

The "Black Bog Ant" *Formica picea* NYLANDER, 1846 – a species different from *Formica candida* SMITH, 1878 (Hymenoptera: Formicidae)

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Abstract

According to morphometrical and genetical evidence, the ant taxa collected by BOLTON (1995) under the name *Formica candida* SMITH, 1878 can be divided into a minimum of two different species with separate zoogeography. The well-known "Black Bog Ant" – distributed over Europe, the Caucasus and the West Siberian Lowland – is identified as *Formica picea* NYLANDER, 1846, but the species found in all Central Asian mountains north to the Gorno-Altai region, in Tibet, Mongolia, the Baikal region and East Siberia is redescribed as *Formica candida* SMITH, 1878 under fixation of a neotype. According to article 23.9.5. of the 4th edition of ICZN (1999), the name *Formica picea* NYLANDER, 1846 (a junior primary homonym of *F. picea* LEACH, 1825) needs not be replaced by one of its junior synonyms. This rule is most appropriate, considering the fact that *F. picea* LEACH is in *Camponotus* MAYR since 1861 and will never return to *Formica*; this application ends the confusing to-and-fro between three names that lasted for 50 years. The separation of *F. picea* and *F. candida* from the three other Palaearctic species with shining blackish body and reduced pubescence (i.e. *F. gagatoides* RUZSKY, 1904, *F. kozlovi* DLUSSKY, 1965 and *F. gagates* LATREILLE, 1798) is explained and morphometric data are given in two tables. An explanation for the peculiar habitat shift of *F. picea* is offered.

Key words: *Formica picea* complex, lectotype, neotype, discriminant analysis, zoogeography, habitat shift

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Introduction

The black and brilliantly shining species of the subgenus *Serviformica*, known to European myrmecologists under the trivial name "Black Bog Ant", is one of the worst examples for unstable and indeterminate taxonomic naming. In Europe, but not outside this area, this ant is one of the few real tytrphophiles among ants though occurrence on mineralic soil is reliably reported for higher mountain ranges (e.g., KUTTER 1917) and moist atlantic *Empetrum-Molinia* heath (SÖRENSEN 2001). Its special habitat selection and the brilliantly shining body surface has led to the rare situation that most European reports on this ant published during the last 150 years can credibly be referred to one and the same species. As a consequence, there is a rather good knowledge on several aspects of its biology.

From 1846 to 1979, this ant has almost constantly been named *Formica picea* NYLANDER, 1846. Considering the junior primary homonymy of *F. picea* NYLANDER, 1846 with *Formica picea* LEACH, 1825 (since 1861 in *Camponotus* MAYR), different junior synonyms were introduced as replacement names in the second half of the 20th century. YARROW (1954) was the first to propose the replacement name *Formica transcaucasica* NASSONOV, 1889. This propos-

al was not followed by a majority of myrmecologists – apparently because they did not consider the homonymy a practical problem (e.g., DLUSSKY 1967, DLUSSKY & PISARSKI 1971, KUTTER 1977, ARNOLDI & DLUSSKY 1978). The name *F. transcaucasica* became more frequently used when COLLINGWOOD (1979) repeated Yarrow's name change in his widely-distributed book on Fennoscandian ants. The most recent name change came, when BOLTON (1995) introduced the replacement name *F. candida* SMITH, 1878 in his important world catalogue of ants. All name changes performed by Yarrow, Collingwood, and Bolton were not based upon type investigation, critical reading of the original description, and consideration which similar species occurred in the type localities.

As shown in the results (section 1), no original material of *F. transcaucasica* and *F. candida* has been identified so far and the original descriptions are insufficient and may refer to several species occurring in the type localities. Hence we are confronted with the problem that nobody knows to which real species the original descriptions of *F. transcaucasica* and *F. candida* must refer and we are in urgent search for a valid and verifiable name of the Black Bog Ant.

A most reasonable solution of this homonymy case is now permitted by a new regulation of the 4th edition of the International Code of Zoological Nomenclature (1999). Article 23.9.5 states: "When an author discovers that a species-group name in use is a junior primary homonym [Art. 53.3] of another species-group name also in use, but the names apply to taxa not considered congeneric after 1899, the author must not automatically replace the junior homonym; the case should be referred to the Commission for a ruling under plenary power and meanwhile prevailing usage of both names is to be maintained." A full applicability of this article is given by the fact that *Formica picea* LEACH, 1825 is named *Camponotus piceus* (LEACH, 1825) since 1861 and will never be returned to *Formica* by any existing or future taxonomist because it belongs to a widely distant clade with a fundamentally deviating morphology. The reasonable decision of myrmecologists such as Pisarski, Dlussky, or Kutter not to replace the name *F. picea* NYLANDER finally became justified by the ICZN.

According to both genetic evidence (GOROPASH-NAYA 2003) and the morphological investigations presented here, the Palaearctic complex of all the taxa attributed by BOLTON (1995) to *Formica candida* SMITH, 1878, consists of two separable entities at least. Redescription and neotype fixation for the Central Asian-Tibetan species *Formica candida* and redescription and lectotype fixation of the European-West Siberian Black Bog Ant, *Formica picea* NYLANDER, 1846, as performed here are hoped to be first steps towards taxonomic determinism in this species complex.

Material and methods

If not explicitly stated otherwise, all material used in this study is stored in the Museum für Naturkunde Görlitz. A total of 105 nest samples with 264 worker specimens belonging to the five related species *Formica picea* NYLANDER, 1846, *F. candida* SMITH, 1878, *F. gagatoides* RUZSKY, 1904, *F. kozlovi* DLUSSKY, 1965, and *F. gagates* LATREILLE, 1798 was morphometrically investigated. Details on the origin and number of specimens are given in the sections treating the species.

All measurements were made on mounted and dried specimens using a goniometer-type pin-holding device, permitting endless rotations around X, Y, and Z axes. A Wild M10 stereomicroscope equipped with a 1.6 x planapochromatic objective was used at magnifications of 50 - 320 x. A mean measuring error of $\pm 1 \mu\text{m}$ is given for small and well-defined structures, such as hair length, but may reach $4 \mu\text{m}$ for measures $> 1700 \mu\text{m}$ with difficult positioning and high influence of air humidity. To avoid rounding errors, all measurements were recorded in μm even for characters for which a precision of $\pm 1 \mu\text{m}$ is im-

possible. Error sources of stereomicroscopic measuring in general and of the particular system used here are properly discussed elsewhere (SEIFERT 2002).

Setae, also called pilosity or simply "hairs", are differentiated from pubescence hairs in having a much larger diameter – usually $4 - 8 \mu\text{m}$ in setae and $1 - 2 \mu\text{m}$ in pubescence. All seta counts (acronyms beginning with "n") are restricted to standing setae projecting $> 10 \mu\text{m}$ from cuticular surface as seen in a profile view specifically defined.

