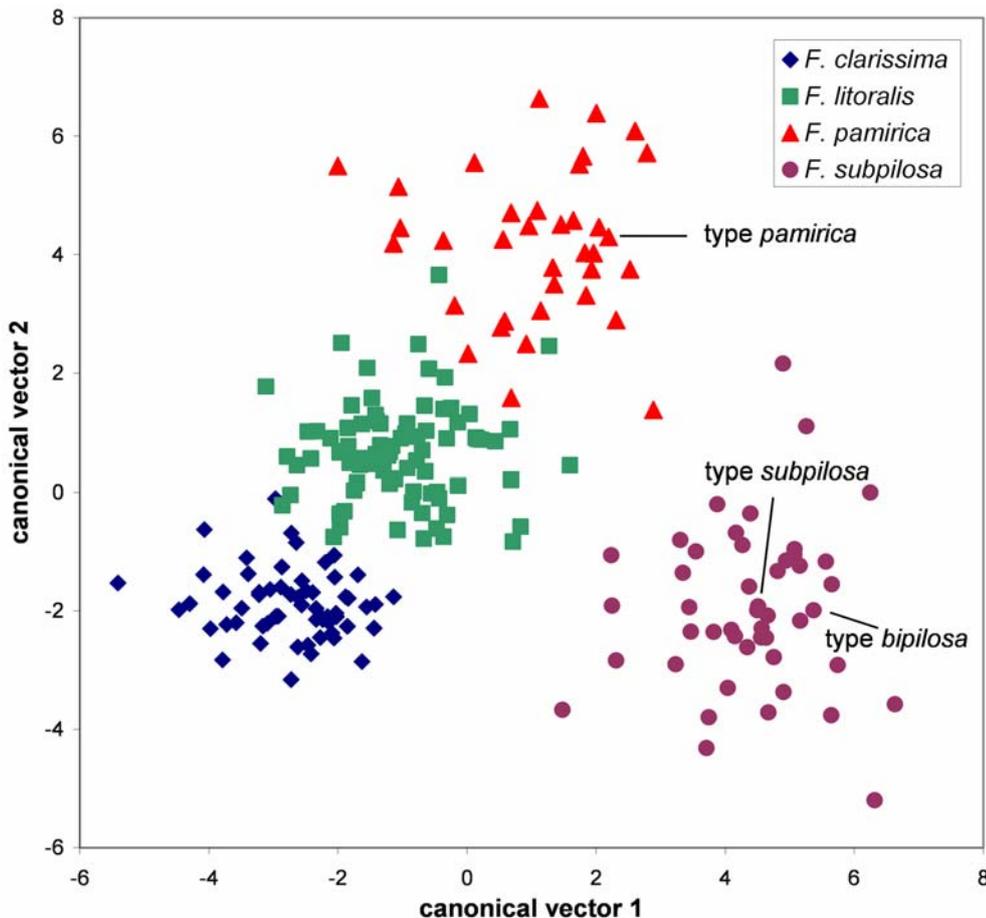


Fig. 7: Separation of *F. subpilosa* (circles) from *F. clarissima* (rhombs), *F. pamirica* (triangles) and *F. litoralis* (quadrats) in a discriminant analysis. Canonical vectors 1 and 2 describe 91.4% of variance.

## Results

### Complete morphological separation of the *F. cinerea*, *F. rufibarbis* and *F. subpilosa* groups by discriminant analysis

The separation of the *F. cinerea*, *F. rufibarbis*, and *F. subpilosa* species groups becomes already obvious when unselectively pooling all available samples of any species from the whole Palearctic. In a first step a discriminant analysis considering all three entities was run with uncorrected nest sample means of the eleven characters CS, CL / CW, SL / CS, PEW / CS, EYE / CS, GHL / CS, nOCC, nGU, nPRME, nPE, and nHFFL. Figure 5 shows that the 96 samples of the *F. cinerea* group are fully separated from the 201 samples of the *F. subpilosa* group and 430 samples of the *F. rufibarbis* group – the errors in both the DA and LOOCV-DA were 0%. However, the latter two groups are not fully separated with this character set: 3.3% misidentifications occur. To improve this situation, we ran a DA considering only these two groups with the uncorrected nest sample means of 16 characters, the above-mentioned 11 characters with the addition of these five: OceD, nPN, nMN, RipD, and sqPDG. This resulted in a clear separation (Fig. 6) with an error rate of only 0.5% both in the DA and LOOCV-DA. The conclusion from these data is that the proposed grouping within the subgenus *Serviformica* is real

and that the next relatives of the *F. subpilosa* group are the members of the *F. rufibarbis* group. This hypothesis should stand as long as a thorough investigation with adequate ncDNA marker genes would not come to other conclusions.

### Complete morphological separation of *F. subpilosa*, *F. clarissima*, *F. litoralis* and *F. pamirica* by discriminant analysis

As first step to discriminate within the *F. subpilosa* group, we ran a DA including all four entities and considering nest sample means of the 16 characters CS, CL / CW<sub>1.4</sub>, SL / CS<sub>1.4</sub>, PEW / CS<sub>1.4</sub>, GHL / CS<sub>1.4</sub>, nOCC<sub>1.4</sub>, nGU<sub>1.4</sub>, nPRME<sub>1.4</sub>, nPE<sub>1.4</sub>, nHFFL<sub>1.4</sub>, OceD / CS<sub>1.4</sub>, nPN<sub>1.4</sub>, nMn<sub>1.4</sub>, PIGM<sub>1.4</sub>, RipD<sub>1.4</sub>, and sqPDG<sub>1.4</sub>. Only *F. subpilosa* is clearly separated from the other three entities (Fig. 7) with an error rate of 0% in both the DA and LOOCV-DA. However, the DA failed to completely separate *F. clarissima*, *F. litoralis*, and *F. pamirica* – the optical separation in the graphics appears even worse because the first two canonical vectors describe only 91.4% of total variance. These more similar entities could be convincingly resolved in three two-class discriminant analyses. In each of these analyses, the error rate in the LOOCV-DA was 0% and the statistics of posterior probabilities (p) was as follows: 97.9% of all samples with  $p > 0.95$  in *F. clarissima* vs. *F. litoralis* (Fig. 8), 100% of

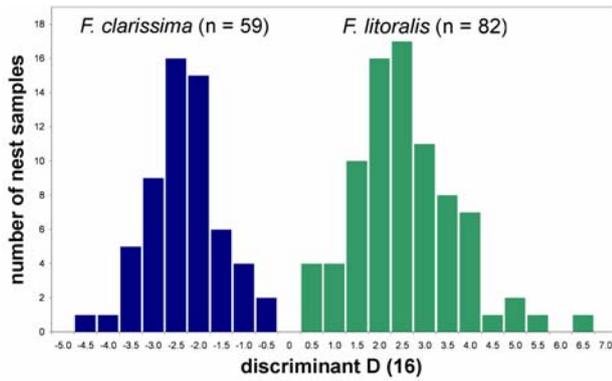


Fig. 8: Separation of *F. clarissima* (blue bars) from *F. litoralis* (green bars) in a discriminant analysis computing nest sample means of 16 RAV-corrected characters.

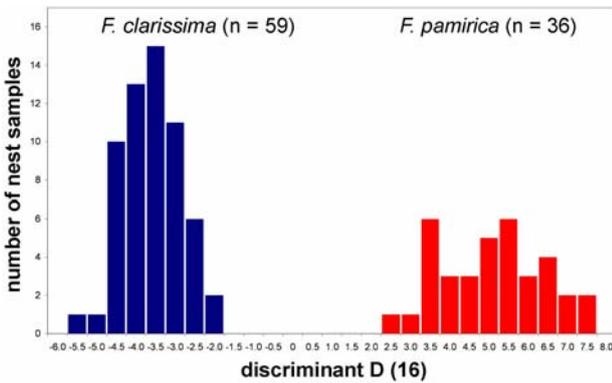


Fig. 9: Separation of *F. clarissima* (blue bars) from *F. pamirica* (red bars) in a discriminant analysis computing nest sample means of 16 RAV-corrected characters.

