



## A taxonomic revision of the Palaearctic members of the *Formica rufa* group (Hymenoptera: Formicidae) – the famous mound-building red wood ants

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### Abstract

A revision of the Palaearctic members of the *Formica rufa* group, the famous mound-building red wood ants, is presented based on Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT) and on genetic information from studies published in cooperation with others. Standardized morphological character systems were described numerically to allow objective hypothesis formation by exploratory data analyses and testing by hypothesis-driven data analyses. NUMOBAT data were recorded in a total of 1200 samples with 5500 worker individuals and 410 gynes. Comparative tables to workers and gynes of all species and the most frequent hybrids and a key to the workers are presented. Considering 54 available names, the survey recognized 13 good species, 32 junior synonyms and eight names not interpretable to species level (incertae sedis). The ratio of junior synonyms against the number of recognized species is elevenfold the ratio found in a revision of Palaearctic *Lasius* s.str. conducted by the same author in 2020 with basically the same methodology. Excessive name production in the *F. rufa* group is partly result of the big attention these eye-catching ants have received by naturalists but it also reflects the enormous difficulties to reasonably interpret a multitude of phenotypes. These difficulties are caused by extraordinary frequency of reticulate evolution, particular mechanisms for the evolution of deviating local populations, and intraspecific polymorphism with differences sometimes being larger than those between species. Hybridization and introgression were shown or made plausible in 46% of the 13 recognized species with regional hybridization frequencies of above 20% in three species. The author assumes that the evolutionary history of *F. rufa* group ants will turn out as extremely reticulate comparable with the situation in *Heliconius* butterflies or Darwin Finches once whole genome analyses will be available for all species. The 13 species of the *F. rufa* group were assigned to four species complexes: (a) the *F. rufa* complex with *F. rufa* LINNAEUS, 1761 and *F. polyctena* FOERSTER, 1850; (b) the *F. lugubris* complex with *F. lugubris* ZETTERSTEDT, 1838, *F. helvetica* sp.n., *F. paralugubris* SEIFERT, 1996, *F. aquilonia* YARROW, 1955 and *F. ussuriensis* sp.n.; (c) the *F. pratensis* complex with *F. pratensis* RETZIUS, 1783 and *F. kupyanskayae* BOLTON, 1995 and (d) the *F. truncorum* complex with *F. truncorum* FABRICIUS, 1804, *F. dusmeti* EMERY, 1909, *F. frontalis* SANTSCHI, 1919 and *F. sinensis* WHEELER, 1913. *Formica yessensis* WHEELER, 1913 is recognized as a new junior synonym of *F. truncorum*. Special sections describe the situation in six hybrid combinations. Comments on species incertae sedis and unavailable names are given in a final chapter.

**Key words:** Reticulate evolution, cryptic species, polymorphism, hybridogenous species, morphometrics, new species.

Received 13 October 2020; revision received 20 January 2021; accepted 2 February 2021

Subject Editor: Herbert Zettel

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## Introduction

With their impressing mound constructions and armies of foragers moving restlessly over any surface of their woodland habitats, wood ants of the *Formica rufa* LINNAEUS, 1761 group are highly visible for everyone. Literature on their life history, ecology and conservation should take more than 10 shelf meters. These ecologically dominant ants are key elements for ecosystem functioning and flow of matter and energy in temperate and boreal forests of the Palaearctic (e.g., FROUZ & al. 2016). The figures are impressive: Small-scale nest density, worker number and worker fresh weight may achieve 20 nests, eight million workers and 80 kg per hectare in *Formica aquilonia* YARROW, 1955 or *Formica polyctena* FOERSTER, 1850 and the maximum large-scale density of *F. aquilonia* was censused as 1070 nests / km<sup>2</sup> on an area of 3 km<sup>2</sup> which corresponds to about three tons fresh weight per km<sup>2</sup> (reviewed in SEIFERT 2018). The same source gives the following estimate: Expressed in energy equivalents, a *F. polyctena* population at saturation density consumes year after year 4% of the net primary production of a mature temperate forest, but only 0.16% of net primary production are finally fixed in ant biomass.

Another remarkable trait of Palaearctic *F. rufa* group ants is reticulate evolution. Reticulate evolution is the horizontal transfer of genes between species lineages and is largely caused through hybridization. Those systematists generally doubting the reality of species will find massive reticulate evolution in *F. rufa* group ants a good example to support their view. It will be shown in this paper that hybridization and introgression are known so far in 46% of the 13 species recognized here. It is predicted that the evolutionary history of Palaearctic *F. rufa* group ants as a whole will turn out as extremely reticulate once whole genome analyses are available for many species as given in the pioneering study on *Heliconius* butterflies (EDELMAN & al. 2019). Regional frequencies of hybrids and backcrosses in *F. polyctena* and *F. rufa* (see SEIFERT 1991, SEIFERT & al. 2010) and *F. aquilonia* and *F. polyctena* (see BERESFORD & al. 2017) may exceed 20% and my estimates of the total hybrid frequency over the whole Palaearctic range of the three parental species is certainly above 5% in both cases. This undeniable gene flow represents a dilemma for taxonomists who want to maintain the long-established names

*F. polycrena* and *F. aquilonia* at species level. According to the Gene And Gene Expression (GAGE) species concept (SEIFERT 2020b), species divergence must be demonstrable through analysis of nuclear gene sequences and / or their expression products by showing gaps between the genetic and / or phenetic clusters or by minimum disagreement in classification between different analysis systems below a defined threshold. The latter becomes difficult or impossible if there are lots of hybrids and introgression from multiple directions in the investigated material. Unavoidably, we will encounter cases with most complicated evolutionary histories in which even the smartest species concept is of little help. Naming should then follow pragmatism in scientific communication.

Uncomfortable feelings for a taxonomist are also produced by occurrence of locally confined geno- / phenotypes showing characters not matching any described species or any identified hybrid. In the case of *Formica helvetica* sp.n., I took the risk to give a genetically but not morphologically clusterable local population a taxonomic status. This is a provocation or an appeal to stimulate future ant students to further investigations. In other cases – a deviating population of *Formica rufa* from the summit of Blansky Les / South Bohemia and two deviating local populations of *Formica lugubris* ZETTERSTEDT, 1838 from near Ambri / Ticino and near Martello / Alto Adige – I did not risk introducing a new taxon. There are reasons to assume that the evolution of deviating local populations is enforced by a combination of the following factors: (a) hybridization, (b) self-isolation in quasi-closed supercolonial systems, (c) strong genotype selection and (d) small-scale geographic barriers (KULMUNI & al. 2010, SEIFERT 2010, KULMUNI & PAMILO 2014). Such a local scenario was assumed by SEIFERT (2018) for the evolution of *Formica paralugubris* SEIFERT, 1996 which developed into one of the most dominant wood ants of the western Alps after the last glaciation.

The third problem is extreme intraspecific polymorphism with intraspecific differences often being larger than those between species. Examples are *Formica pratensis* RETZIUS, 1783 and Fennoscandian *Formica lugubris* (see SEIFERT 1992, 2003). Detection of phenotype polymorphism is done in the best way by an integrative study with parallel investigation of morphology and nuclear DNA. Alternatively, when data on nuclear DNA or breeding experiments are not available, an assessment can be done by the DIMORPH test (SEIFERT 2016b, 2019c). This test is based on analyzing intranidal and large-scale (whole-population) phenotype distributions and comparing the observed distributions with predictions for different scenarios of heterospecificity and intraspecific dimorphism.

Reticulate evolution, occurrence of local variants, extreme intraspecific pilosity polymorphism and the big attention these eye-catching ants have received has led to the production of much more synonyms than usually discovered in other ant groups. There are 54 available names attributable to the Palaearctic *Formica rufa* group

but 32 of these are junior synonyms and eight names are not interpretable to species level (incertae sedis). This mess is completed by 14 unavailable names. The enormous ratio of 32 junior synonyms within a species group of only 13 recognized species is unprecedented in any taxonomic revision conducted by the author since the year 1988. This ratio of junior synonyms against the number of recognized species is elevenfold the ratio found in a revision of Palaearctic *Lasius* s.str. conducted by the same author with basically the same methodology and over the same geographic area (SEIFERT 2020a): Here we have only 12 synonyms within 56 recognized species.

The working philosophy of this revision is Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT, SEIFERT 2009). In distinction from not strictly quantifying approaches that do not aim at generating hypotheses from the data they produce, NUMOBAT demands to describe character systems numerically to allow objective hypothesis formation and testing. Following the GAGE species concept (SEIFERT 2020b), the decisive character systems describing species identities are only nuclear DNA and / or their expression products. The architecture of phenotype is such an expression product and is used here as leading indicator for taxonomic treatment of species identities and assessment of type specimens. Various Nest-Centroid (NC) clustering methods (SEIFERT & al. 2014, Csósz & FISHER 2015) have proven as excellent in indicating the basic taxonomic structure for any ant genus studied during the last seven years. However, there are important limitations to these approaches. Their main weakness is that hybrid samples are usually not exposed as an own cluster as many of them are absorbed by the clusters of either parental species. This disguising might also apply to very rare species present in the material with only single samples. A sample-by-sample supervision in the vectorial space is needed here to avoid misinterpretations. Furthermore, NC-clustering of morphological data is no silver bullet to uncover each cryptic species. This became apparent in *Formica helvetica* sp.n. which was sufficiently separated from *Formica lugubris* by nuclear DNA. This species is either generally inseparable by worker morphology or the character system applied here does not include the specific diagnostic elements.

## Material

Consideration of males is not performed here because males are strongly under-represented in the collections and are in some taxa unknown. Species-level taxonomy should concentrate on the caste which is permanently available throughout the year and this is workers. Furthermore, the author does not know of a single Formicinae genus worldwide where a separation of species which are very similar in the female castes was testably demonstrated by means of male genitalia. NUMOBAT data were recorded in a total of 1200 samples (largely nest samples) with 5500 worker individuals and 410 gynes. With the exception of type specimens and other samples of special relevance,

data of this large material are not presented in detail in the main text of this paper but listed in the electronic supplementary information at the journal's web pages (SI1, SI2, and SI3). The abbreviations of depositories are as follows:

- AMNH New York – American Museum of Natural History, New York, USA  
 FMNH Helsinki – Finnish Museum of Natural History, Helsinki, Finland  
 MCZ Harvard – Museum of Comparative Zoology of the Harvard University, Cambridge, USA  
 MHN Genève – Muséum d'histoire naturelle de Genève, Genève, Switzerland  
 MNCN Madrid – Museo Nacional de Ciencias Naturales, Madrid, Spain  
 MSNB Bruxelles – Muséum des sciences naturelles de Belgique, Bruxelles, Belgium  
 NBC Leiden – Naturalis Biodiversity Center Leiden, Leiden, Netherlands  
 NHM Basel – Naturhistorisches Museum, Basel, Switzerland  
 NHM Maastricht – Natuurhistorisch Museum Maastricht, Maastricht, Netherlands  
 RIFCAF Beijing – Research Institute of Forestry, Chinese Academy of Forestry, Beijing, China  
 SIZ Kiev – Schmalhausen Institute of Zoology, Kiev, Ukraine  
 SMN Görlitz – Senckenberg Museum für Naturkunde, Görlitz, Germany  
 ZM Berlin – Zoologische Sammlungen am Museum für Naturkunde, Berlin, Germany  
 ZM Copenhagen – Zoological Museum of the University, Copenhagen, Denmark  
 ZM Kiel – Zoologisches Museum der Universität, Kiel, Germany  
 ZMLU Lund – Zoologiska Museet, Lunds Universitet, Lund, Sweden  
 ZMLU Moskva – Zoological Museum of Moscow Lomonossov University, Moskva, Russia

## Methods

**The species concept applied:** The GAGE species concept of SEIFERT (2020b) was used. However, the high frequency of hybridization and introgression between *Formica rufa*, *Formica polyctena*, and *Formica aquilonia* led to difficulties to delimit clear clusters and to apply the error threshold of < 4% as it was proposed by SEIFERT (2020a, b). Applying this threshold would have meant synonymizing *F. polyctena* and *F. aquilonia* with *F. rufa*. The author decided against this radical solution for reasons of pragmatism in scientific communication.