Definition of numeric characters:

CL	maximum cephalic length in median line; the head must be carefully tilted to the position with the true maximum. Excavations of occiput and/or clypeus reduce CL.
CS	cephalic size; the arithmetic mean of CL and CW, used as a less variable indicator of body size.
CW	maximum cephalic width; this is either across, behind, or before the eyes.
EYE	eye-size: the arithmetic mean of the large (EL) and small diameter (EW) of the elliptic compound eye.
GHL	length of longest seta on dorsal plane of first gaster tergite excluding the row of setae immediately anterior of the hind tergite margin.
nGU	unilateral number of setae protruding more than $10 \mu\text{m}$ from cuticular surface of the underside of head ("gula") as visible in lateral view.
nHFFL	arithmetic mean of the number of setae protruding more than $10 \mu\text{m}$ from cuticular surface of the flexor profile of hind femora.
nMN	unilateral number of setae on mesonotum protruding more than $10 \mu\text{m}$ from cuticular surface.
nOCC	with the head in measuring position for CL, unilateral number of setae protruding more than $10 \mu\text{m}$ from occipital margin and the 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.
nPR	unilateral number of setae protruding more than $10 \mu\text{m}$ from cuticular surface on propodeum and lateral metapleuron (excluding setae fringing the metapleural gland orifice and those on ventrolateral edge of metapleuron).
PEW	maximum width of petiole.
RipD	average distance of transversal microripples on dorsal plane of first gaster tergite. At least 3 countings along a $90 \mu\text{m}$ distance on different surface spots are averaged – in species of the <i>F. candida</i> complex 5 - 8 coun-

tings may be necessary. Use high-resolution objectives with numeric apertures > 0.200, clean surfaces and light inclined perpendicular to the ripples. Do not include anastomoses between the ripples into the counting.

- 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. Use high-resolution objectives with numeric apertures > 0.200. In each specimen 4 - 6 measuring-lines of 400 μm are averaged under exclusion of surface parts with apparently detached pubescence. If there are no transects with undamaged pubescence possible, PDG can be calculated by the formula $\text{PDG} = \text{BD}^2 / \text{PLG}$ where BD is the mean distance of hair base punctures and PLG the mean length of pubescence hairs.

In most of the species groups of *Formica*, body ratios are strongly influenced by allometric growth. In order to make numeric characters directly comparable between the species, predictions for the assumption of all individuals having an identical cephalic size of 1.4 mm were calculated with the following equations calculated as mean of 24 Palearctic species of the subgenus *Serviformica*:

$$\text{CL} / \text{CW}_{1.4} = \text{CL} / \text{CW} / (-0.1143 * \text{CS} + 1.2936) * 1.1336$$

$$\text{SL} / \text{CS}_{1.4} = \text{SL} / \text{CS} / (-0.1077 * \text{CS} + 1.2062) * 1.0554$$

$$\text{EYE} / \text{CS}_{1.4} = \text{EYE} / \text{CS} / (-0.0594 * \text{CS} + 0.3752) * 0.292$$

$$\text{GHL} / \text{CS}_{1.4} = \text{GHL} / \text{CS} / (-0.0008 * \text{CS} + 0.0852) * 0.0841$$

$$\text{PEW} / \text{CS}_{1.4} = \text{PEW} / \text{CS} / (0.1001 * \text{CS} + 0.3039) * 0.444$$

$$\text{nOCC}_{1.4} = \text{nOCC} / (3.268 * \text{CS} + 1.31) * 5.88$$

$$\text{nGU}_{1.4} = \text{nGU} / (1.635 * \text{CS} + 0.43) * 2.72$$

$$\text{nPN}_{1.4} = \text{nPN} / (10.81 * \text{CS} - 6.50) * 8.63$$

$$\text{nMN}_{1.4} = \text{nMN} / (6.10 * \text{CS} - 5.21) * 3.33$$

$$\text{nPR}_{1.4} = \text{nPR} / (5.50 * \text{CS} - 3.97) * 3.73$$

$$\text{nPE}_{1.4} = \text{nPE} / (3.94 * \text{CS} - 1.80) * 3.71$$

$$\text{nHFFL}_{1.4} = \text{nHFFL} / (4.13 * \text{CS} - 0.45) * 5.34$$

$$\text{sqPDG}_{1.4} = \text{sqPDG} / (0.953 * \text{CS} + 3.086) * 4.42$$

$$\text{RipD}_{1.4} = \text{RipD} / (-0.0632 * \text{CS} + 7.29) * 7.2$$

Negative or positive signs in the divisor indicate a negative or positive allometry of the ratios but not necessarily in the other characters.

Results and Discussion

1. The current taxonomic status of *F. picea* NYLANDER, 1846, *F. transcaucasica* NASSONOV, 1889, and *F. candida* SMITH, 1878

Lectotype fixation for *Formica picea* NYLANDER, 1846

The type localities of *Formica picea* NYLANDER, 1846 mentioned in the original description are Helsingfors (now Helsinki) and Uleaborg (now Oulu). NYLANDER (1846) gave a quite detailed description of the worker with the following characters diagnostic for our Black Bog Ant (translation from the Latin): "... entirely black ... frontal triangle rather well-demarcated, as shining as remaining part of head thorax with extremely sparse whitish pubescence, a number of erect hairs on pronotum ... abdomen brilliantly shining black (without the smallest greyish-silky shine) ...". This character combination allows to exclude a synonymy with *Formica fusca* LINNAEUS, 1758, *F. lemani* BONDROIT, 1917, and *F. cunicularia* LATREILLE, 1798 which are the only blackish (or potentially blackish) ants occurring in South Finland. The description could match *F. gagates* LATREILLE, 1798 and does not clearly contradict the characters of *F. gagatoides* RUZSKY, 1904. *Formica gagates* can be excluded by zoogeography: the next population of this Mediterranean species is found 1150 km south. *Formica gagatoides*, in contrast, is highly boreal and its range begins 250 km north of Helsinki. Hence, the record from Uleaborg could possibly refer to *F. gagatoides*. In the Finnish Museum of Natural History in Helsinki is only one worker being in agreement with the geographic and descriptive statements in the original description. This specimen is labelled: "H: fors", "W. Nyland.", "Coll. Nyland.", "42/vii", "picea Nyl.", "Mus. Zool. H: fors Spec. typ. No. 5035 *Formica picea* Nyl.". It is strongly damaged: petiole, gaster, left legs and parts of the right middle leg are missing. This specimen was designated by Radchenko in 2003 as lectotype of *Formica picea* but this taxonomic act is not published so far (Radchenko, pers. comm., October 2004). However, independent fixation of a lectotype by different authors in objectively the same specimen cannot produce any taxonomic problem and herewith I publish this specimen as lectotype of *Formica picea* NYLANDER under maintenance of Radchenko's label. According to microsculpture, pubescence structure and setae condition on the preserved body parts, the specimen is clearly heterospecific from *F. fusca*, *F. lemani* and *F. gagatoides*, the other black species occurring in Finland. However, the lectotype could not be incorporated into the discriminant ana-