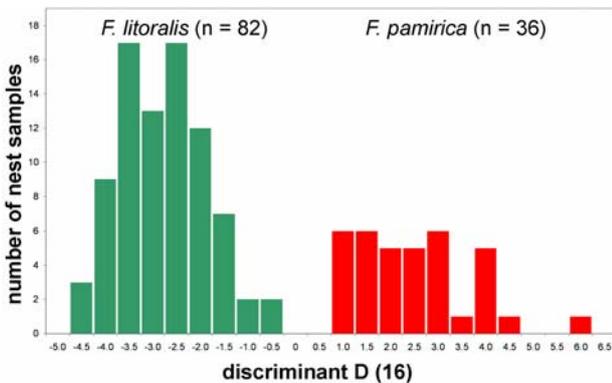


Fig. 10: Separation of *F. litoralis* (green bars) from *F. pamirica* (red bars) in a discriminant analysis computing nest sample means of 16 RAV-corrected characters.

the samples with  $p > 0.999$  in *F. clarissima* vs. *F. pamirica* (Fig. 9), and 98.3% of the samples with  $p > 0.95$  in *F. litoralis* vs. *F. pamirica* (Fig. 10). These data indicate three different morphospecies with *F. pamirica* and *F. litoralis* representing parapatric species while *F. clarissima* appears to be allopatric according to the information presently available (Figs. 11, 12).

### Interspecific morphological distance as function of geographic distance

*Formica pamirica*, *F. litoralis* and *F. clarissima* are most similar species which were considered as subspecies by

DLUSSKY (1967). Figure 11 shows that there is more or less a west-east array of these taxa and one of the referees of this paper asked if there was a cline between these entities. In other words, do these entities show convergence of morphology with increasing geographical proximity as it would be expected for subspecies? When the overall morphological distance, OMD, is plotted against the square root of geographic distance, sqrtGD, the situation between *F. litoralis* and *F. pamirica* is characterised by the following regressions ( $r$  = Pearson correlation coefficient,  $n$  = number of pairs):

*F. litoralis*, intraspecific  
 $OMD = 0.0045 * \text{sqrtGD} + 0.929$  ( $r = 0.1054$ ,  $n = 3291$ )

*F. litoralis* vs. *F. pamirica*  
 $OMD = -0.0010 * \text{sqrtGD} + 1.984$  ( $r = -0.0934$ ,  $n = 2952$ )

*F. pamirica*, intraspecific  
 $OMD = 0.0014 * \text{sqrtGD} + 1.030$  ( $r = 0.3115$ ,  $n = 630$ )

The situation between *F. clarissima* and *F. litoralis* is as follows:

*F. clarissima*, intraspecific  
 $OMD = 0.0075 * \text{sqrtGD} + 1.040$  ( $r = 0.2450$ ,  $n = 1711$ )

*F. clarissima* vs. *F. litoralis*  
 $OMD = -0.0009 * \text{sqrtGD} + 1.713$  ( $r = -0.0136$ ,  $n = 4838$ )

*F. litoralis*, intraspecific  
 $OMD = 0.0079 * \text{sqrtGD} + 1.015$  ( $r = 0.1659$ ,  $n = 2952$ )

For all intraspecific pairings, there is a morphological convergence with falling geographic distance as it would be expected for coherent populations of the same species. In both heterospecific contexts, the data suggest a slightly divergent morphology with falling geographic distance but this indication is unreliable for two reasons:

(1) Though the Pearson correlation coefficient given above would indicate a statistical significance of  $p < 0.0001$  for all except one of the regressions, its use in the context of such distance matrices is most problematic. Changing the position of one sample would change also the positions of  $n - 1$  other samples. The Pearson coefficient is likely to make much too optimistic indications.

(2) Credible analyses of clines must include plenty of closely neighbouring samples because steep hybrid gradients may occur within very narrow contact zones of parapatric species (SHAW & al. 1993, BUNO & al. 1994, SEIFERT 1995, BOZIKOVA & al. 2005, PUSCH & al. 2006, VÖRÖS & al. 2006). In the present case, a sufficient number of pairs with distances  $< 100$  km would be required, but the geographic distribution of samples does not match this condition: *F. litoralis* and *F. clarissima* are probably allopatric – the smallest distance between two samples of these species is 986 km which perfectly excludes a clinal analysis. In *F. pamirica* and *F. litoralis*, the situation is better but there are only 8 data pairs below the 100 km threshold formed by a single sample of *F. litoralis* and 8 samples of *F. pamirica*.

To conclude, there is some indication that the morphologies of *F. litoralis* and *F. pamirica* do not converge with falling geographic distance but only an adequate future sampling combined with a genetic analysis will help us to clearly answer this question.

### The diagnostic characters of *F. subpilosa*, *F. clarissima*, *F. litoralis*, and *F. pamirica*

The interspecific overlap of primary data in individual workers is so strong that the computation of nest sample means

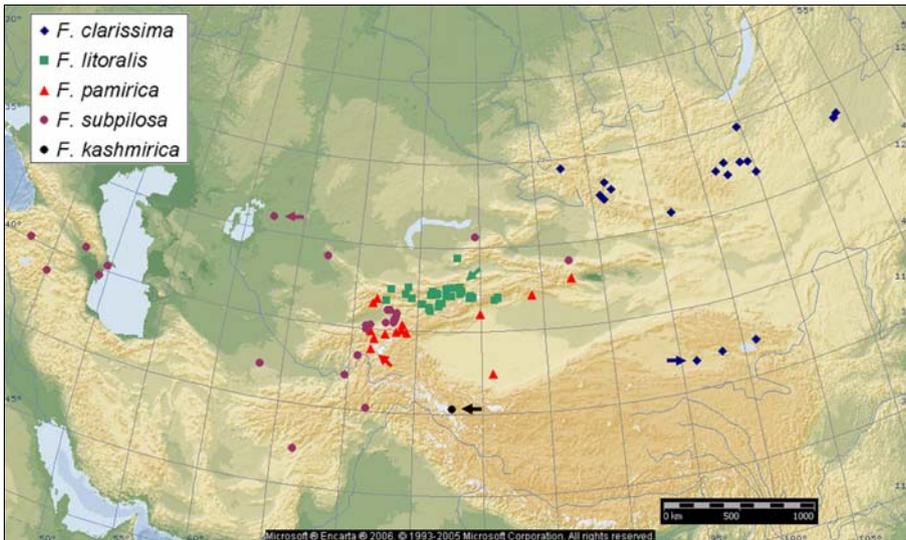


Fig. 11: Distribution map of the five species of the *Formica subpilosa* group in Asia. Arrows indicate type localities. Original map with permission of Microsoft®Encarta ©2006©1993-2005 Microsoft Corporation. All rights reserved.