**Recording of NUMOBAT characters:** A pin-holding stage, permitting full rotations around X-, Y-, and Z-axes and a Leica (Wetzlar, Germany) M165C high-performance stereomicroscope equipped with a 2.0× planapochromatic objective (resolution 1050 lines / mm) were

used for spatial adjustment of specimens at magnifications of 120 - 360×. A Schott KL 1500 cold-light source (Mainz, Germany) 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 visualization of silhouette lines. A Schott KL 2500 LCD cold-light source in combination with a Leica coaxial polarized-light illuminator provided optimal resolution of tiny structures and microsculpture at highest magnifications. Simultaneous or alternative use of the cold-light sources depending upon the required illumination regime was quickly provided by regulating voltage up and down. A Leica cross-scaled ocular micrometer with 120 graduation marks ranging over 52% of the visual field was used. To avoid the parallax error, its measuring line was constantly kept vertical within the visual field. Measurement errors are influenced by some 10 different factors (SEIFERT 2002). Seventeen morphometric characters (four shape and 12 seta characters plus absolute head size) were recorded in workers. In gynes, twenty-four characters (five shape, 16 setae and two surface characters plus absolute head size) were recorded. Figures assisting the definition of these characters are given in SEIFERT (2018). All seta counts (nSc, nCH, nGu, nPn, nMes, nPr, nMet, nPe, nHT, nGfr, nSt) considered only hairs protruding > 10 µm from cuticular surface. The bilateral characters were recorded as arithmetic mean of both sides.

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

**CS** – arithmetic mean of CL and CW as less variable indicator of body size.

**CW** – maximum cephalic width; this is either across, behind, or before the eyes.

**EyeHL** – length of longest hair on eye.

**FodG** – mean distance of foveolae on paramedian (!) dorsum of first gaster tergite in gynes. The number of foveolae n in an area A were counted. FodG is then  $\sqrt{A} / \sqrt{n}$ . Counting was performed within squares of  $10 \times 10$  graduation marks (GRM) at a magnification of 150 ×. In the Leica cross-scaled ocularmicrometer, the space between the GRM and the cross line is exactly 10 GRM wide. Most effective counting is done when the counting squares are aligned longitudinally but in case of polluted surfaces various numbers of  $10 \times 10$  GRM squares, connected or not, can be selected. Pubescence may be patchily removed to reduce the counting error.

**F2L** – Median length of second funiculus segment in dorsal view (dorsal view is given when the swivelling plane of first funiculus segment is positioned in the visual plane). Take care to really measure median length and to recognize the real segment margins.

**F2W** – maximum width of cuticular surface of second funiculus segment in dorsal view.

**GfrHL** – length of longest seta on frontal face of first gaster tergite in gynes.

**GuHL** – length of longest seta on underside of head (“gula”).

**IF2** – ratio F2L / F2W.

**MetHL** – length of the longest seta on a metapleuro-propodeal area below a straight reference line that is directed parallel to the straight section of lower metapleural margin and touches the lower margin of propodeal spiracle (SEIFERT 2018: fig. 353). The area of caudal propodeal slope below this line is included but weir hairs at orifice of metapleural gland and setae near to petiolar junction are excluded. Take care to visualize the lateral suture between meso- and metapleuron.

**ML** – mesosoma length in the alates; measured in lateral view from the caudalmost portion of propodeum to the frontalmost point of the steep anterior pronotal slope (i.e., not to the frontalmost point of the whole pronotum that is usually concealed by the occiput).

**mPnHL** – mean pronotal hair length. Applied measuring schedule: select one of the longest hairs on dorsal pronotum and calculate the arithmetic mean length of this hair and of its six nearest neighbors. If there are less than seven hairs on pronotum, the mean is calculated from the hairs present. The very fine proprioceptive setae on anterior pronotal shield are excluded.

**nCH** – bilateral mean of the number of standing hairs protruding more than 10 µm from head silhouette as seen in full face view. Counting begins at the level of anterior eye margin and ends at median occiput. The full depth of focus is used for counting and the parallax error is considered.

**nGfr** – sum of setae on frontal profile of first gaster tergite in gynes.

**nGu** – bilateral mean of the number of setae protruding from underside of head as visible in lateral view.

**nHT** – bilateral mean of the number of setae on extensor profile of hind tibia.

**nMes** – bilateral mean of the number of setae on mesopleuron protruding from cuticular surface as seen in dorsal view; the specimen is not turned during counting.

**nMet** – bilateral mean of the number of setae on a metapleuro-propodeal area defined under MetHL. Setae positioned directly on the suture are counted as 0.5. Definitely excluded from count are weir hairs fringing the metathoracal gland, hairs standing on the ventrolateral edge of metapleuron and hairs which are very near to the petiolar junction.

**nPe** – bilateral mean of the number of setae surpassing the margin of petiole above the spiracle in frontal / caudal view by more than 10 µm.

**nPn** – bilateral mean of the number of setae on pronotum. Proprioceptive setae on anterior pronotal shield are excluded. Numbers > 50 are often inaccurate estimates. “Precise” nPn<sub>1750</sub> data are generated by allometric corrections (see section “Removal of allometric variance”, p. 137).

**nPr** – bilateral mean of the number of setae on propodeum above the level of the lower spiracular margin.

**nSc** – bilateral mean of number of setae on dorsal plane of scape under exclusion of the most apical setae, counted with view on the small scape diameter.

**nSt** – bilateral sum of setae protruding from ventral surface of first gaster sternite as visible in profile view.

**OccHL** – apparent protrusion length of the longest standing seta over the postocular head contour in full-face view. This value is shorter than the real seta length because setae bases are often concealed and setae axes are inclined compared with visual plane. This traditional mode of measuring (SEIFERT 1992) was maintained to save measurement time.

**PeW** – maximum width of petiole scale.

**PnHL** – length of the longest seta on pronotum.

**SL** – maximum straight-line scape length excluding articular condyle and its neck.

**Smax** – maximum scape width at midpoint; data of both scapes are averaged.

**sqPDG** – pubescence distance on paramedian dorsal plane of first gaster tergite in gynes; the length of a transversal measuring line is divided by the number of pubescence hairs crossing or touching this line; in each specimen this is the mean over four to six 400 µm measuring lines under exclusion of surface parts with apparently damaged pubescence.

**StHL** – length of longest seta on ventral surface of first gaster sternite in gynes.

**Removal of allometric variance:** There is a strong intraspecific variance of body size in *Formica rufa* group ants which is largely determined by age and social structure of the colonies. In order to show interspecific differences independent of body size in comparative tables and to increase resolution of principle component analyses, a removal of allometric variance (RAV) was performed for worker ants following the basic procedure described by SEIFERT (2008). Evaluation of scatter plots suggested the use of linear monophasic allometry functions in 16 characters but of a diphasic function in SL / CS. RAV was calculated assuming all individuals to have a cephalic size of CS = 1750 µm. RAV functions were calculated as the arithmetic mean of the species-specific functions of all 13 Palaearctic species, with separable morphs considered as separate entities. With CS given in mm, the RAV functions of four shape and 12 seta characters are:

$$CL / CW_{1750} = CL / CW / (-0.1064 * CS + 1.2886) * 1.0743$$

$$EyeHL_{1750} = EyeHL / (4.15 * CS + 14.2) * 21.5$$

$$GuHL_{1750} = GuHL / (41.39 * CS + 64.73) * 137.2$$

$$MetHL_{1750} = MetHL / (39.34 * CS + 71.78) * 140.6$$

$$mPnHL_{1750} = mPnHL / (24.07 * CS + 38.28) * 80.4$$

$$nCH_{1750} = nCH / (7.70 * CS + 3.34) * 16.82$$

$$nGu_{1750} = nGu / (6.11 * CS + 0.46) * 11.16$$

$$nMes_{1750} = nMes / (8.93 * CS - 0.29) * 15.34$$

$$nMet_{1750} = nMet / (6.25 * CS - 3.70) * 7.23$$

$$nPn_{1750} = nPn / (13.98 * CS - 6.72) * 17.74$$

$$nPr_{1750} = nPr / (10.08 * CS - 5.77) * 11.87$$

$$nSc_{1750} = nSc / (0.49 * CS + 2.87) * 3.73$$

$$OccHL_{1750} = OccHL / (37.57 * CS + 21.6) * 87.3$$

$$\begin{aligned}
 \text{PeW / CS}_{1750} &= \text{PeW / CS} / (0.0170 * \text{CS} + 0.4493) * 0.4791 \\
 \text{SL / CS}_{1750} &= \text{SL / CS} / (-0.06743 * \text{CS} + 1.04464) \\
 &\quad * 0.9266 \text{ for } \text{CS} \leq 1750 \mu\text{m} \\
 \text{SL / CS}_{1750} &= \text{SL / CS} / (-0.08561 * \text{CS} + 1.07646) \\
 &\quad * 0.9266 \text{ for } \text{CS} > 1750 \mu\text{m} \\
 \text{SL / Smax}_{1750} &= \text{SL / Smax} / (-0.1286 * \text{CS} + 9.994) \\
 &\quad * 9.769
 \end{aligned}$$

**Explorative and supervised data analyses, classification, and statistical testing:** In the first level of analysis, four different forms of exploratory data analyses (EDA) were run using nest centroids as input data (NC-clustering). These were firstly hierarchical NC-Ward clustering, secondly and thirdly the hierarchical method NC-part.hclust and the iterative vector-quantization method NC-part.kmeans – both implemented in partitioning algorithms based on recursive thresholding (for details, see Csősz & FISHER 2015). Accessorily, as fourth method, nonmetric multidimensional scaling combined with iterative vector-quantization NC-NMDS.kmeans (SEIFERT & al. 2014) was applied. The first three methods were run as the standard working routine. Checking samples with controversial classifications was done by an interaction of NC-clustering and a controlling linear discriminant analysis (LDA) in which these samples were run as wild-cards, following the rationale described in SEIFERT & al. (2014). The final classification (“final species hypothesis”) was established by the LDA in an iterative procedure and there remained no undecided cases even if their posterior probabilities were close to 0.5.