Tab. 1: Morphometric data of workers of *Formica picea* and *F. candida* given as arithmetic mean \pm standard deviation [minimum, maximum]. Note the lower sample size in EYE / CS; p = error probability in 2-sided t test, df = degrees of freedom.

primary data of individuals				size-corrected nest sample means(for CS = 1.4 mm)			
	<i>F. picea</i> (n = 62)	p for $df = 174$	<i>F. candida</i> (n = 116)		<i>F. picea</i> (n = 24)	p for $df = 65$	<i>F. candida</i> (n = 43)
CS [μ m]	1218 \pm 95 [1034, 1458]	n.s.	1237 \pm 131 [985, 1565]	CS [μ m]	1219 \pm 80 [1071, 1408]	n.s.	1241 \pm 119 [1018, 1456]
CL / CW	1.142 \pm 0.026 [1.096, 1.207]	0.0001	1.120 \pm 0.025 [1.040, 1.181]	CL / CW _{1.4}	1.123 \pm 0.014 [1.100, 1.152]	0.0001	1.101 \pm 0.017 [1.065, 1.143]
SL / CS	1.049 \pm 0.022 [0.990, 1.105]	0.0001	1.029 \pm 0.034 [0.944, 1.123]	SL / CS _{1.4}	1.030 \pm 0.015 [0.988, 1.047]	0.0001	1.011 \pm 0.028 [0.950, 1.079]
PEW / CL	0.423 \pm 0.024 [0.379, 0.476]	0.041	0.431 \pm 0.025 [0.370, 0.496]	PEW / CL _{1.4}	0.438 \pm 0.016 [0.413, 0.473]	0.027	0.450 \pm 0.021 [0.407, 0.496]
EYE / CS	0.283 \pm 0.009 [0.263, 0.295]	n.s. ($df = 26$)	0.285 \pm 0.010 [0.267, 0.298]	EYE / CS _{1.4}	0.273 \pm 0.006 [0.261, 0.283]	n.s. ($df = 16$)	0.277 \pm 0.003 [0.275, 0.283]
GHL / CS [%]	12.06 \pm 1.47 [8.7, 15.3]	0.0001	11.06 \pm 1.53 [6.6, 14.0]	GHL / CS _{1.4} [%]	12.18 \pm 1.12 [10.67, 14.95]	0.0001	10.95 \pm 1.40 [7.05, 13.63]
nOCC	0.29 \pm 0.38 [0.0, 2.0]	n.s.	0.19 \pm 0.37 [0.00, 1.00]	nOcc _{1.4}	0.36 \pm 0.43 [0.00, 2.00]	0.035	0.18 \pm 0.25 [0.00, 1.00]
nGU	0.40 \pm 0.43 [0.0, 1.5]	n.s.	0.28 \pm 0.32 [0.0, 2.0]	nGu _{1.4}	0.48 \pm 0.34 [0.0, 1.20]	0.048	0.30 \pm 0.33 [0.0, 1.17]
nPN	5.62 \pm 2.77 [1.0, 12.0]	n.s.	4.59 \pm 3.47 [0.0, 17.5]	nPn _{1.4}	6.91 \pm 2.18 [4.05, 11.95]	0.012	5.19 \pm 2.83 [1.23, 12.57]
nMN	3.56 \pm 1.85 [0.5, 8.0]	0.0001	2.33 \pm 2.30 [0.0, 12.5]	nMn _{1.4}	5.32 \pm 1.21 [2.50, 7.83]	0.0001	2.87 \pm 2.09 [0.0, 9.85]
nPR	0.14 \pm 0.40 [0.0, 2.5]	n.s.	0.06 \pm 0.24 [0.0, 2.0]	nPr _{1.4}	0.22 \pm 0.45 [0.0, 1.60]	n.s.	0.06 \pm 0.17 [0.0, 0.90]
nPE	0.50 \pm 0.76 [0.0, 2.7]	0.0001	0.06 \pm 0.22 [0.0, 1.5]	nPe _{1.4}	0.54 \pm 0.69 [0.0, 2.40]	0.002	0.05 \pm 0.18 [0.0, 0.83]
nHFFL	1.94 \pm 0.90 [0.2, 4.0]	0.0001	1.28 \pm 1.26 [0.0, 5.0]	nHFFL _{1.4}	2.34 \pm 0.61 [1.50, 4.10]	0.0001	1.37 \pm 1.12 [0.0, 4.50]
sqPDG	8.62 \pm 0.73 [6.80, 10.08]	0.0001	10.63 \pm 1.66 [8.10, 17.20]	sqPDG _{1.4}	8.92 \pm 0.65 [8.00, 10.48]	0.0001	11.17 \pm 1.57 [9.19, 15.56]
RipD	6.79 \pm 0.60 [5.4, 8.0]	0.0001	7.69 \pm 0.70 [5.8, 9.5]	RipD _{1.4}	6.78 \pm 0.44 [6.03, 7.77]	0.0001	7.72 \pm 0.59 [6.20, 9.30]

lysis because two most discriminative and three less discriminative differential characters to the Central Asian sister species *F. candida* SMITH (see below) are placed on missing body parts. A subjective distinction from this species based upon the preserved body parts seems not possible according to present knowledge. However, heterospecificity is clearly indicated by the most different geographic distribution of *F. picea* and *F. candida*: all 26 morphometrically and another 9 genetically evaluated samples from France to West Siberia (GOROPASHNAYA 2003) belonged to *F. picea*. As a matter of fact it is most unlikely that *F. candida* could occur in Finland.

Formica transcaucasica* NASSONOV, 1889 – a *Formica incertae sedis

YARROW (1954) and COLLINGWOOD (1979) tried to solve the homonymy problem by proposing the name

Formica transcaucasica NASSONOV, 1889 for the Black Bog Ant without presenting conclusive arguments of how they identified Nasonov's taxon. Can it be identified at all? DLUSSKY (1967) casually mentioned to have investigated types of *F. transcaucasica* from the Zoological Museum Moscow without giving any description of their characters or their labelling. Repeated contacts of the present author with the former and present curators of the Moscow collection during the late 1990ies did not result in a discovery of real or alleged types of *F. transcaucasica* (Dlussky, pers. comm., Andropov, pers. comm.). Conclusions on the identity of this taxon can thus only be derived from the original description in which NASSONOV (1889) wrote: "... Found by Gorbatshev in the Caucasus near the town of Tiflis. Worker: Black with dark brownish mandibles, scape, articulations of legs, feet, and lower part of scale. Smooth, shin-

Tab. 2: Nest sample means of workers of all blackish Palaearctic *Formica* species with large pubescence distance given as arithmetic mean \pm standard deviation [minimum, maximum]. To enable more transparent interspecific comparisons, all data except CS are corrected for the assumption of equal body size (CS = 1.4 mm). n = number of nest samples, i = number of individuals.