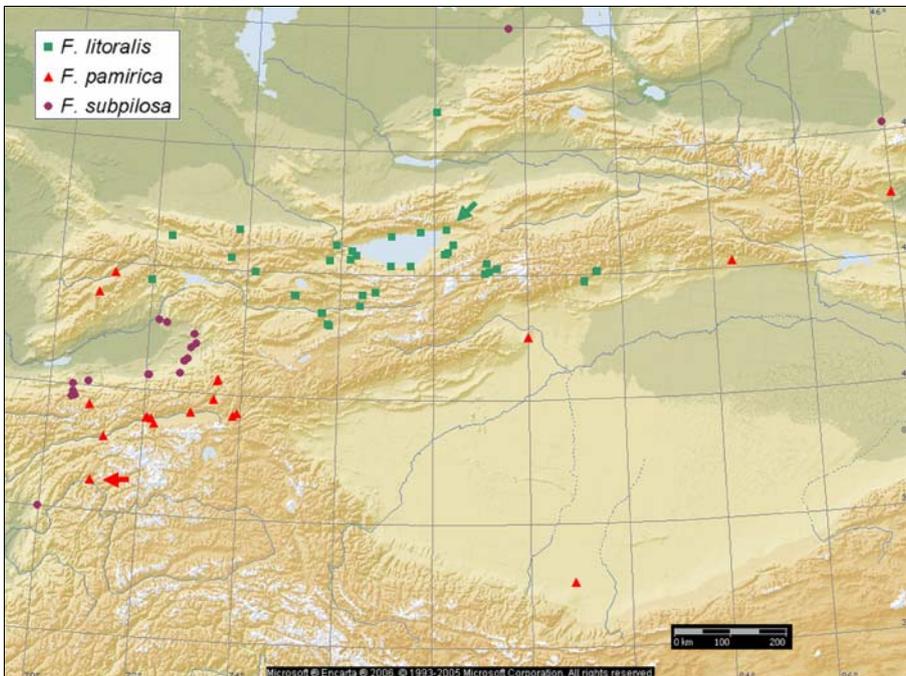


Fig. 12: Distribution map of the three Middle Asian species of the *Formica subpilosa* group. Arrows indicate type localities. Original map with permission of Microsoft®Encarta©2006©1993-2005 Microsoft Corporation. All rights reserved.

of uncorrected data and of nest sample means of RAV-corrected data is necessary to increase the resolution. Over all species and all 17 characters the computation of nest sample means of uncorrected data reduced the variance of data sets by 36% compared to individual workers, whereas the computation of RAV-corrected nest sample means compared to uncorrected nest sample means reduced the variance by a further 25%. Among the linear numeric data, the RAV-effect was 52% in EYE / CS, 22% in CL / CW, 19% in SL / CS, 8% in GH / CS, 7% in PEW / CS, 1% in RipD, and 0% in Ocd / CS and sqPDG. Tables 1 and 2 present the uncorrected and the RAV-corrected nest sample means.

*Formica subpilosa* deviates from the other three species by a combination of wider RipD and smaller Ocd / CS, PIGM, PEW / CS and larger CL / CW and SL / CS – in most cases this species does not cause difficult determination problems. The distinction of *F. clarissima*, *F. litoralis* and *F. pamirica* presents a real problem and is not possible by simple methods. It is tempting to use zoogeography as an easy solution but this would not help in contact zones. Furthermore, the branching outposts in the geographic range of *F. pamirica* (Figs. 11, 12) indicate a less simple distribution pattern. *Formica pamirica* is the most hirsute on any body part and has the narrowest petiole. *Formica clarissima* differs from *F. litoralis* by lower setae

Tab. 1: Nest sample means of morphological data of workers of the *Formica subpilosa* group. Arrangement of data: mean  $\pm$  standard deviation [minimum, maximum]. n = number of nest samples; CS, RipD and sqPDG given in  $\mu\text{m}$ .

	<i>F. pamirica</i> (n = 36)	<i>F. litoralis</i> (n = 82)	<i>F. clarissima</i> (n = 59)	<i>F. subpilosa</i> (n = 47)	<i>F. kashmirica</i> (n = 1)
CS	1313 $\pm$ 87 [1001, 1508]	1282 $\pm$ 100 [997, 1511]	1275 $\pm$ 87 [1093, 1453]	1378 $\pm$ 123 [1142, 1578]	1277
CL / CW	1.149 $\pm$ 0.018 [1.107, 1.184]	1.135 $\pm$ 0.017 [1.080, 1.165]	1.141 $\pm$ 0.022 [1.095, 1.186]	1.153 $\pm$ 0.018 [1.113, 1.187]	1.141
SL / CS	1.062 $\pm$ 0.020 [1.019, 1.108]	1.052 $\pm$ 0.022 [0.997, 1.096]	1.045 $\pm$ 0.025 [0.986, 1.106]	1.075 $\pm$ 0.022 [1.026, 1.115]	1.061
PEW / CS	0.405 $\pm$ 0.028 [0.351, 0.473]	0.430 $\pm$ 0.024 [0.367, 0.490]	0.435 $\pm$ 0.023 [0.383, 0.484]	0.391 $\pm$ 0.017 [0.345, 0.414]	0.435
EYE / CS	0.286 $\pm$ 0.008 [0.274, 0.306]	0.286 $\pm$ 0.007 [0.267, 0.303]	0.285 $\pm$ 0.007 [0.270, 0.300]	0.279 $\pm$ 0.007 [0.267, 0.296]	0.282
OceD / CS	0.183 $\pm$ 0.007 [0.166, 0.196]	0.180 $\pm$ 0.010 [0.163, 0.206]	0.181 $\pm$ 0.008 [0.164, 0.202]	0.165 $\pm$ 0.008 [0.144, 0.181]	0.185
GHL / CS [%]	11.36 $\pm$ 1.11 [8.57, 13.23]	10.41 $\pm$ 0.97 [8.36, 13.38]	8.41 $\pm$ 1.02 [6.73, 10.33]	11.29 $\pm$ 1.04 [9.00, 13.90]	8.20
nOcc	5.49 $\pm$ 3.33 [1.8, 13.3]	1.38 $\pm$ 0.99 [0.9, 4.1]	0.63 $\pm$ 0.49 [0.0, 2.3]	1.20 $\pm$ 1.29 [0.0, 7.5]	1.90
nGu	2.60 $\pm$ 1.28 [1.0, 5.7]	0.82 $\pm$ 0.59 [0.0, 3.8]	0.63 $\pm$ 0.41 [0.0, 1.9]	0.23 $\pm$ 0.35 [0.0, 1.5]	2.17
nPn	32.9 $\pm$ 5.5 [21.8, 48.8]	19.4 $\pm$ 3.9 [10.7, 27.2]	14.9 $\pm$ 3.4 [ 7.8, 22.2]	17.1 $\pm$ 6.6 [ 7.5, 37.8]	3.3
nMn	13.8 $\pm$ 3.4 [ 8.3, 19.2]	9.2 $\pm$ 2.5 [4.2, 15.7]	5.0 $\pm$ 2.0 [1.8, 10.2]	7.1 $\pm$ 3.6 [1.2, 17.7]	0.0
nPrMe	11.7 $\pm$ 3.1 [4.2, 18.8]	5.7 $\pm$ 2.2 [1.7, 13.5]	1.7 $\pm$ 1.1 [0.2, 4.8]	5.1 $\pm$ 2.8 [0.5, 15.3]	1.1
nPe	7.1 $\pm$ 1.7 [2.3, 10.9]	4.4 $\pm$ 1.2 [1.0, 8.0]	3.3 $\pm$ 1.2 [0.8, 6.0]	4.4 $\pm$ 1.6 [1.7, 10.5]	0.7
nHFFL	10.0 $\pm$ 2.9 [3.2, 16.3]	6.3 $\pm$ 1.3 [3.8, 9.3]	3.0 $\pm$ 1.3 [0.2, 7.2]	6.5 $\pm$ 2.2 [2.3, 13.0]	8.8
RipD	4.23 $\pm$ 0.18 [3.9, 4.6]	4.26 $\pm$ 0.37 [3.7, 5.2]	4.28 $\pm$ 0.27 [3.7, 4.9]	5.30 $\pm$ 0.38 [4.5, 6.7]	4.13
sqPDG	3.20 $\pm$ 0.14 [2.8, 3.6]	3.24 $\pm$ 0.11 [3.0, 3.5]	3.23 $\pm$ 0.15 [2.76, 3.52]	3.00 $\pm$ 0.14 [2.68, 3.25]	3.18
PIGM [%]	16.2 $\pm$ 9.3 [0, 40.0]	21.2 $\pm$ 14.8 [0, 65.0]	13.2 $\pm$ 10.4 [0, 66.3]	5.0 $\pm$ 6.0 [0, 22.7]	2.7
CONT	0.18 $\pm$ 0.13 [ 0.0, 0.58]	0.12 $\pm$ 0.12 [0.0, 0.60]	0.12 $\pm$ 0.15 [0.0, 1.00]	0.01 $\pm$ 0.03 [0.0, 0.16]	0.0

numbers, in particular on mesonotum, propodeum + lateral metapleuron and flexor profile of hind femur.