As all these NC-clustering algorithms were run with basically the same morphological data, they are not independent and expected to result in similar classifications. In fact, classifications by all four algorithms are equal if a species discrimination is very clear, but disagreements between the four algorithms increase the more difficult the species separation becomes. As result, parallel runs of different algorithms make sense as this will improve the awareness of a problem. This positive statement on a morphological method does not deny that integration of data from other disciplines, preferentially study of nuclear DNA, is highly required.

It has to be repeated here that the high hybridization frequency in *Formica rufa* group ants and the weakness of NC-clustering to expose hybrids may lead to unrealistic interpretations. Explicitly, NC-clustering generated the illusion that *Formica polyctena* and *Formica rufa* as well as *Formica polyctena* and *Formica aquilonia* are clearly separable species. Revealing the true situation required further analytical steps: checking the data sample by sample and analyzing them in the simple two-dimensional vectorial space. This was preferentially done by a principal component analysis (PCA) with a maximum of three considered entities and often with character selection. Alternatively, the position of suspicious samples was checked by wild-card runs in a linear discriminant analysis (LDA). PCA, LDA, analysis of variance (ANOVA) were run with the SPSS 15.0 software package.

It may be asked if the numeric character system used here is informative from a phylogenetic perspective. This can be clearly denied. Setae characters, that are powerful for species delimitation and form a dominant part of the data, are bad indicators of long-term phylogeny. Earlier attempts of running all species in a single analysis under consideration of the shape and setae characters described above resulted in unrealistic dendograms. For instance, *Formica dusmeti* EMERY, 1909, clearly a species of the *Formica truncorum* complex, clustered together with *Formica polyctena*, which is very distant in any known genetic tree and by assessment of overall morphology. The same extreme misplacement occurred with *F. truncorum* FABRICIUS, 1804 and *Formica sinensis* WHEELER, 1913, which are placed within the *Formica lugubris* species complex. Reasonably good morphology-based phylogenies should be possible but require intelligent selection of accessory character systems and other algorithms which incorporate both qualitative and quantitative characters.

## Results

**Diagnosis and subdivision of the Palaearctic *Formica rufa* group:** There is evidence from mtDNA sequences that the Nearctic species of the *F. rufa* group form a monophyletic branch that is the sister clade to the monophyletic branch formed by the Palaearctic species (TRAGER 2016). This appears to be in agreement with subjective assessment of phenotype. Yet, in the absence of thorough studies based on nuDNA, I do not further comment on this issue and restrict the consideration to the Palaearctic species and their subdivision. The Palaearctic members of the *F. rufa* group can be separated from other Palaearctic species of the genus *Formica* in having the following character combination: anteromedian margin of clypeus not notched and posterior margin of head in dorsal view not clearly excavated, frontal triangle contrastingly more shiny than the surrounding surface of head, basal margin of mandibles without small denticles, above-ground nest parts made as regular mounds or irregular piles of plant particles, all species are incapable of independent single-queen nest foundation. An attempt to subdivide the *F. rufa* group into four species complexes is as follows.

The *Formica rufa* species complex contains only *F. rufa* and *Formica polyctena* and has its main distribution within the temperate to subboreal or planar to submontane zones. **Workers:** Hind margin of head without setae. Scape slender with SL / Smax 10.0 - 10.3. With view on the swivelling plane of the first segment of antennal funiculus, ratio of median length of second funicular segment against its maximum width < 2.0. **Gynes:** dorsum of first gaster tergite shiny with widely spaced microfoveolae having a mean distance of about 25 - 80 µm and a very dilute pubescence, sqPDG 9.0 - 12.2 (Figs. 1, 2).

The *Formica lugubris* species complex contains *F. lugubris*, *Formica helvetica* sp.n., *Formica aquilonia*, *Formica ussuriensis* sp.n., and *Formica paralugubris*. The main distribution characteristics are subboreal to boreal

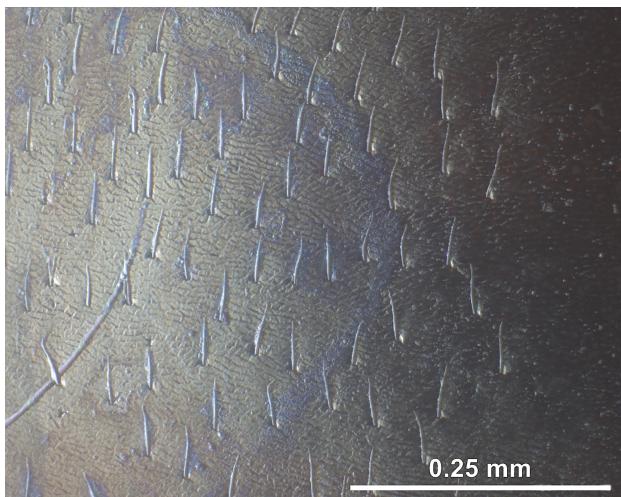


Fig. 1: *Formica rufa*, gyne; paramedian surface of the dorsum of first gaster tergite.

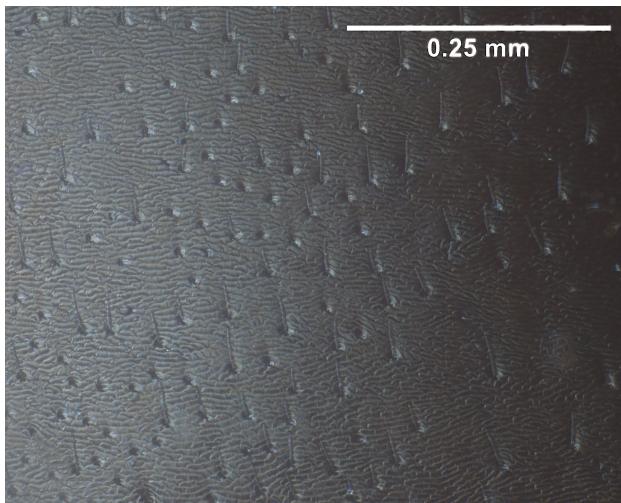


Fig. 2: *Formica polycrena*, gyne; paramedian surface of the dorsum of first gaster tergite. There is some trend to show stronger transverse microripples and a more dilute pubescence than *Formica rufa*.

and submontane to subalpine. **Workers:** Hind margin of head hirsute, at least laterally with few standing setae. Scape more thickset, SL / Smax 9.2 - 9.5. With view on the swivelling plane of the first segment of antennal funiculus, ratio of median length of second funiculus segment against its maximum width < 2.0. **Gynes:** dorsum of first gaster tergite with more densely arranged microfoveolae having a mean distance of 22 - 28 µm and a denser pubescence, sqPDG 4.0 - 10.0 (Fig. 3).

The *Formica pratensis* species complex contains *F. pratensis* and *Formica kupyanskayae* BOLTON, 1995. The main distribution characteristics are submediterranean to temperate and planar to submontane. **Workers:** Hind margin of head hirsute, at least laterally with few standing setae. Scape more slender, SL / Smax 9.8 - 10.7. With view on the swivelling plane of the first seg-

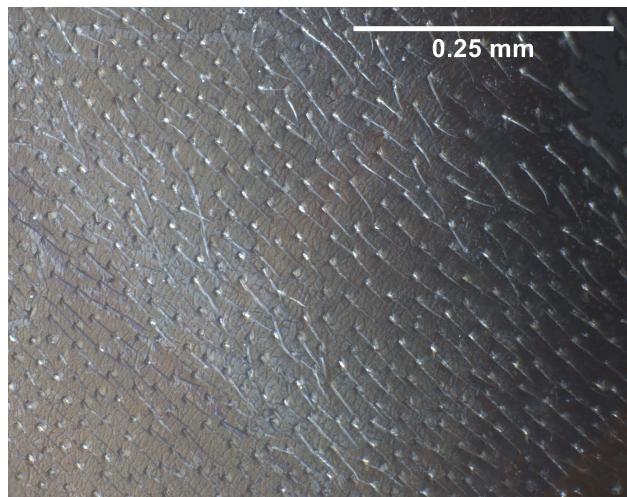


Fig. 3: *Formica lugubris*, gyne; paramedian surface of the dorsum of first gaster tergite. The transverse microsculpture is as weak as in *Formica rufa*, but the density of pubescence and microfoveolae is much higher.

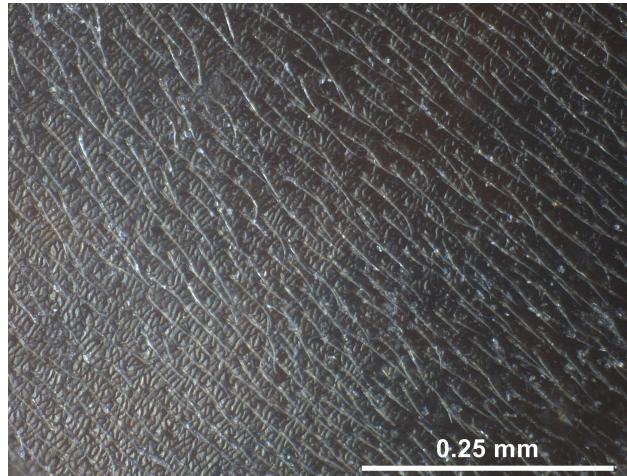


Fig. 4: *Formica pratensis*, gyne; paramedian surface of the dorsum of first gaster tergite. The strength of transverse microripples is at maximum within the *Formica rufa* group and pubescence density comparable with *Formica lugubris*.

ment of antennal funiculus, ratio of median length of second funiculus segment against its maximum width < 2.0. **Gynes:** dorsum of first gaster tergite matt, showing at larger magnification densely packed transverse microripples and a denser pubescence, sqPDG 3.6 - 4.0 (Fig. 4). Scape much more slender than in the *Formica rufa* and *F. lugubris* species complexes, SL / Smax 9.66 - 9.75.

The *Formica truncorum* species complex contains *F. truncorum*, *Formica dusmeti*, *Formica frontalis* SANTSCHI, 1919, and *Formica sinensis*. The distribution characteristics are heterogeneous from submediterranean to boreal and planar to montane. **Workers:** Lateral clypeus deeply depressed, as result anterior portion of lateral clypeus forming a bead. With view on the swivelling plane

of the first segment of antennal funiculus, ratio of median length of second funiculus segment against its maximum width  $\geq 2.0$ . Scape longer than in the other three species complexes, SL / CS 0.985 - 1.015. Reddish pigmentation on whole body on average more extended than in the other three species complexes. **Gynes:** Shape of clypeus and funiculus segments similar to worker. Dorsum of first gaster tergite matt or silky shiny, showing at larger magnification densely packed transverse microripples; microfoveolae, when present, are widely spaced, FodG 50 - 90; pubescence dilute, sqPDG 9.8 - 12.2.