	<i>F. picea</i> (n = 24; i = 60)	<i>F. candida</i> (n = 43; i = 116)	<i>F. gagatoides</i> (n = 14; i = 36)	<i>F. kozlovi</i> (n = 7; i = 18)	<i>F. gagates</i> (n = 14; i = 31)
CS [μ m]	1219 \pm 80 [1071, 1408]	1241 \pm 119 [1018, 1456]	1277 \pm 71 [1162, 1426]	1333 \pm 48 [1263, 1415]	1431 \pm 159 [1262, 1508]
CL / CW _{1.4}	1.123 \pm 0.014 [1.100, 1.152]	1.101 \pm 0.017 [1.065, 1.143]	1.129 \pm 0.018 [1.089, 1.158]	1.128 \pm 0.007 [1.120, 1.139]	1.129 \pm 0.014 [1.099, 1.157]
SL / CS _{1.4}	1.030 \pm 0.015 [0.988, 1.047]	1.011 \pm 0.028 [0.950, 1.079]	1.031 \pm 0.016 [0.999, 1.053]	1.071 \pm 0.016 [1.045, 1.092]	1.110 \pm 0.019 [1.081, 1.154]
PEW / CL _{1.4}	0.438 \pm 0.016 [0.413, 0.473]	0.450 \pm 0.021 [0.407, 0.496]	0.470 \pm 0.015 [0.443, 0.492]	0.455 \pm 0.011 [0.446, 0.477]	0.447 \pm 0.018 [0.424, 0.470]
EYE / CS _{1.4}	0.273 \pm 0.006 [0.261, 0.283]	0.277 \pm 0.003 [0.275, 0.283]	0.271 \pm 0.005 [0.262, 0.281]	0.274 \pm 0.004 [0.271, 0.281]	0.264 \pm 0.006 [0.252, 0.272]
GHL / CS _{1.4} [%]	12.18 \pm 1.12 [10.67, 14.95]	10.95 \pm 1.40 [7.05, 13.63]	7.76 \pm 0.94 [6.37, 9.97]	6.79 \pm 0.73 [5.67, 7.60]	13.54 \pm 0.81 [11.60, 15.10]
nOcc _{1.4}	0.36 \pm 0.43 [0.00, 2.00]	0.18 \pm 0.25 [0.00, 1.00]	0.00 \pm 0.00 [0.0, 0.0]	0.04 \pm 0.08 [0.0, 0.17]	0.00 \pm 0.00 [0.0, 0.00]
nGu _{1.4}	0.48 \pm 0.34 [0.0, 1.20]	0.30 \pm 0.33 [0.0, 1.17]	0.15 \pm 0.21 [0.0, 0.75]	0.28 \pm 0.36 [0.0, 0.80]	0.04 \pm 0.07 [0.0, 0.13]
nPn _{1.4}	6.91 \pm 2.18 [4.05, 11.95]	5.19 \pm 2.83 [1.23, 12.57]	0.33 \pm 0.30 [0.00, 0.97]	1.57 \pm 0.96 [0.37, 2.90]	2.71 \pm 1.94 [0.00, 6.03]
nMn _{1.4}	5.32 \pm 1.21 [2.50, 7.83]	2.87 \pm 2.09 [0.0, 9.85]	0.29 \pm 0.56 [0.0, 2.10]	0.37 \pm 0.34 [0.0, 0.93]	0.83 \pm 0.78 [0.00, 3.25]
nPr _{1.4}	0.22 \pm 0.45 [0.0, 1.60]	0.06 \pm 0.17 [0.0, 0.90]	0.00 \pm 0.00 [0.0, 0.00]	0.00 \pm 0.00 [0.0, 0.00]	0.08 \pm 0.20 [0.0, 0.50]
nPe _{1.4}	0.54 \pm 0.69 [0.0, 2.40]	0.05 \pm 0.18 [0.0, 0.83]	0.00 \pm 0.00 [0.0, 0.0]	0.00 \pm 0.00 [0.0, 0.00]	0.00 \pm 0.00 [0.0, 0.00]
nHFFL _{1.4}	2.34 \pm 0.61 [1.50, 4.10]	1.37 \pm 1.12 [0.0, 4.50]	0.42 \pm 0.50 [0.0, 1.80]	0.91 \pm 0.96 [0.17, 3.00]	0.24 \pm 0.32 [0.0, 0.80]
sqPDG _{1.4}	8.92 \pm 0.65 [8.00, 10.48]	11.17 \pm 1.57 [9.19, 15.56]	5.11 \pm 0.58 [3.82, 6.01]	4.37 \pm 0.53 [3.76, 5.20]	4.73 \pm 0.38 [4.19, 5.58]
RipD _{1.4}	6.78 \pm 0.44 [6.03, 7.77]	7.72 \pm 0.59 [6.20, 9.30]	7.86 \pm 0.59 [6.95, 9.30]	6.58 \pm 1.08 [4.60, 7.63]	8.35 \pm 0.51 [7.60, 8.80]

ing with widely spaced punctures and poorly notable rugosity on head and mesosoma. Decumbent hairs absent. Erect hairs rare, occurring only on lower surface of gaster and rarely on the thighs and between the antennae. Otherwise as in *F. gagates*. L. 3.5 - 4.5 mm ..." (translation from the Russian).

The present author has collected four weeks "near to the town of Tiflis" in 1985. A spectrum of most different habitats is found there, including hot steppes, warm deciduous forests, coniferous mountain forests, and subalpine meadows. The number of black, shining *Serviformica* morphospecies is four at least in this region and only one of them is *F. picea*. Furthermore, the full absence of erect setae on whole mesosoma strongly indicates a heterospecificity of *F. transcaucasica* and *F. picea*: A completely bare dorsal mesosoma and gaster was not observed in any specimen of the Black Bog Ant within its West Palaearctic range. Full absence of mesosomal setae is sometimes observed in four other black and shining spe-

cies of the Palaearctic (see Tab. 2) and frequently seen in the other three species existing around Tiflis (Seifert, unpubl. results). As a consequence, the name must be deposited under "*Formica incertae sedis*". I urgently recommend future taxonomists not to speculatively use this name for any species as long as a type is not reliably identified. Nasonov did not label types and a well-founded identification of a lectotype must fulfil the following minimum requirements: (a) the specimen must be at least 115 years old, (b) it must carry an original label of Nasonov referring to a locality in the vicinity of Tiflis and (c) its dorsal mesosoma and dorsum of gaster must be completely without setae and its body surface should be very shining. As a consequence, it is most unlikely that ever a type specimen of *F. transcaucasica* will be credibly identified which is conspecific with *F. picea* and a neotype fixation must be done in agreement with the descriptive statements and the explained need to save nomenclatoric stability.