#### Key to the workers of the *F. (Serviformica) subpilosa* group

The highly complex methods of numeric morphology-based alpha-taxonomy (NUMOBAT) presented here are indis-

pensable for taxonomic fundamental research in which subjective guesswork cannot provide a solution. A practitioner, however, who is confronted during ecological or faunistic field work with thousands of samples and hundreds of species wants to have more simple methods. We have tried to find a less time-consuming determination method by strongly reducing the number of required characters and

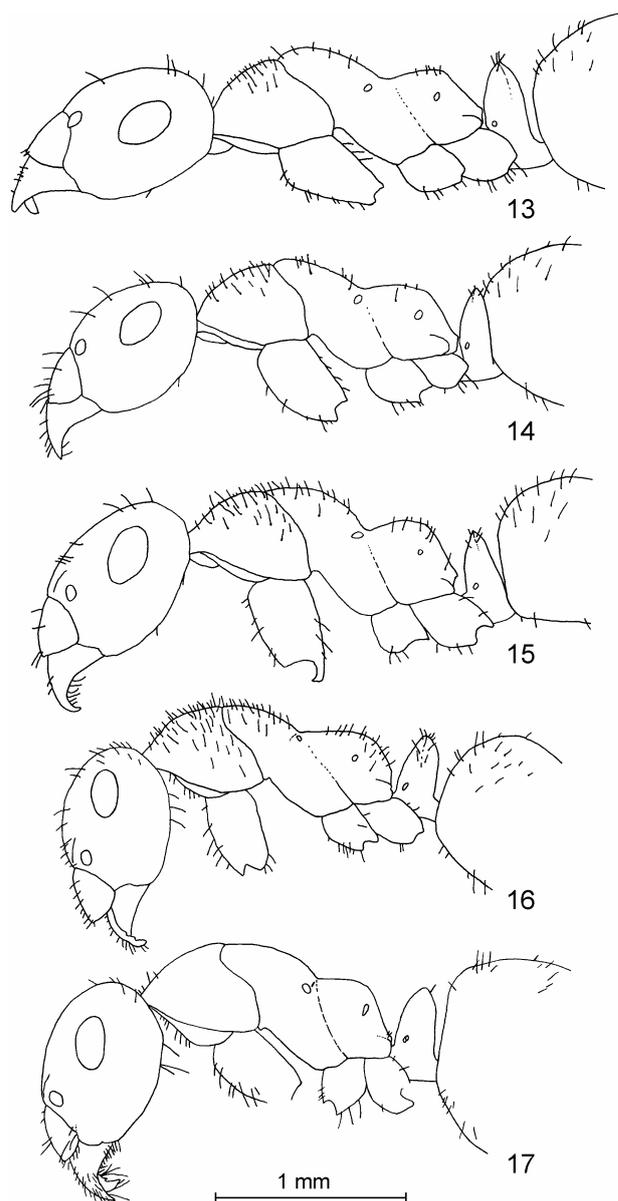
Tab. 2: RAV-corrected nest sample means of morphological data of workers of the *Formica subpilosa* group. All data indexed with "1.4" are corrected for the assumption that all specimens have an equal head size of CS = 1.4 mm. Arrangement of data: mean  $\pm$  standard deviation [minimum, maximum]. n = number of nest samples; CS, RipD and sqPDG given in  $\mu\text{m}$ .

	<i>F. pamarica</i> (n = 36)	<i>F. litoralis</i> (n = 82)	<i>F. clarissima</i> (n = 59)	<i>F. subpilosa</i> (n = 47)	<i>F. kashmirica</i> (n = 1)
CS	1313 $\pm$ 87 [1001, 1508]	1282 $\pm$ 100 [997, 1511]	1275 $\pm$ 87 [1093, 1453]	1378 $\pm$ 123 [1142, 1578]	1277
CL / CW <sub>1.4</sub>	1.141 $\pm$ 0.017 [1.109, 1.180]	1.125 $\pm$ 0.016 [1.071, 1.157]	1.131 $\pm$ 0.019 [1.088, 1.168]	1.151 $\pm$ 0.013 [1.125, 1.175]	1.130
SL / CS <sub>1.4</sub>	1.053 $\pm$ 0.019 [1.021, 1.111]	1.040 $\pm$ 0.019 [0.987, 1.077]	1.033 $\pm$ 0.022 [0.985, 1.086]	1.073 $\pm$ 0.020 [1.029, 1.114]	1.048
PEW / CS <sub>1.4</sub>	0.413 $\pm$ 0.024 [0.375, 0.471]	0.441 $\pm$ 0.021 [0.395, 0.498]	0.448 $\pm$ 0.021 [0.399, 0.499]	0.393 $\pm$ 0.019 [0.338, 0.438]	0.447
EYE / CS <sub>1.4</sub>	0.281 $\pm$ 0.006 [0.272, 0.296]	0.279 $\pm$ 0.004 [0.267, 0.292]	0.278 $\pm$ 0.005 [0.267, 0.290]	0.277 $\pm$ 0.005 [0.267, 0.287]	0.276
OceD / CS <sub>1.4</sub>	0.185 $\pm$ 0.006 [0.168, 0.198]	0.180 $\pm$ 0.010 [0.163, 0.206]	0.184 $\pm$ 0.009 [0.165, 0.207]	0.165 $\pm$ 0.008 [0.148, 0.184]	0.188
GHL / CS <sub>1.4</sub> [%]	11.39 $\pm$ 1.07 [8.82, 13.23]	10.44 $\pm$ 0.93 [8.50, 13.38]	8.61 $\pm$ 0.92 [7.23, 10.33]	11.28 $\pm$ 1.05 [9.00, 13.90]	8.36
nOcc <sub>1.4</sub>	5.45 $\pm$ 2.48 [2.5, 12.0]	2.12 $\pm$ 0.73 [0.9, 4.8]	1.53 $\pm$ 0.52 [0.8, 3.3]	1.66 $\pm$ 0.82 [0.8, 5.8]	2.50
nGu <sub>1.4</sub>	2.12 $\pm$ 0.71 [1.2, 4.0]	1.10 $\pm$ 0.34 [0.5, 2.6]	0.99 $\pm$ 0.26 [0.5, 1.7]	0.69 $\pm$ 0.19 [0.5, 1.4]	1.93
nPn <sub>1.4</sub>	35.9 $\pm$ 5.0 [28.7, 48.4]	22.3 $\pm$ 3.3 [12.0, 28.1]	17.5 $\pm$ 3.6 [9.7, 26.0]	17.6 $\pm$ 5.4 [8.7, 35.3]	4.8
nMn <sub>1.4</sub>	15.6 $\pm$ 3.3 [10.8, 24.2]	11.2 $\pm$ 1.8 [7.3, 15.6]	6.6 $\pm$ 2.0 [3.6, 12.0]	7.4 $\pm$ 2.7 [2.9, 15.8]	1.1
nPrMe <sub>1.4</sub>	12.8 $\pm$ 2.2 [6.9, 17.6]	7.0 $\pm$ 1.7 [3.9, 11.1]	2.9 $\pm$ 1.1 [1.0, 5.6]	5.5 $\pm$ 2.2 [2.0, 13.3]	2.2
nPe <sub>1.4</sub>	7.6 $\pm$ 1.2 [4.9, 9.5]	5.3 $\pm$ 1.0 [2.5, 7.8]	4.3 $\pm$ 1.1 [1.8, 7.3]	4.7 $\pm$ 1.2 [2.7, 9.2]	1.6
nHFFL <sub>1.4</sub>	10.5 $\pm$ 2.5 [4.3, 15.6]	7.2 $\pm$ 1.0 [5.1, 10.1]	3.9 $\pm$ 1.3 [1.3, 8.8]	6.6 $\pm$ 1.7 [2.8, 11.7]	9.9
RipD <sub>1.4</sub>	4.28 $\pm$ 0.18 [3.9, 4.6]	4.33 $\pm$ 0.36 [3.7, 5.3]	4.35 $\pm$ 0.28 [3.8, 5.0]	5.32 $\pm$ 0.37 [4.7, 6.8]	4.13
sqPDG <sub>1.4</sub>	3.20 $\pm$ 0.14 [2.9, 3.6]	3.25 $\pm$ 0.11 [3.0, 3.5]	3.23 $\pm$ 0.15 [2.76, 3.53]	3.00 $\pm$ 0.14 [2.68, 3.25]	3.19
PIGM <sub>1.4</sub> [%]	13.9 $\pm$ 7.9 [0, 31.6]	17.3 $\pm$ 11.7 [0, 56.0]	10.7 $\pm$ 8.2 [0, 55.8]	4.6 $\pm$ 5.4 [0, 18.5]	2.0
CONT <sub>1.4</sub>	0.15 $\pm$ 0.11 [0.0, 0.52]	0.10 $\pm$ 0.10 [0.0, 0.55]	0.10 $\pm$ 0.12 [0.0, 0.75]	0.00 $\pm$ 0.01 [0.0, 0.22]	0.0