**Key to the workers of the Palaearctic *Formica rufa* group:** This key can certainly solve a good number of determinations in a rather simple way but the best results are achieved when own discriminant functions are run using the data of SI1 as reference. In contrast to Tables 1 - 5 and for more simplicity, this key works with primary, not allometrically corrected data, and all linear measurements are given in mm. Because of the enormous intraspecific and intranidal variation, nest sample means should be considered in critical cases. The percentage of reddish pigmentation follows a positive allometric trend and is of rather little indicative value. Figures 5-20 with z-stacking photos of the species from different viewing positions are presented after the key.

- 1a** With view on the swivelling plane of the first segment of antennal funiculus, ratio of median length of second funiculus segment against its maximum width  $\geq 2.0$  (movement within only a swivelling plane is defined by the hinge joint of distal scape with the first funiculus segment). Lateral clypeus deeply depressed, as result anterior portion of lateral clypeus forming a bead. Medium to large-sized workers usually with whole surface of head, mesosoma and petiole light reddish brown. *Formica truncorum* group ..... 2
- 1b** Ratio of median length of second funiculus segment against its maximum width  $< 2.0$ . Lateral clypeus less deeply depressed and anterior portion of lateral clypeus not forming a bead. Percentage of surface with dark or blackish brown pigmentation usually larger ..... 5
- 2a** Iberian Peninsula and Pyrenees ..... 3
- 2b** Outside Iberian Peninsula and Pyrenees ..... 4
- 3a** Gula and dorsal mesosoma without or with very few setae; nGu + nPn + nPr + nMet  $< 30$  ..... *Formica dusmeti*
- 3b** Gula and dorsal mesosoma with more setae; nGu + nPn + nPr + nMet  $> 30$  ..... *Formica frontalis*
- 4a** More hirsute on all body positions. Discriminant  $76.03 * \text{EyeHL} + 0.073 * \text{nCH} - 0.057 * \text{nGu} + 0.08 * \text{nMet} + 12.36 * \text{mPnHL} - 14.75 * \text{MetHL} - 1.33 > 0$  (error 0% in 92 individuals, Tab.5) ..... *Formica truncorum*
- 4b** Less hirsute on all body positions. Often a disparity between rather few setae on dorsal mesosoma and rather many setae on gula is visible. Discriminant

- $< 0$  (error 0% in 70 individuals, Tab.5). Only E Tibet and China. .... *Formica sinensis*
- 5a** Palaearctic with exception of Russian Far East, NE China, Korea, Japan ..... 6
- 5b** Russian Far East, NE China, Korea, Japan ..... 12
- 6a** Hind margin of head without or only occasional small setae, nCH 0 - 1; if nCH is slightly larger, then scape slender with SL / Smax  $10.08 \pm 0.39$ . Eyes with only short microsetae, EyeHL  $0.020 \pm 0.004$ . Mesopleuron with rather few setae, nMes  $10.5 \pm 7.4$ . Discriminant  $0.024 * \text{nCH} + 0.08 * \text{nMes} - 0.046 * \text{nPr} - 11.451 * \text{SL} + 72.20 * \text{Smax} + 62.96 * \text{EyeHL} + 3.879 < 0$  (error 0% in 114 nest sample means) ..... 7
- 6b** Hind margin of head usually with many setae, nCH  $> 1$ ; if nCH is near zero (occasional in *F. aquilonia*), then scape thickset with SL / Smax  $9.27 \pm 0.34$ . Eyes with longer microsetae, EyeHL  $0.030 \pm 0.008$ . Mesopleuron with rather many setae, nMes  $21.6 \pm 10.4$ . Discriminant  $> 0$  (error 1.7% in 180 nest sample means) ..... 8
- 7a** Weakly haired; nest means: nGu 0.1 - 3.0, GuHL  $0.007 - 0.097$ , nPn 0.1 - 5.6, mPnHL 0.006 - 0.055, nPr 0 - 5.2, nCH 0 - 0.9 (microsetae) ..... *Formica polycetena*
- 7b** Moderately hairy; nest means: nGu 1.9 - 6.6, GuHL  $0.096 - 0.197$ , nPn 5.8 - 16.0, mPnHL 0.047 - 0.083, nPr 4.4 - 11.2, nCH 0 - 1.2 (microsetae) ..... *Formica polycetena × rufa*
- 7c** More strongly haired; nest means: nGu 5.1 - 11.0, GuHL  $0.155 - 0.224$ , nPn 12.5 - 45.0, mPnHL 0.061 - 0.102, nPr 8.5 - 25.1, nCH 0 - 3.6 (setae small) ..... *Formica rufa*
- 8a** Longest propodeo-metapleural hair below level of propodeal spiracle shorter: MetHL 0 - 0.142. With maximum CL in focal plane, contour of head from median occiput to anterior eye margin with fewer setae: nCH 1.3 - 12.3. In doubtful cases: discriminant  $0.0503 * \text{nCH} + 22.213 * \text{MetHL} - 3.481 < 0$  (error 0% in 75 nest samples) ..... *Formica aquilonia*
- 8b** Longest propodeo-metapleural hair below level of propodeal spiracle longer: MetHL 0.134 - 0.237. With maximum CL in focal plane, contour of head from median occiput to anterior eye margin with more setae: nCH 5.2 - 65.2. Discriminant  $> 0$  (error 0% in 305 nest samples) ..... 9
- 9a** Scape more compact: SL / Smax 8.45 - 10.07. Frons appears at low magnification not perfectly matt, with a mild silky shine. This overall impression is produced by a weaker microsculpture with more longitudinal and less reticulate elements, particularly along the frontal line and anteriolaterally from mid ocellus. With all measurements in mm, discriminant  $2.524 - 3.89 * \text{CW} - 12.25 * \text{SL} + 5.889 * \text{PeW} + 117.36 * \text{Smax} > 0$  (error 0% in 291 nest samples for whole Palaearctic range). Boreo-montane species ..... 10

- 9b** Scape slender: SL / Smax 9.94 - 11.74. Frons matt. This overall impression is produced by a stronger more reticulate microsculpture. Discriminant < 0 (error 0% in 94 nest samples for whole Palaearctic range). More xerothermous woodland and woodland-steppe habitats ..... *Formica pratensis*
- 10a** Only W Alps, ranging east to approximately 11° E. Pronotal setae shorter: mPnHL 0.061 - 0.093. Propodeo-metapleural area below level of propodeal spiracle with fewer and shorter setae: nMet 3.3 - 9.7, MetHL 0.130 - 0.174. Discriminant 48.8 \* mPnHL + 16.6 \* MetHL - 0.100 \* nCH + 0.087 \* nMet - 0.072 \* nSc - 5.535 < 0 (error 0% in 70 nest sample means of four individuals, function only valid for Central Europe) ..... *Formica paralugubris*
- 10b** Widely distributed. Pronotal setae longer: mPnHL 0.079 - 0.127; nMet 6.5 - 14.8, MetHL 0.153 - 0.225. Discriminant > 0 (error 3.1% in 98 nest sample means of four individuals; function only valid for Central Europe) ..... **11**
- 11a** Whole Palaearctic. Population from the Alps poorly separable from *F. helvetica* sp.n. Discriminant 36.64 \* Smax + 0.128 \* nMet + 0.110 \* nSc + 0.068 \* nCH - 53.54 \* mPnHL - 3.224 > 0 (error 20.5% in 380 individuals and 14.6% in 89 nest samples) ..... *Formica lugubris*
- 11b** Only known from a local population in Mingèr Valley in the Eastern Swiss Alps. Separation from *F. lugubris* very weak. Discriminant 36.64 \* Smax + 0.128 \* nMet + 0.110 \* nSc + 0.068 \* nCH - 53.54 \* mPnHL - 3.224 < 0 (error 13.3% in 30 individuals and 11.1% in nine nest samples) ..... *Formica helvetica* sp.n.
- 12a** Gula, mesopleuron, propodeum and metapleuron with many setae; nGu + nMes + nPr + nMet = 38 - 110. Discriminant 0.092 \* nGu + 0.048 \* nMes + 0.235 \* nMet + 0.051 \* nPr - 3.8554 > 0 (error 4.9% in 161 individuals and 0% in 44 nest samples) ..... *Formica lugubris*
- 12b** Gula, mesopleuron, propodeum and metapleuron with fewer setae; nGu + nMes + nPr + nMet = 3 - 46. Discriminant < 0 (error 0.9% in 424 individuals and 0% in 95 nest samples) ..... **13**
- 13a** Gular setae much longer, GuHL 0.217 ± 0.021; setae in all other body positions longer. Mesopleuron with fewer setae, nMes 6.6 ± 2.1. Discriminant 20.041 \* GuHL + 30.455 \* mPnHL + 2.661 \* MetHL - 0.147 \* nMes - 4.466 > 0 (error 0% in 38 individuals). Ussuri region ..... *Formica kupyanskayae*
- 13b** Gular setae much shorter, GuHL 0.098 ± 0.033; setae in all other body positions shorter. Mesopleuron with more setae, nMes 13.3 ± 4.9. Discriminant < 0 (error 0% in 386 individuals) ..... **14**
- 14a** Dorsal plane of scape and hind margin of head with rather many setae, nSc 10.5 ± 4.3, nCH 9.8 ± 4.2. Metapleuron with rather long setae, MetHL 0.133 ± 0.029. Discriminant 6.56 \* PeW - 11.58 \* Smax - 3.155 \* CW + 0.013 \* nCH + 0.357 \* nSc + 3.505 \* MetHL - 1.224 > 0 (error 9.8% in 41 individuals and 0% in 10 nest sample means). Ussuri and Sichote Alin range ..... *Formica ussuriensis* sp.n.
- 14b** Dorsal plane of scape and hind margin of head with very few setae, nSc 0.3 ± 1.3, nCH 4.3 ± 3.8. Metapleuron with short setae, MetHL 0.074 ± 0.047. Discriminant < 0 (error 1.0% in 102 individuals and 0% in 31 nest sample means) ..... *Formica aquilonia*



Figs. 5-13: (5-ussu) *Formica ussuriensis* sp.n., worker, holotype, head. (6-ussu) *Formica ussuriensis* sp.n., worker, holotype, lateral. (7-ussu) *Formica ussuriensis* sp.n., gyne, head; note the more trapezoid head shape. (8-aqui) *Formica aquilonia*, gyne, head; note the more rounded head shape. (9-prat) *Formica pratensis*, worker, neotype, head; note the more reticulate microsculpture of central vertex compared with *Formica lugubris* (Figs. 14, 15), producing a matt surface appearance. (10-prat) *Formica pratensis*, worker, neotype, lateral aspect. (11-prat) *Formica pratensis*, gyne, P morph, lateral; almost no setae on head, mesosoma, and first gaster tergite. (12-prat) *Formica pratensis*, gyne, N morph, lateral; many setae on head, mesosoma, and first gaster tergite. (13-kupy) *Formica kupyanskayae*, gyne, head.