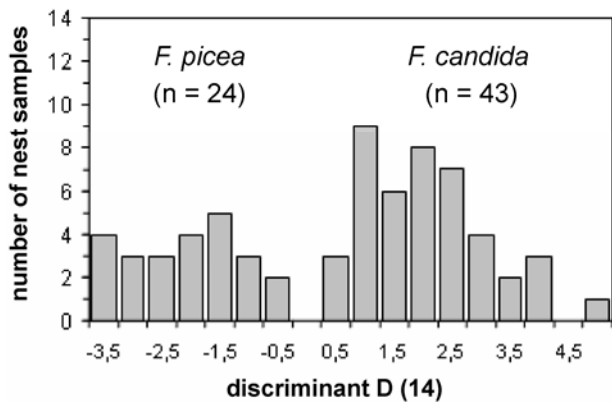


Fig. 1: Frequency distribution of discriminant values D(14) of worker nest samples to separate *Formica picea* NYLANDER, 1846 and *Formica candida* SMITH, 1879.

Neotype fixation for *Formica candida* SMITH, 1878

BOLTON (1995), following EMERY (1925) and DLUSSKY (1967), who both considered *Formica candida* SMITH as junior synonym of *F. picea* NYLANDER, automatically introduced *Formica candida* as oldest available name for *F. picea*. Both, Emery and Dlussky did not present a conclusive argument and their idea can also not be supported by the information stored in the original description or in collections.

Formica candida has been described based upon a single gyne that was found "... On the road across the Pámir, from Sarikol to Panja ..." (SMITH 1878). According to the curators of the collections in Oxford University Museum and British Museum of Natural History (Chris O'Toole and Barry Bolton, pers. comm., 2001), the whereabouts of this material are unknown. Inquiries sent to the National Zoological Survey of India Calcutta, another possible depository, where not answered. For the latter institution, it was not even possible to discover the name of a responsible curator for any of the probably existing insect collections. The description of Smith is insufficient even in terms of his time. It allows to exclude a blackish *Camponotus*, most probably to exclude a *Proformica* and to assume that *F. candida* should be a blackish *Formica* with a shining gaster in the gyne. The elevation of the locus typicus is between 2000 and 3500 m. The author has no material from the type locality (about 36°50'N, 73°20'E) in his collection but he has specimens from 315 km north (39°42'N, 73°27'E). Here, two blackish species with shining gasters in the gyne are sympatric and abundant between 2000 and 3000 m – a species most similar to *F. picea* and another one equal or near to *Formica lemani* BONDROIT, 1917. As a consequence, not even an assumption is possible to which of the two species *F. candida* should refer.

As solution of this dilemma and estimating a low risk of preservation of the original specimen, a neotype fixation for *Formica candida* SMITH, 1878 in a worker specimen is performed here:

The specimen is labelled "KYRGHYZTAN: Alai-Valley 39.42.09 N, 73.27.24 E, 3200 m, leg. R.Schultz 1999.07.21-67" and "Neotype *Formica candida* Smith 1878 det. Seifert". It is the bottom specimen of three workers on the same pin which were collected from the same nest and stored in SMN Görlitz. The neotype has the data CS 1.112 mm, CL / CW 1.132, SL / CS 1.032. The neotype locality is about 315 km N of the site given by Smith which is "very near" in terms of Asian dimensions. The mtDNA sequence data of the neotype sample No. 67 is stored under GenBank Accession No. AY786154 (Haplotype "Kyrgyzstan-II"), those of samples No. 64 and No. 66 from the neotype locality under No. AY786153 (Haplotype "Kyrgyzstan-I").

2. Evidence for heterospecificity of *F. picea* and *F. candida* and their distribution in the Palaearctic

The Palaearctic ants collected by BOLTON (1995) under the name *F. candida* can be subdivided into a minimum of two entities which are considered here as different species. According to examination of three mtDNA loci with 1500 base pairs (GOROPASHNAYA 2003), the *F. candida* complex shows a rather strong phylogeographic structure and can be subdivided in two main clades – a European-West Siberian clade and a clade occurring in the Central Asian Mountains. The two main clades showed a net sequence divergence of 1.2 % which is much in terms of the genus *Formica* in which clearly different species such as *F. pratensis* and *F. lugubris* or *F. truncorum* and *F. frontalis* differ by only 0.85 to 1.2 % (GOROPASHNAYA & al. 2004a, b).

This genetic separation could be confirmed on the morphological level by a discriminant analysis using absolute cephalic size and 13 size-corrected characters of 67 nest samples where a minimum of two workers per sample was available. The discriminant D(14) with

$$D(14) = 42.98 - 2.65 CS - 44.11 CL / CW_{1.4} + 0.58 SL / CS_{1.4} - 8.88 PEW / CS_{1.4} + 4.18 GH / CS_{1.4} + 0.12 nOCC_{1.4} + 0.79 nGU_{1.4} + 0.48 nPN_{1.4} - 0.54 nMN_{1.4} + 0.29 nPR_{1.4} - 1.25 nPE_{1.4} - 0.25 nHFFL_{1.4} + 0.72 RipD_{1.4} + 0.67 sqPDG_{1.4}$$

provided a reasonable separation of the Palaearctic samples into two groups which are interpreted here as *Formica picea* and *Formica candida*.

$$F. picea: D(14) -2.049 \pm 0.894 [-0.49, -3.58] n = 24$$

$$F. candida: D(14) 2.054 \pm 1.053 [0.49, 4.81] n = 43$$

94 % of 67 determinations had error probabilities < 0.05. This clear result indicates that the grouping is basically real which, however, does not exclude that the *F. candida* cluster could be subdivided further. There are suggestions on heterogeneity of the *F. candida* cluster, meaning that one of Ruzsky's, Forel's or Stärcke's names could be revived some day for referring to a third species, but the data available do not allow to demonstrate this at the present stage. There

is one sample from Tibet which seemed to show genetic proximity to the West Palaearctic clade (GOROPASHNAYA 2003). However, its position is only weakly supported by bootstrap values and more samples from this region are needed to find phylogenetic relationships of the *F. candida* from Tibet and from Western Europe.

A detailed consideration shows significant differences in primary data of individuals for 9 characters and in size-corrected nest sample means for 13 characters (Tab. 1). The best discriminators are RipD, sqPDG, and CL / CW.

Despite the apparently good discrimination of both species, the difficulties to measure RipD and sqPDG with the accuracy required here must be kept in mind. Accidental selection and insufficient number of measuring spots as well as surface pollution may affect the results and further errors would occur in sqPDG when damaged surface areas are included without considering the basal points and length of missing hairs. As a consequence, the separation of the two sister species needs a very careful consideration of the measuring schedule described in Methods.