using primary (absolute) data. The entry values in the key are arithmetic means of usually three workers per nest. The error estimations given in the discriminant functions refer to this sample size and our accuracy of data recording. To

reduce working time when using discriminant functions, we recommend beginning with one worker per sample and only extending the sample size when the resulting discriminant value is close to zero.

- 1a** Sum of setae numbers on dorsal mesosomal sclerites clearly larger than sum of setae on caudal margin and underside of head and flexor profile of hind tibia: ratio  $(nPN + nMN + nPRME) / (nOCC + nGU + nHFFL) > 2.1$ . Figures 13 - 16. .... **2**
- 1b** Sum of setae numbers on dorsal mesosomal sclerites not clearly larger than sum of setae on caudal margin and underside of head and flexor profile of hind tibia: ratio  $(nPN + nMN + nPRME) / (nOCC + nGU + nHFFL) < 2.1$ . Colour of mesosoma, coxae and petiole light reddish; head mainly reddish or infuscated on central and posterior vertex. Only type sample known. Figure 17. .... ***F. kashmirica***
- 2a** Colour of mesosoma usually clear reddish; head often mainly reddish, in smaller specimens infuscated on central and posterior vertex. Mean distance of transverse microripples on dorsum of first gaster tergite larger, RipD  $5.32 \pm 0.37 \mu\text{m}$ . Discriminant [0% error; insert RipD in  $\mu\text{m}$ ; SL, PEW, OceD in mm]:  $15.788 * SL - 45.689 * OceD - 11.55 * PEW + 2.624 * RipD - 18.035 > 0$ . .... ***F. subpilosa***
- 2b** Colour of mesosoma usually not clear reddish, with a stronger brown colour component, dark brown spots may be present; head not mainly reddish, usually notably infuscated on central and posterior vertex and in postocular region. Mean distance of transverse microripples on dorsum of first gaster tergite smaller, RipD  $4.33 \pm 0.30 \mu\text{m}$ . Discriminant [0% error; insert RipD in  $\mu\text{m}$ ; SL, PEW, OceD in mm]:  $15.788 * SL - 45.689 * OceD - 11.55 * PEW + 2.624 * RipD - 18.035 < 0$ . .... **3**
- 3a** Setae number on all body positions larger, nOCC 2 - 13, nPN 22 - 49. Discriminant [0% error; insert SL and PEW in mm]:  $2.122 * SL - 11.565 * PEW + 0.284 * nOCC + 0.166 * nPN - 1.762 > 0$ . .... ***F. pamirica***
- 3b** Setae number on all body positions lower, nOCC 0 - 4, nPN 8 - 27. Discriminant [0% error; insert SL and PEW in mm]:  $2.122 * SL - 11.565 * PEW + 0.284 * nOCC + 0.166 * nPN - 1.762 < 0$ . .... **4**
- 4a** Setae longer and more numerous: GHl 85 - 177  $\mu\text{m}$ , nPRME 1.7 - 13.5, nHFFL, nMN, nPN 10.7 - 27.2. Range west of 85° E. Discriminant [0.7% error; insert CW, GHl in mm]:  $52.971 * GHl + 0.302 * nPRME + 0.497 * nHFFL - 14.33 * CW + 7.195 > 0$ . .... ***F. litoralis***
- 4b** Setae shorter and less numerous: GHl 75 - 149  $\mu\text{m}$ , nPRME 0.2 - 4.8, nHFFL, nMN, nPN 7.8 - 22.2. Range east of 85° E. Discriminant [0.7% error; insert CW, GHl in mm]:  $52.971 * GHl + 0.302 * nPRME + 0.497 * nHFFL - 14.33 * CW + 7.195 < 0$ . .... ***F. clarissima***



Figs. 13 - 17: Lateral aspect of (13) *F. subpilosa*, (14) *F. clarissima*, (15) *F. litoralis*, (16) *F. pamirica* and (17) the holotype of *F. kashmirica*. Setae numbers in the first four species show the average situation.

#### Taxonomic treatment: descriptions, diagnoses, nomenclature, and biology

After presenting arguments for heterospecificity of the proposed entities, we treat in the following sections the formal taxonomic aspects and comment on biology and distribution. The basis of a name allocation is given in the taxonomic listing in square brackets. The text of labels is directly cited under inclusion of possible writing errors. Cyrillic letters are transliterated according to the US Library of Congress system.

#### Diagnosis of the *Formica (Serviformica) subpilosa* group

Within the Palaearctic members of the subgenus *Serviformica*, the *F. subpilosa* group is characterised by the following character combination: mesosoma between 40

to 100% reddish; moderate body size (nest means of CS 1.00 - 1.56 mm); moderate eye size (nest means of EYE / CS<sub>1.4</sub> 0.267 - 0.296); posterior margin and underside of head with a few setae at least (nest means of nOCC<sub>1.4</sub> 0.8 - 12.0, nGU<sub>1.4</sub> 0.5 - 4.0), mesosoma with few to numerous setae (nest means of nPN<sub>1.4</sub> 5 - 48, nMn<sub>1.4</sub> 1 - 24, nPRME<sub>1.4</sub> 2 - 18); petiole scale rather wide (nest means of PEW / CS<sub>1.4</sub> 0.338 - 0.499), with a broadly rounded or bluntly angulate dorsal crest; gaster tergites with a dense, usually silvery pubescence (sqPDG<sub>1.4</sub> 2.7 - 3.6) and with dense transverse microripples (RipD<sub>1.4</sub> 3.7 - 6.8), thus appearing completely matt at low magnifications. Range West to Central Asia. Thermophilic, found in open, sun-exposed habitats, but avoiding such with a dense grass or herb layer. Primary habitats are on alluvial soils along creeks and rivers, margins of lakes and other standing waters; halotolerant; has invaded rural or suburban areas. Monodomous to polydomous colonies with single to few queens. Simple, sometimes extended soil nests, rarely with a flat mound of mineral soil particles, frequently under stones. Predacious and trophobiotic.