Figs. 14-20: (14-lugu) *Formica lugubris*, worker, normal morph, head; central vertex suggestedly shiny due to weaker transverse microsculpture. (15-lugu) *Formica lugubris*, worker, Hippie morph, head; central vertex suggestedly shiny due to weaker transverse microsculpture. (16-helv) *Formica helvetica* sp.n., worker, holotype, head. (17-helv) *Formica helvetica* sp.n., worker, holotype, lateral. (18-trun) *Formica truncorum*, worker, head. (19-trun) *Formica truncorum*, gyne, head. (20-sine) *Formica sinensis*, worker, lateral; note the contrast between weak pronotal and strong gular pilosity.

Tab. 1: Workers of species and hybrids close to *Formica rufa*; head size and RAV-corrected data for the assumption of each individual having a head size of 1750 µm; data given as arithmetic mean ± standard deviation (lower extreme, upper extreme) number of individuals.

	<i>F. lugubris × rufa</i>	<i>F. rufa</i>	<i>F. rufa × polycetna</i> all	<i>F. rufa × polycetna</i> Continental	<i>F. rufa × polycetna</i> British	<i>F. polycetna</i>	
CS	1875 ± 90 [1698, 2071]	19	1891 ± 188 [1233, 2274] 331	1774 ± 191 [1263, 2197] 345	1794 ± 187 [1263, 2197] 256	1718 ± 193 [1295, 2047] 89	1670 ± 182 [1154, 2067] 309
CL/CW	1.113 ± 0.014 [1.083, 1.139]	19	1.109 ± 0.017 [1.062, 1.149] 330	1.104 ± 0.018 [1.041, 1.150] 345	1.105 ± 0.018 [1.054, 1.150] 256	1.103 ± 0.017 [1.041, 1.139] 89	1.103 ± 0.018 [1.048, 1.147] 309
SL/CS	0.934 ± 0.017 [0.899, 0.965]	19	0.939 ± 0.023 [0.882, 1.000] 330	0.936 ± 0.023 [0.866, 1.004] 345	0.937 ± 0.023 [0.866, 1.004] 256	0.934 ± 0.022 [0.872, 0.999] 100	0.932 ± 0.023 [0.846, 0.995] 309
SL/Smax	10.08 ± 0.16 [9.73, 10.37]	19	10.10 ± 0.40 [9.18, 11.29] 227	10.17 ± 0.38 [9.21, 11.10] 212	10.15 ± 0.39 [9.21, 11.10] 158	10.23 ± 0.36 [9.33, 10.91] 54	9.96 ± 0.37 [8.98, 11.10] 220
PeW/CS	0.470 ± 0.018 [0.430, 0.492]	19	0.467 ± 0.021 [0.410, 0.523] 234	0.476 ± 0.019 [0.424, 0.524] 200	0.477 ± 0.019 [0.433, 0.519] 118	0.476 ± 0.019 [0.424, 0.524] 82	0.483 ± 0.025 [0.426, 0.570] 115
EyeHL	24.2 ± 2.6 [20, 28]	19	21.8 ± 4.4 [10, 54] 234	19.2 ± 4.4 [0, 33] 247	19.7 ± 4.1 [0, 33] 165	18.1 ± 4.7 [0, 28] 82	17.4 ± 3.8 [0, 28] 285
nSc	0.6 ± 1.1 [0, 3.9]	19	0.0 ± 0.1 [0, 1.2] 330	0.0 ± 0.04 [0, 0.5] 345	0.0 ± 0.04 [0, 0.5] 256	0.0 ± 0.0 [0, 0.0] 89	0.0 ± 0.1 [0, 1.0] 309
nCH	13.5 ± 4.5 [4.1, 19.5]	19	0.81 ± 1.53 [0, 9.1] 330	0.10 ± 0.41 [0, 6.1] 345	0.10 ± 0.44 [0, 6.1] 256	0.11 ± 0.30 [0, 1.9] 89	0.06 ± 0.28 [0, 2.5] 309
OccHL	102.5 ± 21.7 [65, 133]	19	22.6 ± 28.9 [0, 120] 330	6.5 ± 16.6 [0, 93] 345	6.5 ± 17.0 [0, 93] 256	6.7 ± 15.6 [0, 56] 89	3.0 ± 12.0 [0, 76] 309
nGu	11.34 ± 2.67 [5.8, 16.6]	19	6.28 ± 1.89 [2.1, 12.6] 330	4.44 ± 1.83 [0.0, 10.7] 345	4.50 ± 1.95 [0.0, 10.7] 256	4.29 ± 1.42 [0.5, 8.0] 89	1.45 ± 1.59 [0.0, 6.4] 309
GuHL	193.4 ± 17.8 [167, 238]	19	188.5 ± 25.7 [106, 269] 330	153.5 ± 45.6 [0, 247] 345	149.1 ± 46.7 [0, 247] 256	166.3 ± 39.7 [24, 242] 89	50.8 ± 45.4 [0, 173] 309
nPn	26.1 ± 6.6 [13.3, 37.9]	21	20.2 ± 7.3 [3.5, 41.8] 330	8.6 ± 5.8 [0.0, 27.1] 345	9.0 ± 5.7 [0.0, 27.1] 256	7.6 ± 6.0 [0.0, 24.5] 89	2.4 ± 3.4 [0.0, 20.0] 309
mPnHL	94.8 ± 8.9 [71.9, 108.6]	19	81.0 ± 13.8 [36.2, 113.0] 330	64.5 ± 17.6 [0.0, 113.0] 345	63.7 ± 16.6 [0.0, 101.4] 256	66.9 ± 19.5 [0.0, 113.0] 89	30.1 ± 23.6 [0.0, 89.3] 309
nMes	26.2 ± 4.1 [18.8, 32.2]	19	15.4 ± 5.6 [3.5, 32.9] 330	10.4 ± 4.0 [2.0, 25.4] 345	10.9 ± 4.2 [2.0, 25.4] 256	9.0 ± 3.0 [2.1, 17.4] 89	5.9 ± 3.8 [0.0, 19.4] 309
nPr	16.2 ± 3.3 [10.6, 22.7]	19	12.9 ± 4.4 [2.2, 29.3] 330	7.2 ± 3.9 [0.0, 21.4] 345	7.4 ± 3.8 [0.0, 21.4] 256	6.6 ± 4.1 [0.0, 17.2] 89	2.3 ± 2.8 [0.0, 13.1] 309
nMet	6.3 ± 2.1 [3.6, 12.9]	19	1.9 ± 1.3 [0.0, 9.0] 330	0.9 ± 1.0 [0.0, 6.0] 345	0.9 ± 1.0 [0.0, 6.0] 256	1.0 ± 1.0 [0.0, 4.9] 89	0.3 ± 0.6 [0, 3.4] 309
MetHL	170.7 ± 18.8 [135, 205]	19	143.8 ± 48.9 [0, 240] 330	87.9 ± 65.4 [0, 222] 345	85.2 ± 65.0 [0, 222] 256	95.7 ± 66.3 [0, 189] 89	26.5 ± 47.7 [0, 180] 309

Tab. 2: Workers of species and hybrids similar to *Formica rufa* and *Formica aquilonia*; head size and RAV-corrected data for the assumption of each individual having a head size of 1750 µm; data given as arithmetic mean ± standard deviation (lower extreme, upper extreme) number of individuals.

	<i>F. polyctena</i>	<i>F. aquilonia</i> × <i>polyctena</i>	<i>F. aquilonia</i>	<i>F. ussuriensis</i>	<i>F. opaca</i>	<i>F. rufa</i>						
CS	1669 ± 182 [1154, 2067]	306	1682 ± 183 [1177, 2164]	148	1575 ± 150 [1099, 1902]	381	1537 ± 152 [1205, 1808]	41	1745 ± 184 [1380, 2068]	38	1901 ± 190 [1233, 2209]	313
CL/CW	1.103 ± 0.018 [1.048, 1.147]	306	1.096 ± 0.018 [1.052, 1.146]	148	1.094 ± 0.017 [1.045, 1.165]	381	1.104 ± 0.015 [1.071, 1.142]	41	1.121 ± 0.018 [1.067, 1.146]	38	1.111 ± 0.016 [1.066, 1.149]	313
SL/CS	0.932 ± 0.023 [0.846, 0.995]	6	0.910 ± 0.019 [0.861, 0.960]	148	0.908 ± 0.021 [0.850, 1.020]	345	0.903 ± 0.018 [0.858, 0.935]	41	0.917 ± 0.021 [0.847, 0.957]	38	0.941 ± 0.021 [0.882, 1.000]	313
SL/Smax	9.97 ± 0.37 [8.98, 11.10]	217	9.53 ± 0.36 [8.74, 10.57]	148	9.25 ± 0.34 [8.38, 10.34]	345	9.51 ± 0.34 [8.80, 10.26]	41	9.78 ± 0.30 [8.99, 10.51]	38	10.07 ± 0.40 [9.18, 11.29]	213
PeW/CS	0.483 ± 0.025 [0.426, 0.570]	15	0.485 ± 0.028 [0.415, 0.562]	144	0.498 ± 0.027 [0.440, 0.586]	102	0.518 ± 0.023 [0.466, 0.579]	41	0.476 ± 0.018 [0.437, 0.514]	38	0.470 ± 0.020 [0.410, 0.523]	218
EyeHL	17.3 ± 3.7 [0, 28]	282	21.1 ± 3.6 [12, 32]	148	24.2 ± 3.9 [13, 36]	345	25.6 ± 2.8 [18, 31]	41	35.1 ± 4.0 [26, 44]	38	20.9 ± 3.9 [10, 34]	220
nSc	0.0 ± 0.1 [0, 1.0]	306	0.05 ± 0.16 [0, 1.0]	148	0.17 ± 0.90 [0, 12.0]	345	10.8 ± 4.4 [0.0, 20.2]	41	0.6 ± 0.6 [0.0, 3.0]	38	0.0 ± 0.1 [0, 1.0]	313
nCH	0.06 ± 0.28 [0, 2.5]	306	0.47 ± 1.00 [0, 6.3]	148	5.14 ± 4.76 [0.0, 23.2]	345	10.9 ± 4.8 [2.4, 23.9]	41	5.8 ± 1.8 [2.4, 10.9]	38	0.41 ± 0.87 [0, 8.2]	313
OccHL	3.0 ± 12.1 [0, 76]	306	17.3 ± 26.3 [0, 97]	148	63.6 ± 24.0 [0, 134]	345	79.7 ± 16.3 [57, 123]	41	118.4 ± 19.0 [63, 159]	38	15.4 ± 23.4 [0, 92]	313
nGu	1.46 ± 1.60 [0.0, 6.4]	306	2.82 ± 2.03 [0.0, 8.5]	148	5.39 ± 2.64 [0.0, 13.5]	345	5.57 ± 2.62 [0.5, 13.5]	41	7.03 ± 1.86 [3.9, 10.7]	38	5.95 ± 1.85 [2.1, 11.5]	313
GuHL	50.8 ± 45.3 [0, 173]	306	90.2 ± 49.8 [0, 186]	148	102.7 ± 34.8 [0, 180]	345	117.4 ± 28.2 [62, 170]	41	217.2 ± 20.9 [164, 250]	38	187.8 ± 24.6 [106, 269]	313
nPN	2.5 ± 3.4 [0.0, 20.0]	306	3.9 ± 4.4 [0.0, 20.9]	148	7.9 ± 7.0 [0.0, 31.8]	381	7.1 ± 7.9 [0.0, 38.2]	41	18.9 ± 4.4 [12.1, 30.3]	38	19.2 ± 7.8 [3.0, 41.8]	313
mPnHL	30.1 ± 23.6 [0.0, 89.3]	306	44.8 ± 25.2 [0.0, 98.7]	148	42.2 ± 16.6 [0.0, 87.1]	381	44.3 ± 14.6 [0.0, 75.5]	41	97.5 ± 7.8 [78.2, 113.9]	38	78.7 ± 13.5 [41.5, 106.1]	313
nMes	5.9 ± 3.8 [0.0, 19.4]	306	8.1 ± 3.8 [1.4, 20.6]	148	14.7 ± 5.1 [2.2, 33.1]	345	15.4 ± 4.9 [5.0, 25.4]	41	6.6 ± 2.1 [2.5, 11.2]	38	14.8 ± 5.6 [4.5, 32.9]	313
nPr	2.3 ± 2.8 [0.0, 13.1]	306	3.1 ± 3.1 [0.0, 15.3]	148	5.8 ± 5.1 [0.0, 23.5]	345	3.5 ± 3.5 [0.0, 12.1]	41	9.0 ± 2.0 [3.5, 12.2]	38	12.4 ± 4.7 [0.7, 29.3]	313
nMet	0.3 ± 0.6 [0, 3.4]	306	0.8 ± 0.9 [0.0, 3.7]	148	1.8 ± 1.7 [0.0, 8.0]	381	3.8 ± 1.8 [0.0, 7.7]	41	3.4 ± 0.9 [1.8, 5.7]	38	1.7 ± 1.2 [0.0, 9.0]	313
MetHL	26.8 ± 47.9 [0, 180]	306	53.9 ± 55.4 [0, 172]	148	86.3 ± 53.3 [0, 183]	381	141.3 ± 30.1 [0, 195]	41	198.2 ± 19.8 [152, 233]	38	141.9 ± 52.0 [0, 240]	313