According to the morphological and genetical identifications we have so far, *Formica picea* is distributed from Europe to the West Siberian lowland and is also found in the high Caucasus. The apparent absence from the Baikal region or North Mongolia needs to be confirmed. *Formica candida* is known so far only from the Central Asian mountain regions (Himalayas, Pamirs, Tien Shan, Tarbagatai, Saur east to the Altai region), the Baikal region, Mongolia, Tibet and East Siberia. The present information does not allow to state if there is some geographic overlap of the sister species or a clear parapatry. The idea that both species are separated in the east-west direction by the Johansen Line (a division of East and West Palaearctic faunas due to postglacial ecological reasons) and in the north-south direction by the western section of the Reinig Line (a division of faunas for glacial ecological reasons, DE LATTIN 1967) is suggested by the known data but the big capacity of both species to survive cold continental winters should make these borders penetrable.

If a third species should be identified some day within the *F. candida* cluster, the following six taxa with type localities more than 2000 km outside the geographic range of *F. picea* and deeply within the range of *F. candida* should be checked. These are *F. fusca* ssp. *gagates* var. *filchneri* FOREL, 1907 [unavailable name] from Lanshou in East Tibet, *F. picea* var. *lochmatteri* STÄRCKE, 1935 from the West Himalayas and four taxa of Ruzsky, all collected during the Kozlov expedition in northeastern Tibet in 1901: *F. fusca* subsp. *orientalis* RUZSKY, 1915, *F. picea* var. *inplana* EMERY, 1925 [first available use of *F. fusca picea* var. *inplana* RUZSKY, 1915], *F. fusca* var. *piceoimplana* EMERY, 1925 [first avail-

able use of *F. fusca picea* var. *piceo-inplana* RUZSKY, 1915] and *Formica fusca* ssp. *orientalis* var. *piceo-orientalis* RUZSKY, 1915 [unavailable name].

3. Redescription of *Formica candida* SMITH, 1878

Material investigated: Altogether 44 samples with 117 specimens from the following sites were morphometrically investigated:

Bhutan: Dorjee-Khandu, IX.1975, 3600 m; Paro 19.V.1972, 2300 m. China: Tibet: Oring Nor (35.00 N, 97.29 E), 4285 m, 30.VI.1990; Tibet: Madoi (35.01 N, 96.23 E), 4700 m, 22.VI.1990; Tibet: Heka (35.47 N, 99.52 E), 4000 m, 14.VII.1990; Tibet: Gonghe (36.16 N, 100.37 E), 3500 m, 8.V.1992; Tibet: Gonghe (36.20 N, 100.40 E), 3500 m, 21.VI.1998; Tibet: Xining (36.34 N, 101.53 E), 18.VII.1990; Tibet: Heimahe (36.44N, 99.35E), 24.V.1990; Tibet: Koko Nur, Niao Dao (36.48 N, 99.53 E), 29.V.1990; Tibet: Koko Nur, Nia Dao (36.45 N, 99.47 E), 25.VI.1998; Tibet: Chaka (36.49 N, 99.16 E), 16.VI.1990; Tibet: Chaka (36.45 N, 99.12 E), 3400 m, 29.VI.1998; Tibet: Beishan Nat. Park (36.56 N, 102.29 E), 25.V.1996 (No 911, No 912). India: Kashmir: Dras-Zojjla, 3200 m, 18.VII.1976. Kazakhstan: Saur Mts. (47.18 N, 85.37 E), 1486 m, 24.VII.2001 (No 237, No 324); Manrak Mts. (47.19 N, 84.37 E), 1168 m, 27.VII.2001 (No 270, No 345). Kirgisia: Tien Shan: Alai valley (39.42 N, 73.27 E), 3200 m, 21.VII.1999 (No 64, 66, 67); Tien Shan: Otuk valley (41.48 N, 75.45 E), 2600 m, 16.VII.1999 (No 16, No 17); Tien Shan: Dolon pass (41.50 N, 75.45 E), 3000 m, 16.VII.1999 (No 11); Tien Shan: Enyltshak valley (42.04 N, 79.12 E), 2700 m, 25.VII.2000 (No 260, No 267); Tien Shan: Sousamyr valley (42.12 N, 73.20 E), 2500 m, 18.VII.1998; Tien Shan: Kirgisky Alatau (42.25 N, 73.45 E), 3000 m, 17.VII.1998. Mongolia: Charchorin (47.04 N, 102.37 E), 2.X.1985; without locality name (47.04 N, 113.35 E), 11.VIII.1999; without locality name (47.16 N, 107.38 E), 18.VII.1997; without locality name (47.17 N, 107.38 E), 22.VIII.1999; without locality name (47.54 N, 106.25 E), 1405 m, 30.VII.2003; Dormod-Aimag, 16.VIII.1997. Russia: Baikal region (106.23 E, 53.47 N), 22.VIII.2001; Baikal region (106.31 E, 53.02 N), 22.VIII.2001; Baikal region (106.54 E, 53.01 N), 22.VIII.2001; Baikal region, (107.29 E, 53.15 N), 24.VIII.2001; Barnaul (53.17 N, 83.46 E), 19.VII.2000; Yakutia: Nat. Park Lensky Stolby (66.40 N, 126.10 E), 1999; Ussuri region: (43.16 N, 134.08 E), 174 m, V.2001; Ussuri region (42.54 N, 133.51 E), 35 m, 1999.

Description of the worker: Mean size smaller than *Serviformica* average: CS 1.240 mm. Head and scape shorter than in the next related species, i.e. *F. picea*, *F. gagatoides* and *F. kozlovi*: CL / CW_{1.4} 1.101, SL / CS_{1.4} 1.010 (Tab. 2). Frontal triangle as shining as the adjacent surfaces. Cuticular surface of head, mesosoma and gaster, as result of strongly reduced pubes-

cence and very weak microsculpture, very shining; a denser pubescence is usually developed only on propodeum and petiole. On dorsal surface of first gaster tergite, average distance of transverse microripples 7.7 μm (RipD) and of pubescence hairs 113 μm (PDG). Clypeus, procoxae, ventral parts of meso- and metacoxae and all ventral and dorsal gaster sclerites with quite numerous and very long erect setae. Seen in lateral profile, hind vertex with 3 - 7 and central vertex with 2 - 8 setae. Both sides of pronotum usually with 2 - 16 and of mesonotum with 1 - 9 long, erect setae. Propodeum and petiole scale only very occasionally with single short and weak setae. Flexor sides of both hind tibiae with a sum of 0 - 5 semierect to subdecumbent setae. Petiole scale variable, its dorsal margin in frontal view fully convex or with a straight or concave median part; scale in lateral view not very thick and with a tapering apex. An average colouration pattern is: head, mesosoma, coxae and gaster blackish brown; appendages lighter, mandibles light to dark reddish brown. Slightly lighter or darker specimens may occur. For morphometric details of 117 worker specimens see Tab. 1.