***Formica (Serviformica) subpilosa* RUZSKY, 1902**

*Formica rufibarbis* ssp. *subpilosa* RUZSKY, 1902; Kazakhstan: Lake Aral [name allocation by type investigation]

*Formica cinerea* var. *bipilosa* KARAVAJEV, 1926; Caucasus: Vataga Khurshud [name allocation by type investigation]

**Type material examined:** *Formica subpilosa*: 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.)", ZMLSU Moskva. *Formica cinerea* var. *bipilosa*: 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], ZMU Kiev.

**Description of worker** (Figs. 11 - 13, Tabs. 1, 2): significantly larger than the four related species (mean CS 1.378 mm), head more elongated (CL / CW<sub>1.4</sub> 1.151), lateral ocelli more approached (OceD / CS<sub>1.4</sub> 0.165) and petiole narrower (PEW / CS<sub>1.4</sub> 0.393). Clypeus with fine longitudinal microcarinulae and sharp median keel. Frontal triangle finely transversely rippled and with 40 - 70 short pubescence hairs. Eyes with microsetae of 10 - 13 µm maximum length. Dorsal plane of scape without setae. Total mean of unilateral setae numbers on different body parts predicted for a specimen with CS = 1.4 mm: posterior margin of vertex 1.7, underside of head 0.7, pronotum 17.6, mesonotum 7.4, propodeum plus dorsolateral metanotum 5.5, petiole 4.7 (setae here only dorsal of spiracle), flexor profile of hind tibia 6.6. Ventral coxae and gaster tergites with long setae. Mesonotum in lateral aspect more slender and more constricted than in the four related species: shortest distance from bottom of metanotal groove to ventral mesosomal profile (near anterior corner of mesopleuron) 29 - 31% of mesonotopropodeal length. Profile formed by dorsal and caudodorsal propodeum more angulate in smaller and more convex in larger workers. Dorsal crest of petiole in frontal view convex to bluntly angled (approaching wedge-shaped). Petiole scale in lateral aspect rather thick, wedge-shaped, with convex anterior and

more straight posterior profile. Gaster with transverse microripples, their distance clearly larger than in the four related species (RipD 5.3 µm) and covered by dense silvery pubescence (sqPDG 3.0). 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.

**Comments, distribution and notes on biology:** In a DA, simultaneously considering the four entities *F. clarissima*, *F. litoralis*, *F. pamirica*, and *F. subpilosa*, the latter appears as a clearly separate cluster with an error rate of 0% (Fig. 7). The same DA also places the type series of *F. subpilosa* and *F. cinerea* var. *bipilosa* near to the centre of the *F. subpilosa* cluster with posterior probabilities of  $p = 1.000$  both in the DA and LOOCV-DA. This is fully supported by a subjective comparison of the type series. Hence we can confirm the synonymy of *F. subpilosa* and *F. cinerea* var. *bipilosa* which had already been stated in a verbal argumentation of DLUSSKY (1967).

An overview on the geographic distribution is given in Figs. 11 and 12, detailed site data in the section "Material". Compared to the related species, *F. subpilosa* is apparently more thermophilic, occurring in clearly lower altitudes and penetrating the true desert zone along moist river valleys or in oases. It is typical of 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). Altitudinal records: sea level to 1500 m a.s.l. (Turkestan Range, 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.

***Formica (Serviformica) clarissima* EMERY, 1925, stat.n.**

*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)] [name allocation by type investigation]

*Formica subilosa ruzskyi* DLUSSKY, 1965 [unnecessary replacement name for *F. rufibarbis* ssp. *subpilosa* var. *clarior* RUZSKY 1915]

**Type material examined:** *Formica clarissima*: 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 "Lectoergatotype F. subpilosa ruzskyi (Ruzk) Dluss.", ZMLU Moscow.

**Description of worker** (Figs. 11, 12, 14, Tabs. 1, 2): the smallest species of the *F. subpilosa* group (mean CS 1.275 mm), with the lowest number of setae on mesosoma and legs and shortest setae on dorsal plane of first gaster tergite within the group. Total mean of unilateral setae numbers on different body parts predicted for a specimen with CS = 1.4 mm: posterior margin of vertex 1.5, underside of head 1.0, pronotum 17.5, mesonotum 6.6, propodeum plus dorsolateral metanotum 2.9, petiole 4.3 (setae here only dorsal of spiracle), flexor profile of hind tibia 3.9. Clypeus with

sharp median keel and fine longitudinal microcarinulae. Frontal triangle with fine transverse ripples and short pubescence. Eyes with short microsetae (length max. 13  $\mu\text{m}$ ). Dorsal plane of scape without setae. Mesonotum relatively shorter: distance from anterior mesonotal to posterior propodeal margin 112.4% of CS (in 10 workers). Metanotal depression as shallow as in *F. pamirica*, shallower than in *F. subpilosa* and *F. litoralis*. Propodeal dome in profile more or less flat, especially in smaller workers. Dorsal crest of petiole in frontal aspect rounded, especially in larger workers bluntly angled. Petiole scale in lateral aspect rather slender, wedge-shaped, with convex anterior and more straight posterior profile. Gaster with transverse microripples, clearly more dense than in *F. subpilosa* (RipD 4.28  $\mu\text{m}$ ). Head, mesosoma, petiole and gaster covered with silvery pubescence, on gaster more dense (sqPDG 3.23). 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.

**Comments, distribution and notes on biology:** The lectotype from E Tsajdam is placed close to the cluster centre of *F. clarissima* with  $p = 1.000$  both by DA and LOOCV-DA. This data point is not depicted in Figure 7 because we received the type specimen after the proof corrections were finished. *Formica clarissima* is the species with the most eastern distribution (Fig. 11) and can be considered as an allopatric sister species of *F. litoralis*. We have so far no information if there exists a direct contact zone of both species somewhere east of the Tian Shan. The habitat selection of this species shows similarities to that of *F. litoralis* and *F. pamirica*. B. Pisarski (cited in DLUSSKY 1967) found the nests on rubble soils or sand banks of flooding terraces along the river Kergulen / Mongolia. RS 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 on salty semidesert soil; higher shrubs or trees were frequently absent from these sites. Alate gynes were found within the nests on 6 August 2003 (lakes Shine Us Nur and Nar Us Nur) and on 15 August 2003 (semidesert W of mount Chara Obo). Altitudinal records: 900 m to 2700 m a.s.l. (Eastern Zaidam, RUZSKY 1914).

***Formica (Serviformica) litoralis* KUZNETZOV-UGAMSKY, 1926, stat.n.**

*Formica subpilosa* ssp. *litoralis* KUZNETZOV-UGAMSKY, 1926; Lake Issyk-Kul: village Kurminty [name allocation by description of DLUSSKY (1967) and zoogeography.]