Tab. 3: Workers of species similar to *Formica pratensis* and *Formica lugubris*; head size and RAV-corrected data for the assumption of each individual having a head size of 1750 µm; data given as arithmetic mean ± standard deviation (lower extreme, upper extreme) number of individuals.

	<i>F. pratensis</i>	<i>F. lugubris</i> N+N3+Nm	<i>F. lugubris</i> P	<i>F. lugubris</i> A1+A3+B+E	<i>F. helvetica</i> sp.n.	<i>F. paralugubris</i>
range	West and Central Palaearctic	Fennoscandia	Pyrenees	Central Europe, Balkans, Siberia	Switzerland: near Scuol	Western Alps
CS	1820 ± 208 [1177, 2239] 334	1805 ± 207 [1178, 2184] 495	1664 ± 200 [1214, 2082] 80	1828 ± 196 [1240, 2164] 526	1663 ± 156 [1272, 1966] 30	1680 ± 142 [1203, 2020] 355
CL/CW	1.111 ± 0.021 [1.055, 1.165] 334	1.102 ± 0.019 [1.050, 1.169] 495	1.082 ± 0.019 [1.029, 1.123] 80	1.102 ± 0.019 [1.049, 1.157] 526	1.096 ± 0.019 [1.057, 1.135] 30	1.091 ± 0.018 [1.043, 1.147] 355
SL/CS	0.927 ± 0.022 [0.849, 1.007] 334	0.896 ± 0.027 [0.812, 0.998] 495	0.882 ± 0.019 [0.835, 0.931] 80	0.894 ± 0.023 [0.806, 0.960] 488	0.904 ± 0.016 [0.876, 0.933] 30	0.902 ± 0.020 [0.846, 0.983] 326
SL/Smax	10.66 ± 0.49 [9.64, 12.44] 332	9.41 ± 0.48 [8.17, 11.02] 471	9.27 ± 0.39 [8.40, 10.13] 71	9.19 ± 0.40 [8.15, 10.25] 482	9.47 ± 0.43 [8.68, 10.64] 30	9.22 ± 0.38 [8.29, 10.35] 337
PeW/CS	0.453 ± 0.025 [0.374, 0.511] 334	0.487 ± 0.025 [0.419, 0.560] 490	0.475 ± 0.030 [0.399, 0.572] 80	0.494 ± 0.030 [0.404, 0.573] 482	0.497 ± 0.025 [0.456, 0.553] 30	0.495 ± 0.025 [0.408, 0.554] 337
EyeHL	35.0 ± 9.0 [9, 60]	41.6 ± 12.0 [21, 71]	29.3 ± 5.9 [15, 40]	32.8 ± 5.4 [5, 45]	37.1 ± 4.4 [25, 44]	34.5 ± 4.2 [15, 47] 205
nSc	1.6 ± 2.3 [0.0, 13.0]	6.8 ± 10.5 [0.0, 42.2]	0.8 ± 1.2 [0.0, 5.8]	1.3 ± 2.5 [0.0, 18.0]	0.3 ± 0.4 [0.0, 1.5]	5.2 ± 5.6 [0.0, 24.2] 355
nCH	21.9 ± 7.9 [4.1, 51.3]	30.1 ± 11.7 [3.1, 69.3]	18.2 ± 4.0 [8.8, 27.9]	21.3 ± 5.6 [1.3, 39.8]	20.0 ± 3.5 [12.7, 27.3]	24.9 ± 5.6 [6.1, 39.1] 355
OccHL	117.4 ± 31.5 [46, 208]	131.7 ± 31.3 [55, 235]	114.8 ± 14.7 [76, 147]	115.1 ± 21.2 [56, 177]	131.8 ± 21.0 [95, 193]	108.3 ± 18.5 [59, 160] 342
nGu	12.3 ± 3.7 [5.4, 25.2]	20.0 ± 8.6 [7.9, 43.2]	12.7 ± 3.9 [3.9, 19.8]	14.7 ± 3.4 [5.7, 22.8]	14.0 ± 3.0 [8.9, 19.5]	14.2 ± 3.2 [7.2, 22.1] 68
GuHL	193.2 ± 33.4 [131, 285]	204.1 ± 32.8 [125, 267]	181.6 ± 25.7 [115, 240]	187.0 ± 22.8 [122, 256]	204.8 ± 27.4 [155, 267]	164.1 ± 18.6 [103, 211] 68
nPN	> 25	> 25	> 25	> 25	> 25	> 25
mPnHL	116.9 ± 16.5 [54.2, 179.5]	105.8 ± 19.3 [49.5, 175.7]	94.0 ± 9.6 [63.9, 119.3]	98.1 ± 14.0 [44.3, 144.4]	111.1 ± 12.6 [74.0, 130.5]	77.8 ± 12.5 [46.1, 127.4] 355
nMes	34.0 ± 9.3 [4.1, 51.1]	33.9 ± 6.5 [24.7, 50.5]	26.3 ± 6.4 [13.5, 38.8]	27.4 ± 5.2 [11.2, 43.6]	24.4 ± 3.8 [16.3, 33.9]	29.6 ± 4.6 [18.2, 41.2] 64
nPr	27.3 ± 7.6 [2.2, 45.7]	27.1 ± 9.4 [12.0, 54.5]	21.5 ± 5.5 [8.8, 32.8]	20.8 ± 4.6 [3.2, 34.7]	22.2 ± 5.0 [13.7, 30.3]	16.0 ± 5.1 [7.5, 32.3] 64
nMet	12.7 ± 3.1 [4.6, 21.6]	11.34 ± 3.55 [2.1, 24.0]	9.2 ± 2.6 [2.7, 15.3]	9.5 ± 2.5 [3.2, 17.1]	8.7 ± 2.0 [5.8, 13.8]	7.7 ± 2.4 [1.0, 15.2] 355
MetHL	169.9 ± 22.9 [106, 265]	185.3 ± 22.7 [119, 261]	169.7 ± 16.0 [134, 211]	180.6 ± 20.5 [132, 249]	187.6 ± 16.3 [152, 240]	154.3 ± 18.0 [98, 205] 355

Tab. 4: Workers of *Formica aquilonia*, *Formica paralugubris*, *Formica aquilonia × paralugubris*, and collected data of all Palaearctic phenotypes of *Formica lugubris*; head size and RAV-corrected data for the assumption of each individual having a head size of 1750 µm; data given as arithmetic mean ± standard deviation (lower extreme, upper extreme) number of individuals.