4. Redescription of *Formica picea* NYLANDER, 1846

Material investigated: Altogether 26 samples with 62 specimens from the following sites were morphometrically investigated:

Austria: Gerlosplatte (12.15 E, 47.23 N), 1600 m, 11.VII.1982. Czechia: Volary, 16.V.1981. France: Pontarlier vic.: Le Belieu, 11.VII.1990; Pontarlier vic.: Les Granges, 19.VII.1990. Georgia: Kazbegi (44.37 E, 42.41 N), 2100 m, 27.VII.1985 (No 656, No 657); Schenako (45.42 E, 42.23 N), 1500 m, 1.VIII.1985; Schatili (45.10 E, 42.40 N), 1450 m, 14.VIII.1985. Germany: Baden-Württemberg: Oggelshausen - 0.5 km W, 25.V.1991; Baden-Württemberg: Eisenharz - 2 km SE, 7.V.1993; Mecklenburg-Vorpommern: Reinkenhagen, Manhäger Moor, 18.IV.1984; Mecklenburg-Vorpommern: Neustrehlitz-NE, 28.VII.1974; Niedersachsen: NSG Rössenbergheide, 1.IX.1991; Sachsen: Geyer, Hermannsdorfer Wiesen, 30.VII.1965; Sachsen: Battaune - 3.2 km NE, 21.VIII.1994 (No g28, No g29); Sachsen: Dubring - 2.1 km NNE, 12.VIII.1982; Sachsen: Lauchhammer-Süd, FND Laug, 9.V.1984; Sachsen: Milkel - 3.8 km N, Milkeler Moor, 9.VIII.1988; Sachsen: Schleife - 2 km E, 30.VIII.1987; Sachsen: Wildenhainer Bruch, 23.IX.1980. Russia: Moscow - 60 km W, Svenigorod, 24.VIII.1985; Caucasus: Baksan valley: Azau Polje (42.29 E, 43.17 N), 3000 m, 9.VII.1974; Baksan valley: Mt. Tubasanty, 3000 m, 10.VII.1980. Sweden: Bjärröd-6 km E, 16.VI.1992; Lindshammar - 5 km SE, 11.VI.1992.

Description of the worker: Mean size distinctly smaller than *Serviformica* average: CS 1.22 mm. Head and scape significantly longer than in *F. candida*: CL / CW_{1,4} 1.123, SL / CS_{1,4} 1.030 (Tab. 1). Frontal

triangle as shining as the adjacent surfaces. Cuticular surface of head, mesosoma and gaster as result of reduced pubescence and weak microsculpture shining; a denser pubescence is usually developed only on propodeum and petiole. However, pubescence and microsculpture significantly denser than in *F. candida*: on dorsal surface of first gaster tergite, average distance of transverse microripples 6.8 μm (RipD) and of pubescence hairs 74 μm (PDG). Clypeus, procoxae, ventral parts of meso- and metacoxae and all ventral and dorsal gaster sclerites with quite numerous and very long erect setae which are longer than in *F. candida*, GH / CS 12.1 %. Setae numbers a little larger than in *F. candida*: Seen in lateral profile, hind vertex with 3 - 16 and central vertex with 2 - 7 setae. Both sides of pronotum usually with 5 - 17 and of mesonotum with 3 - 11 long, erect setae. Propodeum occasionally and petiole scale usually with single short setae. Flexor sides of both hind tibiae with a sum of 2 - 6 semierect to subdecumbent setae. Petiole scale variable, on the average narrower than in *F. candida*; its dorsal margin in frontal view fully convex or with a straight or concave median part; scale in lateral view not very thick with a tapering apex. Colouration pattern similar to situation in *F. candida*. For morphometric details of 62 worker specimens see Tab. 1.

5. Comments on separation from other species

Any of the species presented in Tab. 2 can be separated from each other by discriminant functions based upon nest sample means. Values and formulae of discriminant functions are not presented here but the most useful character combinations can be derived from Tab. 2. *Formica gagates* can be separated from any other species by a character combination of extremely large SL / CS, GH / CS, less large sqPDG and large RipD. Furthermore its identification is facilitated by the much deviating habitat selection and zoogeography. Leading characters for the distinction of the collective clusters *F. gagatoides* + *F. kozlovi* and *F. candida* + *F. picea* are the much lower GH / CS, sqPDG and lower setae numbers on promesonotum in the first cluster. Remains the separation between *F. gagatoides* and *F. kozlovi*: A discriminant function offers a very clear separation between the two taxa but further samples of *F. kozlovi* are desired. The types of both these taxa (lectotype of *F. gagatoides* from Zoological Museum St. Petersburg, holotype of *F. kozlovi* from Zoological Museum Moscow) could be investigated and clearly match to either cluster with error probabilities of $p < 0.001$. *Formica kozlovi* differs from *F. gagatoides* by a significantly longer scape, larger nPN and smaller RipD. A further good difference of *F. kozlovi* is that pubescence distance on the second gaster tergite is much larger than on the first while pubescence distance on both tergites is quite similar in *F. gagatoides*.

6. The habitat change of *Formica picea*

The primary habitats of *F. picea* and *F. candida* are obviously continental or mountain grasslands with cold winters. As adaptation to these habitats, both species should have very low supercooling points during hibernation (BERMAN & al. 1987, here data for *F. candida*). Furthermore, both species should strongly tolerate water saturation, should have a much weaker avoidance behaviour against water surfaces and a very long survival time when submerged. This idea is supported by the following observations in *F. picea*. For peat bog habitats, ADLERZ (1914) reported that ants escaped during nest opening under the surface of water and BÖNNER (1915) observed hibernation clusters a few centimetres above the water surface. During my own investigations, when opening *F. picea* nests in extremely wet *Sphagnum*-areas, workers actively escaped under the water surface, climbing down on *Sphagnum*-stems. Evidence for highest survival times of Siberian ants in submerged condition is presented by observations in *F. picea*'s social parasite *F. uralensis* (GYLLENBERG & ROSENGREN 1984). This performance is especially important in Siberia during thawing in spring when the upper layers of deeply frozen soils are transformed to water-soaked mud areas for several weeks each year. In climates with higher winter temperatures this advantage of *F. picea* has lost importance and it can only stand against its competitors in bog habitats or moist heath. The habitat shift of *F. picea* from bog habitats to grasslands on mineralic soil as seen in higher mountain ranges and in continental climate is thus mainly a function of decreasing winter temperatures and, in the continental lowland range, also of extreme water-saturation of the soil in spring.