**Type material of *Formica litoralis*:** According to DLUSSKY (1967) there should exist a lectotype worker either in the collection of St. Petersburg or Moscow with the supposed labelling "neogergatotyp: s. Kurminty, severovostochnij bereg osera Issyk Kul, leg. Dlussky". This material was not available for investigation.

**Description of worker** (Figs. 11, 12, 15, Tabs. 1, 2): rather small (mean CS 1.282 mm), with least elongated head (CL / CW<sub>1.4</sub> 1.125). Clypeus with sharp median keel and fine longitudinal microcarinulae. Frontal triangle with

fine transverse ripples and short pubescence. Eyes with short microsetae of 10 - 13  $\mu\text{m}$  maximum length. Dorsal plane of scape without setae. Setae numbers on different body parts between *F. clarissima* and *F. pamirica*; total mean of unilateral setae numbers predicted for a specimen with CS = 1.4 mm: posterior margin of vertex 2.1, underside of head 1.1, pronotum 22.3, mesonotum 11.2, propodeum and dorsolateral metanotum 7.0, petiole 5.3 (setae here only dorsal of spiracle), flexor profile of hind tibia 7.2. Gaster tergites and ventral coxae with long setae. Mesonotopropodeal length intermediate between *F. clarissima* and *F. pamirica*: distance from anterior mesonotal to posterior propodeal margin 114% of CS (in 10 workers). Metanotal depression deeper than in *F. pamirica* and *F. clarissima* (8.7% of CS). Propodeal dome steeper than in *F. clarissima* and *F. pamirica*, more strongly developed in larger workers. Dorsal crest of petiole in frontal view convex, rarely straight or with flat median emargination. Petiole scale in lateral aspect wedge-shaped with convex anterior and more or less straight posterior profile. Gaster with transverse microripples, their distance similar to *F. clarissima* (RipD 4.26  $\mu\text{m}$ ). Whole body covered by silvery pubescence, somewhat more 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.

**Comments, distribution and notes on biology:** Our feeling that DLUSSKY (1965, 1967) most probably did not confuse species of the *F. rufibarbis* and *F. subpilosa* group, his brief descriptive statements and our observation that there was only one species of the *F. subpilosa* group present at the type locality of *F. litoralis* at the northeastern shores of Lake Issyk-Kul, give us hope for a stable nomenclature, should the lectotype eventually be rediscovered by later revisors.

Figure 12 gives the geographical distribution of *F. litoralis*. DLUSSKY (1967) and TARBINSKY (1976) erroneously reported this species also from the western Tian Shan. However, our discriminant analyses have shown that all samples west of the Soussamyr valley belonged to *F. pamirica*. 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 peak, 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 colonies 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 if his observations referred to *F. litoralis* or *F. pamirica* or to both species. According to our direct observations on fine-scale nest distribution, both species 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.

DLUSSKY (1967) assumed a later development of alates than in *F. pamirica*: *F. litoralis* nests in the valley of

the river Gulchi at 1700 m contained only larvae during 15 - 16 June 1963, while the nuptial flight of *F. pamirica* in the Alai Valley at 2600 - 3200 m was already finished at the same time. This assumption is not directly confirmed by TARBINSKY (1976) who reported flights of *F. litoralis* in Kyrgyzstan for 16 June at 1600 m and 8 July at 2300 m. We cannot clarify this question because all our expeditions took place after June. We found alates on 17 July 1998 (males within a nest in the Soussamyr valley), 23 July 2000 (alate gynes in a nest near Dsheti Orgus / Inner Tian Shan) and 26 July 2000 (one alate gyne in a yellow bowl). Altitudinal records: 740 m (Byshy river, Kazakhstan) to 2800 m a.s.l. (Central Tian Shan, Kyrgyzstan).

***Formica (Serviformica) pamirica* DLUSSKY, 1965, stat.n.**

*Formica subpilosa pamirica* DLUSSKY, 1965; West Pamirs [name allocation by type investigation]

**Type material examined:** *Formica pamirica*: 1 paratype worker and 1 paratype gyne from the same nest as the holotype, labelled "Khorogski trakt, Darvazski Khrebet, 11.VIII. 59, A.Rasnizyn." and "Paratype *F. subpilosa pamirica* Dlussky"; 5 paratype workers labelled "Dzhirgatal' Tadzhik. 8.VIII.1939, O.Kryzhanovskij" and "Paratype *F. subpilosa pamirica* Dlussky"; all in ZMLSU Moskva.

**Description of worker** (Figs. 11, 12, 16, Tabs. 1, 2): slightly larger than *F. litoralis* (mean CS 1.313 mm), head elongated (CL / CW<sub>1.4</sub> 1.149), lateral ocelli widely distant (OceD / CS<sub>1.4</sub> 0.185) and petiole relatively narrow (PEW / CS<sub>1.4</sub> 0.413). Most hirsute species of the *F. subpilosa* group – total mean of unilateral setae numbers on different body parts predicted for a specimen with CS = 1.4 mm: posterior margin of vertex 5.5, underside of head 2.2, pronotum 35.9, mesonotum 15.6, propodeum and lateral metanotum 12.8, petiole 7.6 (setae here only dorsal of spiracle), flexor profile of hind tibia 10.5. Ventral coxae and gaster tergites with long setae. Clypeus with sharp median keel and fine longitudinal microcarinulae. Frontal triangle finely transversely rippled and with short pubescence hairs. Eyes with microsetae of 12 - 16 µm maximum length. Dorsal plane of scape sometimes with semierect pubescence hairs. Depth of metanotal depression rather low (8.3% of CS), mesonotopropodeal length longer than in *F. clarissima* and *F. litoralis*: distance from anterior mesonotal to posterior propodeal margin 116% of CS (in 10 workers). Dorsal propodeal profile flatter than in *F. litoralis*: curvature formed by base and declivity angulate to convex. Dorsal crest of petiole in frontal aspect convex to bluntly angled, sometimes straight. Petiole scale in lateral view thicker than in *F. litoralis*, with convex anterior and slightly convex posterior profile. Gaster with transverse microripples, their distance distinctly lower than in *F. subpilosa* (RipD 4.23 µm). Pubescence on gastral tergites dense and silvery (sqPDG 3.2) but on mesosoma and head of average *Serviformica* condition. Colour similar to *F. clarissima* and *F. pamirica*. Mesosoma usually reddish with dark brown patches on dorsum and metapleuron (in the types concolourous reddish). Vertex, coxae, all appendages and petiole in most cases brown to dark brown (sometimes lighter with a reddish tinge), gaster always dark brown.

**Comments, distribution and notes on biology:** The geographical distribution of *F. pamirica*, which can be con-

sidered as a parapatric sister species of *F. litoralis*, is given in Figures 11 and 12. Originating from its compact distributional centre in West Tian Shan and Pamirs, *F. pamirica* moved east some 1100 km along the whole southern slope of Tian Shan and obviously it also moved southeast along the northern slope of the Karakorum Mountains to Kunlun Shan. One collecting site along the south Tian Shan route (labelled only "Tarim VIII 66 China HH") is a very rough estimation. It was assumed to be a point next to the Tian Shan Mountains where the stream begins to bear the name Tarim. Along the South Tian Shan, *F. pamirica* should be in contact with *F. litoralis*, but unfortunately there were no further samples available to us from this region, just as there were no samples from the putative contact zone in the West Tian Shan. The collecting point in the southern Tarim Basin, labelled "Tarim Basin: Ceele Station 1966-08-26", refers to Qira (Cele) oasis on the northern foothills of Kunlun Shan. The real collecting point is probably south of the oasis up in the mountains.

The ecology of *F. pamirica* most probably is very similar to that of *F. litoralis* (see there). According to TARBINSKY (1976), a significant percentage of the diet of *F. pamirica* is arthropods stranded at the margins of rivers. The same most certainly applies to *F. litoralis* and *F. clarissima*.