	<i>F. aquilonia</i>	<i>F. aquilonia</i> × <i>paralugubris</i>	<i>F. paralugubris</i>	<i>F. lugubris</i>	<i>F. pratensis</i>					
CS	1575 ± 150 [1099, 1902]	381	1539 ± 162 [1307, 1752]	18	1680 ± 142 [1203, 2020]	355	1805 ± 205 [1178, 2184]	1108	1820 ± 208 [1177, 2239]	334
CL/CW	1.094 ± 0.017 [1.045, 1.165]	381	1.070 ± 0.018 [1.046, 1.101]	18	1.091 ± 0.018 [1.043, 1.147]	355	1.101 ± 0.019 [1.029, 1.169]	1108	1.111 ± 0.021 [1.055, 1.165]	334
SL/CS	0.908 ± 0.021 [0.850, 1.020]	345	0.910 ± 0.013 [0.882, 0.934]	18	0.902 ± 0.020 [0.846, 0.983]	342	0.894 ± 0.025 [0.806, 0.998]	1070	0.927 ± 0.022 [0.849, 1.007]	334
SL/Smax	9.25 ± 0.34 [8.38, 10.34]	345	9.32 ± 0.14 [9.01, 9.59]	18	9.22 ± 0.38 [8.29, 10.35]	337	9.30 ± 0.45 [8.15, 11.02]	1031	10.66 ± 0.49 [9.64, 12.44]	332
PeW/CS	0.498 ± 0.027 [0.440, 0.586]	102	0.496 ± 0.034 [0.436, 0.546]	18	0.495 ± 0.025 [0.408, 0.554]	337	0.489 ± 0.028 [0.399, 0.573]	1059	0.453 ± 0.025 [0.374, 0.511]	334
EyeHL	24.2 ± 3.9 [13, 36]	345	29.9 ± 6.2 [17, 37]	18	34.5 ± 4.2 [15, 47]	205	33.4 ± 7.4 [5, 71]	219	35.0 ± 9.0 [9, 60]	40
nSc	0.17 ± 0.90 [0, 12.0]	345	2.6 ± 2.9 [0.0, 10.1]	18	5.2 ± 5.6 [0.0, 24.2]	355	3.7 ± 7.7 [0.0, 42.2]	1106	1.6 ± 2.3 [0.0, 13.0]	269
nCH	5.14 ± 4.76 [0.0, 23.2]	345	18.8 ± 4.6 [12.3, 32.0]	18	24.9 ± 5.6 [6.1, 39.1]	355	25.0 ± 9.9 [1.3, 69.3]	1106	21.9 ± 7.9 [4.1, 51.3]	268
OccHL	63.6 ± 24.0 [0, 134]	345	101.9 ± 18.7 [72, 136]	18	108.3 ± 18.5 [59, 160]	342	122.8 ± 27.3 [55, 235]	1068	117.4 ± 31.5 [46, 208]	268
nGu	5.39 ± 2.64 [0.0, 13.5]	345	12.7 ± 2.8 [6.6, 16.7]	18	14.2 ± 3.2 [7.2, 22.1]	68	15.1 ± 4.9 [3.9, 43.2]	219	12.3 ± 3.7 [5.4, 25.2]	39
GuHL	102.7 ± 34.8 [0, 180]	345	167.8 ± 21.5 [129, 209]	18	164.1 ± 18.6 [103, 211]	68	188.4 ± 25.3 [115, 267]	219	193.2 ± 33.4 [131, 285]	39
nPN	7.9 ± 7.0 [0.0, 31.8]	381	32.8 ± 9.6 [12.2, 49.5]	18	30.0 ± 9.9 [15.0, 54.8]	20	36.4 ± 26.7 [2.5, 119.6]	43	> 25	
mPnHL	42.2 ± 16.6 [0.0, 87.1]	381	78.2 ± 14.0 [56.0, 102.3]	18	77.8 ± 12.5 [46.1, 127.4]	355	101.2 ± 16.9 [44.3, 175.7]	1106	116.9 ± 16.5 [54.2, 179.5]	268
nMes	14.7 ± 5.1 [2.2, 33.1]	345	22.7 ± 5.2 [16.5, 35.0]	18	29.6 ± 4.6 [18.2, 41.2]	64	28.1 ± 6.0 [11.2, 50.3]	219	34.0 ± 9.3 [4.1, 51.1]	39
nPr	5.8 ± 5.1 [0.0, 23.5]	345	11.6 ± 3.4 [5.1, 17.2]	18	16.0 ± 5.1 [7.5, 32.3]	64	21.7 ± 5.9 [3.2, 54.5]	219	27.3 ± 7.6 [2.2, 45.7]	39
nMet	1.8 ± 1.7 [0.0, 8.0]	381	6.5 ± 1.8 [4.0, 10.7]	18	7.7 ± 2.4 [1.0, 15.2]	355	10.3 ± 3.2 [2.1, 24.0]	1106	12.7 ± 3.1 [4.6, 21.6]	268
MetHL	86.3 ± 53.3 [0, 183]	381	152.4 ± 21.7 [121, 197]	18	154.3 ± 18.0 [98, 205]	355	182.1 ± 21.8 [119, 261]	1106	169.9 ± 22.9 [106, 265]	268

Tab.5: Workers of the *Formica truncorum* species complex; head size and RAV-corrected data for the assumption of each individual having a head size of 1750 µm; data given as arithmetic mean ± standard deviation (lower extreme, upper extreme) number of individuals.

	<i>F. dusmeti</i>	<i>F. frontalis</i>	<i>F. truncorum</i> W +C Palaearctic	<i>F. sinensis</i>	<i>F. truncorum</i> E Palaearctic	<i>F. truncorum</i> whole range						
CS	1706 ± 247 [1437, 2074]	7	1792 ± 177 [1527, 2045]	26	1763 ± 201 [1348, 2177]	77	1773 ± 212 [1312, 2134]	70	1710 ± 205 [1319, 1938]	15	1754 ± 201 [1319, 2177]	92
CL/CW	1.113 ± 0.023 [1.066, 1.132]	7	1.102 ± 0.015 [1.076, 1.127]	26	1.099 ± 0.017 [1.057, 1.136]	77	1.113 ± 0.020 [1.021, 1.182]	70	1.100 ± 0.019 [1.057, 1.123]	15	1.099 ± 0.017 [1.057, 1.136]	92
SL/CS	1.001 ± 0.019 [0.970, 1.030]	7	0.993 ± 0.026 [0.939, 1.068]	26	0.979 ± 0.022 [0.933, 1.018]	77	0.997 ± 0.031 [0.934, 1.091]	70	1.015 ± 0.025 [0.960, 1.056]	15	0.985 ± 0.026 [0.933, 1.056]	92
SL/Smax	11.08 ± 0.27 [10.82, 11.43]	4	10.60 ± 0.48 [9.54, 11.53]	26	10.86 ± 0.41 [9.53, 11.88]	77	11.18 ± 0.50 [10.03, 13.00]	70	10.94 ± 0.33 [10.04, 11.45]	15	10.87 ± 0.41 [9.53, 11.88]	92
PeW/CS	0.438 ± 0.021 [0.424, 0.470]	4	0.450 ± 0.029 [0.387, 0.507]	26	0.437 ± 0.021 [0.388, 0.491]	77	0.430 ± 0.024 [0.364, 0.504]	70	0.459 ± 0.027 [0.403, 0.496]	15	0.442 ± 0.023 [0.388, 0.496]	92
EyeHL	14.4 ± 6.1 [8, 26]	7	16.4 ± 10.8 [0, 29]	26	39.5 ± 9.6 [4, 62]	77	5.1 ± 7.6 [0, 24]	70	43.9 ± 8.3 [28, 59]	15	40.2 ± 9.5 [4, 62]	92
nSc	0.0 ± 0.0 [0.0, 0.0]	7	0.7 ± 0.9 [0.0, 3.0]	26	11.0 ± 8.9 [0.0, 35.5]	77	0.0 ± 0.1 [0.0, 0.5]	70	6.7 ± 3.6 [0.0, 12.5]	15	10.3 ± 8.4 [0.0, 35.5]	92
nCH	0.0 ± 0.0 [0.0, 0.0]	7	14.5 ± 7.2 [0.0, 28.7]	26	41.8 ± 14.5 [6.2, 78.0]	77	8.2 ± 5.2 [0.6, 25.2]	70	46.1 ± 8.7 [27.4, 60.4]	15	42.5 ± 13.8 [6.2, 78.0]	92
OccHL	0.0 ± 0.0 [0.0, 0.0]	7	114.2 ± 33.0 [0, 183]	26	137.6 ± 26.2 [85, 216]	77	113.8 ± 22.6 [64, 168]	70	128.4 ± 16.4 [102, 147]	15	136.1 ± 25.0 [85, 216]	92
nGu	2.9 ± 1.8 [0.5, 5.3]	7	19.5 ± 5.3 [9.2, 29.9]	26	39.5 ± 15.3 [5.2, 76.9]	77	26.1 ± 8.3 [7.0, 51.6]	70	46.2 ± 8.3 [34.1, 59.0]	15	40.6 ± 14.6 [5.2, 76.9]	92
GuHL	156.1 ± 29.5 [144, 221]	7	203.6 ± 28.7 [162, 263]	26	188.6 ± 25.3 [142, 256]	77	183.6 ± 25.9 [123, 250]	70	176.5 ± 17.8 [153, 208]	15	186.7 ± 24.6 [142, 256]	92
nPN	0.3 ± 0.7 [0.0, 1.8]	7	59.5 ± 18.6 [16.6, 102.5]	26	77.8 ± 22.2 [22.3, 124.1]	77	26.6 ± 16.8 [3.8, 72.5]	70	101.2 ± 14.5 [66.4, 123.3]	15	81.6 ± 22.8 [22.3, 124.1]	92
mPnHL	18.2 ± 31.1 [0.0, 66.4]	7	97.4 ± 14.0 [74.0, 128.1]	26	91.3 ± 14.7 [63.7, 138.3]	77	70.3 ± 16.5 [38.5, 106.2]	70	88.4 ± 10.2 [67.1, 108.2]	15	90.9 ± 14.0 [63.7, 138.3]	92
nMes	2.4 ± 2.5 [0.0, 7.0]	7	26.1 ± 11.3 [8.2, 47.1]	26	34.7 ± 10.0 [12.8, 63.4]	77	24.2 ± 5.1 [15.1, 42.5]	70	41.2 ± 6.7 [30.6, 54.1]	15	35.8 ± 9.8 [12.8, 63.4]	92
nPr	0.8 ± 1.4 [0.0, 3.3]	7	29.2 ± 7.1 [16.7, 48.7]	26	45.5 ± 13.9 [15.4, 99.8]	77	20.5 ± 9.0 [0.4, 39.9]	70	51.9 ± 8.3 [36.9, 64.7]	15	46.5 ± 13.3 [15.4, 99.8]	92
nMet	0.4 ± 0.7 [0.0, 1.9]	7	10.2 ± 3.2 [4.2, 19.1]	26	16.8 ± 4.7 [7.1, 30.7]	77	7.7 ± 3.9 [0.0, 17.3]	70	21.9 ± 4.0 [18.1, 31.6]	15	17.6 ± 4.9 [7.1, 31.6]	92
MetHL	27.9 ± 48.5 [0, 114]	7	161.2 ± 22.5 [129, 200]	26	141.7 ± 17.0 [90, 204]	77	140.0 ± 33.2 [0, 221]	70	142.5 ± 20.9 [96, 177]	15	141.9 ± 17.6 [90, 204]	92

Tab.6: Gynes of species and hybrids with sparse pilosity; data given as arithmetic mean  $\pm$  standard deviation (lower extreme, upper extreme) number of individuals.