Zusammenfassung

Gemäss morphometrischer und genetischer Befunde können die von BOLTON (1995) unter dem Namen *Formica candida* SMITH, 1878 zusammengefassten Arten in mindestens zwei Arten unterschiedlicher Zoogeographie aufgetrennt werden. Die weithin bekannte "Schwarze Moorameise", die über Europa, den Kaukasus und das Westsibirische Tiefland verbreitet ist, wird als *Formica picea* NYLANDER, 1846 identifiziert, während die in sämtlichen zentralasiatischen Gebirgen nordwärts bis zur Region Gorno-Altai, in Tibet, der Mongolei, der Baikalsee-Region und Ostsibirien verbreitete Art als *Formica candida* SMITH, 1878 unter Neotypus-Fixierung wiederbeschrieben wird. Gemäß Artikel 23.9.5 der 4. Auflage des ICZN (1999) muss der Name *Formica picea* NYLANDER, 1846 (ein jüngeres Homonym von *F. picea* LEACH, 1825) nicht durch ein jüngeres Synonym ersetzt werden. Diese Regel scheint hier besonders vernünftig, da *F. picea* LEACH seit 1861 zu *Camponotus* MAYR gestellt wird und niemals zu *Formica* zurückkehren

wird. Ihre Anwendung beendet die verwirrende, 50 Jahre andauernde Verwendung dreier verschiedener Namen. Die Unterscheidung von *F. picea* und *F. candida* von den anderen drei paläarktischen Arten mit schwarzer glänzender Körperoberfläche und reduzierter Pubeszenz – *F. gagatoides* RUZSKY, 1904, *F. kozlovi* DLUSSKY, 1965 und *F. gagates* LATREILLE, 1798 – wird erklärt und hinreichende morphometrische Daten werden in einer Tabelle präsentiert. Eine Erklärung für den eigentümlichen Habitatwechsel von *F. picea* wird angeboten.

Acknowledgements

I am very grateful to Izya Kerzhner (St. Petersburg) for most important comments on nomenclatoric aspects of the manuscript; to Axel Gebauer (Görlitz) and Roland Schultz (Greifswald) for repeatedly providing material of their collecting expeditions to Central Asia and Tibet; to Anya Goropashnaya (Fairbanks) for providing genetic information; and to Chris O' Toole (Oxford) and Barry Bolton (Ventnor) for information on the Smith collection and providing of literature.

References

- ADLERZ, G. 1914: *Formica fusca picea* NYL., en torfmossarnas myra. – Arkiv för Zoologi 8 (No 26): 1-5.
- ARNOLDI, K. & DLUSSKY, G. 1978: Nadsem. Formicoidea. 1. Sem. Formicidae - muravi. In: MEDVEDJEV, G.S. (Ed.): Opredelitel nasekomykh evropejskoj chasti SSSR. Tom 3. Pereponchatokryluyi, pervaya chast. – Opredeliteli k Faune SSSR 119: 519-556.
- BERMAN, D.I., SHIGULSKAJA, S.A. & LEIRICH, A.N. 1987: Simnaya ecologia polarnovo muravya (*Formica gagatoides*) v verchovyach Kolymy. – Zoologicheskij Zhurnal 66: 373-384.
- BOLTON, B. 1995: A New General Catalogue of the Ants of the World. – Harvard University Press, Cambridge, Massachusetts and London, 504 pp.
- BÖNNER, W. 1915: Die Überwinterung von *Formica picea* und andere biologische Beobachtungen. – Biologisches Zentralblatt 35: 65-77.
- COLLINGWOOD, C.A. 1979: The Formicidae of Fennoscandia and Denmark. – Fauna Entomologica Scandinavica 8: 1-174.
- DE LATIN, G. 1967: Grundriss der Zoogeographie. – Fischer, Jena, 602 pp.
- DLUSSKY, G. 1967: Muravi roda *Formica*. Izdatel'stvo "Nauka". – Nauka Publishing House, Moskva, 236 pp.
- DLUSSKY, G. & PISARSKI, B. 1971: Rewiizja polskich gatunkow mrowek (Hymenoptera: Formicidae) z rodzaju *Formica* L. – Fragmenta Faunistica 16: 145-224.
- EMERY, C. 1925: Hymenoptera. Fam. Formicidae. Subfam. Formicinae. – Genera Insectorum 183: 1-302.

- GOROPASHNAYA, A. 2003: Phylogeographic structure and genetic differentiation in *Formica* Ants. Acta Universitatis Upsaliensis. – Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology 912: 1-36.
- GOROPASHNAYA, A., FEDOROV, V.B., SEIFERT, B. & PAMILO, P. 2004a: Limited phylogeographic structure across Eurasia in two red wood ant species *Formica pratensis* and *F. lugubris* (Hymenoptera, Formicidae). – Molecular Ecology 13: 1849-1858.
- GOROPASHNAYA, A., FEDOROV, V.B. & PAMILO, P. 2004b: Recent speciation in the *Formica rufa* group ants (Hymenoptera: Formicidae): inference from mitochondrial DNA phylogeny. – Molecular Phylogenetics and Evolution 32: 198-206.
- GYLLENBERG, G. & ROSENGREN, R. 1984: The oxygen consumption of submerged *Formica* queens (Hymenoptera, Formicidae) as related to habitat and hydrochoric transport. – Annales Entomologici Fennici 50: 76-80.
- KUTTER, H. 1917: Myrmecologische Beobachtungen. – Biologisches Zentralblatt 37: 429-437.
- KUTTER, H. 1977: Hymenoptera-Formicidae. In: SAUTER, W. (Ed.): Fauna Insecta Helvetica 6. – Schweizerische Entomologische Gesellschaft Zürich, Zürich, 298 pp.
- NASSONOV, N.V. 1889: Materialy po estestvennoi istorii murav'ev preimushchestvenno Rossii. – Trudy Laboratorii Zoologicheskago Musea Imperatorskago Moskovskago Universiteta 58: 1-78.
- NYLANDER, W. 1846: Adnotationes in monographiam formicarum borealium Europae. – Acta Societatis Scientiarum Fennicae 2: 875-944.
- SEIFERT, B. 2002: How to distinguish most similar insect species - improving the stereomicroscopic and mathematical evaluation of external characters by example of ants. – The Journal of Applied Entomology 126: 445-454.
- SMITH, F. 1878: Scientific Results of the Second Yarkand Mission; based upon the collections and notes of the late Ferdinand Stoliczka, Ph.D. Hymenoptera. – Superintendent of Government Printing (Government of India), Calcutta, 22 pp.
- SÖRENSEN, U. 2001: Untersuchung zur Variabilität der Neststandorte von *Coptoformica forsslundi* LOHMANN, 1949 (Hymenoptera:Formicidae) im Naturschutzgebiet "Süderlögümer Binnendünen" (Nordfriesland). – Myrmecologische Nachrichten 4: 17-24.
- YARROW, I.H.H. 1954: The British ants allied to *Formica fusca* L. – Transactions of the Society for British Entomology 11: 229-224.