A relocation of a *Formica pamirica* colony from a grassy site above the mean flooding level down to the river was observed by RS 27 July 1998. Workers transported pupae and dealate gynes (at least 3) along a trail of about 50 m in the late afternoon. The target nest was established below some *Salix* bushes. Next morning no further relocation activities could be observed. The cause of this colony moving is possibly avoidance of ant competitors better adapted to grassy habitats and occupation of a space free of such competitors. On the Kok-Suu River in the upper Alai Valley large soil nests were constructed in sand and below stones at the edge of the average flooding level. Up to five dealate gynes could be observed within these nests. Altitudinal records: 1500 m (Tian Shan north of Yengisar, China) to 3200 m a.s.l. (upper Alai valley, Kyrgyzstan).

***Formica (Serviformica) kashmirica* STÄRCKE, 1935, stat.n.**

*Formica rufibarbis* var. *kashmirica* STÄRCKE, 1935; India: Kashmir [name allocation by type investigation]

**Type material examined:** 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 "PARATYPE *Formica (Serviformica) rufibarbis rufibarbis* var. *kashmirica* 1933 Stärcke"; 2 paratype workers, 1 paratype male and 1 alate paratype gyne, each on a different pin, 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.

Note: There are also further specimens with the same printed paratype labels in ZM Amsterdam: a series of 6 damaged workers from "Nubra Valley 3700 m 7-26 VI. 1929" and 1 damaged worker from "4125 m 20-26.VI. 1929", "Tehrong valley near Siachen gletscher". Completely missing scapes and ablations of setae and pubescence do not

allow a conclusive determination but most probably these specimens belong to a species of the *F. rufibarbis* group.

**Description of worker** (Fig. 17, Tabs. 1, 2), type series: head moderately elongated (CL / CW<sub>1.4</sub> 1.141), lateral ocelli more distant than in *F. subpilosa* (OceD / CS<sub>1.4</sub> 0.185) and petiole wider (PEW / CS<sub>1.4</sub> 0.435). Clypeus with very fine longitudinal microcarinulae and sharp median keel. Frontal triangle finely transversely rippled and with 40 - 50 short pubescence hairs. Eyes with microsetae of 10 - 14 µm maximum length. Dorsal plane of scape in the two larger workers with single semierect seta, frontal edge of scape with 5 - 7 semierect setae (if repeated in other samples, a clear difference from all related species). Total mean of unilateral setae numbers on different body parts predicted for a specimen with CS = 1.4 mm: posterior margin of vertex 2.5, underside of head 1.9, pronotum 4.8, mesonotum 1.1, propodeum plus dorsolateral metanotum 2.2, petiole 1.6 (setae here only dorsal of spiracle), flexor profile of hind tibia 9.9 (long setae!). Ventral coxae and gaster tergites with long setae. Depth of metanotal depression rather deep (8.9% of CS); profile formed by dorsal and caudodorsal propodeum more convex than angulate. Petiole scale in frontal view wide, reaching its largest width in upper third, with slightly convex sides, dorsal crest only slightly convex (almost straight). Gaster with transverse microripples, their distance clearly smaller than in *F. subpilosa* (RipD 4.1 µm), covered by dense silvery pubescence (sqPDG 3.2) and with a number of long and tapering setae, GHL / CS 8.2%. Colour pattern most similar to *F. subpilosa*: mesosoma, coxae, all appendages and petiole yellowish red; in holotype, whole head yellowish red, in paratypes, frons and posterior vertex infuscated. Gaster medium brown with red tinge, frontal face of first tergite in two specimens yellowish red.

**Comments, distribution and notes on biology:** This species, known only by the type series, is clearly not a species of the *F. rufibarbis* group but clusters in a DA in the centre of the *F. subpilosa* group: the squared Mahalanobis distance from the centroid is only 0.194 in a DA against the *F. cinerea* and *F. rufibarbis* group (Fig. 5) and 0.092 in a DA only against the *F. rufibarbis* group (Fig. 6). 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. There is no information on habitat and biology – the actual landscape picture of the type locality is an open, treeless mountain valley with a river and alluvial soils.

#### Acknowledgements

We wish to thank Alexander Radchenko (Kiev, Ukraine), Ivan Löbl (Geneva, Switzerland), Alexander Antropov (Moscow, Russia), Rob de Vries (Amsterdam, The Netherlands), Martin Pfeiffer (Ulm, Germany), Karla Schneider (Halle, Germany), Ilja Kabak (St. Petersburg, Russia), Andreas Schulz (Leverkusen, Germany), Cedric Collingwood (Skipton, UK), Harold Heatwole (Raleigh, USA), Gerd Müller-Motzfeld, Jonathan Etzold, Thomas Büchner, and Peter Michalik (all Greifswald, Germany) for providing material. We are also indebted to the two (non-anonymous) referees, Sandor Czósz and James Trager, for critically

reading the manuscript and the latter in particular for making linguistic improvements.

#### Zusammenfassung

Die Angehörigen der west- bis zentralasiatischen *Formica subpilosa*-Gruppe wurden mittels numerischer, morphologiebasierter Alpha-Taxonomie (NUMOBAT) untersucht. 18 phänotypische Merkmale wurden anhand von 201 Nestproben mit 591 Arbeiter-Individuen beschrieben. Es wurden fünf Morphospezies unterschieden: *Formica subpilosa* RUZSKY, 1902, *F. litoralis* KUZNETZOV-UGAMSKY, 1926, *F. clarissima* EMERY, 1925, *F. pamirica* DLUSSKY, 1965 und *F. kashmirica* STÄRCKE, 1935. Eine Leave-One-Out Cross-Validation-Diskriminanzanalyse (LOOCV-DA) trennte die ersten vier Arten mit einer Fehleranzeige von 0 % und platzierte alle verfügbaren Typenserien mit a-posteriori-Wahrscheinlichkeiten von  $p = 1.000$  in die Nähe der Clusterzentren. Die Artverschiedenheit von *Formica kashmirica*, die nur durch die Typenserie vertreten war und somit in einer DA nicht sinnvoll testbar war, wird durch eine bei keiner der anderen Arten gefundene Merkmalskombination gerechtfertigt. *Formica litoralis*, *F. clarissima*, *F. pamirica* und *F. kashmirica* werden in den Artstatus erhoben. *F. litoralis* und *F. pamirica* sind parapatrische Zwillingsspezies, die anscheinend keine morphologische Konvergenz mit abnehmendem geographischen Abstand zeigen – die Frage einer möglichen Hybridisierung in Kontaktzonen kann mit dem vorhandenen Datenmaterial nicht beantwortet werden. *Formica cinerea* var. *bipilosa* KARAVAJEV, 1926 wurde als jüngerer Synonym von *F. subpilosa* bestätigt. Die Auftrennung der paläarktischen, rote Pigmentierung aufweisenden *Serviformica*-Arten in eine *Formica cinerea* MAYR, 1853-, eine *F. rufibarbis* FABRICIUS, 1793- und eine *F. subpilosa*-Gruppe wurde durch eine Diskriminanzanalyse bestätigt. Alle Arten werden abgebildet und ein vereinfachter Bestimmungsschlüssel wird präsentiert. Die Arten der *F. subpilosa*-Gruppe bevorzugen Habitate mit spärlich bewachsenen und besonnten Böden alluvialen, limnischen oder aeolischen Ursprunges. Sie nehmen in der Zentralpaläarktis die gleiche ökologische Position ein, die die *F. cinerea*-Gruppe in der Westpaläarktis innehat.

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