	<i>F. rufa</i>	<i>F. rufa</i> $\times$ <i>polyctena</i>	<i>F. polyctena</i>	<i>F. aquilonia</i> $\times$ <i>polyctena</i>	<i>F. aquilonia</i>	<i>F. ussuriensis</i>	<i>F. opaca</i>							
CS	2140 $\pm$ 60 [1978, 2250]	2125 $\pm$ 66 [2030, 2224]	29	16	2037 $\pm$ 68 [1899, 2165]	33	2058 $\pm$ 63 [1978, 2167]	18	2015 $\pm$ 61 [1840, 2173]	59	2225 $\pm$ 173 [2026, 2357]	3	2348 $\pm$ 35 [2318, 2386]	3
CL/CW	1.026 $\pm$ 0.017 [1.003, 1.061]	1.015 $\pm$ 0.017 [0.977, 1.038]	29	16	1.035 $\pm$ 0.022 [1.001, 1.074]	33	1.038 $\pm$ 0.012 [1.018, 1.057]	18	1.016 $\pm$ 0.022 [0.969, 1.077]	59	1.018 $\pm$ 0.021 [0.994, 1.035]	3	1.030 $\pm$ 0.008 [1.021, 1.036]	3
SL/CS	0.868 $\pm$ 0.017 [0.830, 0.888]	0.867 $\pm$ 0.020 [0.829, 0.904]	29	16	0.864 $\pm$ 0.025 [0.802, 0.912]	33	0.832 $\pm$ 0.015 [0.796, 0.855]	18	0.810 $\pm$ 0.024 [0.752, 0.893]	59	0.806 $\pm$ 0.009 [0.796, 0.814]	3	0.903 $\pm$ 0.018 [0.886, 0.922]	3
SL/Smax	9.13 $\pm$ 0.31 [8.48, 9.76]	9.13 $\pm$ 0.28 [8.71, 9.89]	29	16	9.17 $\pm$ 0.43 [8.30, 10.10]	33	8.71 $\pm$ 0.22 [8.26, 9.07]	18	8.32 $\pm$ 0.34 [7.54, 8.82]	29	8.27 $\pm$ 0.41 [7.80, 8.55]	3	9.66 $\pm$ 0.18 [9.48, 9.84]	3
ML/CS	1.738 $\pm$ 0.042 [1.653, 1.822]	1.760 $\pm$ 0.039 [1.669, 1.809]	29	16	1.752 $\pm$ 0.063 [1.523, 1.843]	33	1.789 $\pm$ 0.033 [1.730, 1.846]	18	1.681 $\pm$ 0.041 [1.550, 1.758]	29	1.685 $\pm$ 0.027 [1.655, 1.706]	3	1.776 $\pm$ 0.014 [1.765, 1.791]	3
PeW/CS	0.643 $\pm$ 0.025 [0.587, 0.695]	0.654 $\pm$ 0.029 [0.609, 0.711]	29	16	0.679 $\pm$ 0.033 [0.613, 0.751]	33	0.667 $\pm$ 0.025 [0.626, 0.710]	18	0.681 $\pm$ 0.041 [0.619, 0.788]	29	0.622 $\pm$ 0.064 [0.560, 0.687]	3	0.647 $\pm$ 0.020 [0.635, 0.670]	3
EyeHL	24.6 $\pm$ 2.9 [18, 30]	22.4 $\pm$ 2.9 [19, 29]	29	16	21.3 $\pm$ 3.0 [14, 29]	33	22.6 $\pm$ 3.1 [19, 33]	18	28.7 $\pm$ 4.3 [22, 37]	29	33.0 $\pm$ 4.4 [30, 38]	3	43.7 $\pm$ 15.1 [33, 61]	3
nSc	0.0 $\pm$ 0.0 [0, 0.5]	0.0 $\pm$ 0.0 [0, 0.0]	29	16	0.0 $\pm$ 0.0 [0, 0.0]	33	0.0 $\pm$ 0.0 [0, 0.0]	18	0.5 $\pm$ 1.0 [0, 3.5]	29	3.2 $\pm$ 5.5 [0, 9.5]	3	0.0 $\pm$ 0.0 [0, 0.0]	3
nCH	0.0 $\pm$ 0.0 [0, 0.0]	0.0 $\pm$ 0.0 [0, 0.0]	29	16	0.0 $\pm$ 0.0 [0, 0.0]	33	0.0 $\pm$ 0.1 [0, 0.5]	18	2.1 $\pm$ 2.8 [0, 10.0]	29	15.0 $\pm$ 6.9 [11.0, 23.0]	3	4.8 $\pm$ 1.0 [4.0, 6.0]	3
OccHL	0.0 $\pm$ 0.0 [0, 0]	0.0 $\pm$ 0.0 [0, 0]	29	16	0.0 $\pm$ 0.0 [0, 0]	33	3.3 $\pm$ 10.5 [0, 42]	18	29.8 $\pm$ 38.3 [0, 189]	29	64.7 $\pm$ 20.0 [44, 84]	3	87.0 $\pm$ 27.0 [56, 105]	3
nGu	1.5 $\pm$ 1.4 [0.0, 5.0]	0.1 $\pm$ 0.4 [0, 1.5]	29	16	0.0 $\pm$ 0.1 [0, 0.3]	33	0.9 $\pm$ 0.6 [0, 2.0]	18	3.1 $\pm$ 2.4 [0.0, 8.5]	29	10.8 $\pm$ 3.5 [7.0, 14.0]	3	9.3 $\pm$ 0.8 [8.5, 10.0]	3
GuHL	93.3 $\pm$ 92.5 [0, 280]	14.4 $\pm$ 57.8 [0, 231]	29	16	0.5 $\pm$ 2.8 [0, 16]	33	37.5 $\pm$ 20.0 [0, 67]	18	51.4 $\pm$ 23.8 [0, 107]	29	107.3 $\pm$ 39.7 [64, 142]	3	258.3 $\pm$ 5.7 [252, 263]	3
PnHL	8.1 $\pm$ 15.1 [0, 44]	0.0 $\pm$ 0.0 [0, 0]	29	16	5.4 $\pm$ 11.9 [0, 42]	33	1.9 $\pm$ 8.2 [0, 35]	18	43.3 $\pm$ 15.7 [0, 116]	29	46.0 $\pm$ 4.6 [42, 51]	3	55.7 $\pm$ 10.4 [44, 64]	3
MetHL	12.4 $\pm$ 46.3 [0, 244]	0.0 $\pm$ 0.0 [0, 0]	29	16	1.8 $\pm$ 10.4 [0, 60]	33	0.0 $\pm$ 0.0 [0, 0]	18	30.4 $\pm$ 26.2 [0, 87]	29	166.7 $\pm$ 71.7 [90, 232]	3	125.3 $\pm$ 41.0 [79, 157]	3
nPe	0.0 $\pm$ 0.0 [0, 0]	0.0 $\pm$ 0.00 [0, 0.0]	29	16	0.1 $\pm$ 0.3 [0, 1.0]	33	0.2 $\pm$ 0.4 [0, 1.0]	18	3.7 $\pm$ 2.2 [0, 9.5]	29	3.3 $\pm$ 0.6 [3.0, 4.0]	3	0.2 $\pm$ 0.3 [0.0, 0.5]	3
sqPDG	9.00 $\pm$ 1.76 [5.71, 14.96]	9.35 $\pm$ 1.52 [6.13, 13.21]	29	16	12.21 $\pm$ 2.85 [8.00, 22.85]	33	17.49 $\pm$ 4.68 [13.40, 29.23]	18	9.23 $\pm$ 3.74 [4.16, 20.67]	29	10.12 $\pm$ 4.22 [5.77, 14.20]	3	3.64 $\pm$ 0.26 [3.35, 3.84]	3
FoDG	56.6 $\pm$ 15.4 [38.0, 109.2]	52.0 $\pm$ 12.2 [29.7, 71.3]	29	16	58.2 $\pm$ 10.9 [34.5, 83.7]	33	43.1 $\pm$ 10.5 [20.3, 58.2]	18	27.7 $\pm$ 7.8 [19.0, 48.8]	29	25.3 $\pm$ 6.2 [18.4, 30.3]	3	20.5 $\pm$ 2.7 [18.4, 23.5]	3
nMes	0.5 $\pm$ 0.7 [0, 2.5]	0.1 $\pm$ 0.3 [0, 1.0]	29	16	0.1 $\pm$ 0.3 [0, 1.5]	33	0.2 $\pm$ 0.4 [0, 1.5]	18	2.5 $\pm$ 2.6 [0, 10.5]	29	7.8 $\pm$ 1.9 [6.5, 10.0]	3	2.7 $\pm$ 2.1 [1.0, 5.0]	3
nMet	0.1 $\pm$ 0.4 [0, 2.0]	0.0 $\pm$ 0.0 [0, 0.0]	29	16	0.0 $\pm$ 0.1 [0, 0.5]	33	0.0 $\pm$ 0.0 [0, 0]	18	1.4 $\pm$ 2.0 [0, 6.5]	29	12.2 $\pm$ 1.6 [11.0, 14.0]	3	4.8 $\pm$ 2.4 [3.0, 7.5]	3
nHT	0.4 $\pm$ 0.5 [0, 1.5]	0.0 $\pm$ 0.1 [0, 5]	29	16	0.1 $\pm$ 0.5 [0, 3]	33	0.3 $\pm$ 0.5 [0, 2]	18	3.9 $\pm$ 4.0 [0.0, 14.0]	29	6.7 $\pm$ 2.2 [4.7, 9.0]	3	2.5 $\pm$ 0.5 [2.0, 3.0]	3
GfrHL	10.5 $\pm$ 38.3 [0, 200]	0.0 $\pm$ 0.0 [0, 0]	29	16	2.4 $\pm$ 13.8 [0, 79]	33	25.7 $\pm$ 36.1 [0, 160]	18	64.4 $\pm$ 47.4 [0, 205]	29	257.3 $\pm$ 53.3 [196, 292]	3	43.7 $\pm$ 6.5 [37, 50]	3
nGfr	0.1 $\pm$ 0.4 [0, 1]	0.0 $\pm$ 0.0 [0, 0]	29	16	0.1 $\pm$ 0.4 [0, 2]	33	1.7 $\pm$ 1.5 [0, 4]	18	8.1 $\pm$ 6.1 [0, 25]	29	26.3 $\pm$ 6.0 [20, 32]	3	2.3 $\pm$ 1.2 [1, 3]	3
StHL	350.1 $\pm$ 86.9 [0, 425]	315.7 $\pm$ 79.0 [127, 402]	29	16	122.9 $\pm$ 104.1 [0, 370]	33	295.2 $\pm$ 25.7 [252, 339]	18	232.4 $\pm$ 82.4 [55, 342]	29	335.3 $\pm$ 31.3 [307, 369]	3	336.0 $\pm$ 20.7 [317, 358]	3
nSt	18.8 $\pm$ 8.5 [0, 35]	13.7 $\pm$ 4.3 [6, 21]	29	16	6.2 $\pm$ 3.9 [0, 17]	33	16.1 $\pm$ 7.5 [2, 35]	30	16.6 $\pm$ 7.1 [2, 35]	29	39.7 $\pm$ 8.4 [30, 45]	3	22.0 $\pm$ 5.3 [18, 28]	3

Tab. 7: Gynes of species with richer pilosity; data given as arithmetic mean  $\pm$  standard deviation (lower extreme, upper extreme) number of individuals.

	<i>F. aquilonia</i>	<i>F. paralugubris</i>	<i>F. lugubris</i> A3	<i>F. lugubris</i> A1	<i>F. lugubris</i> N	<i>F. helvetica</i> sp.n.	<i>F. pratensis</i>							
CS	2015 $\pm$ 61 [1840, 2173]	59	2095 $\pm$ 54 [1997, 2238]	53	2262 $\pm$ 81 [2093, 2374]	18	2207 $\pm$ 81 [1996, 2382]	74	2189 $\pm$ 63 [2072, 2291]	12	2126 $\pm$ 78 [2011, 2273]	28	2296 $\pm$ 68 [2169, 2432]	21
CL/CW	1.016 $\pm$ 0.023 [0.969, 1.077]	59	1.005 $\pm$ 0.022 [0.952, 1.068]	53	1.001 $\pm$ 0.017 [0.970, 1.032]	18	0.998 $\pm$ 0.020 [0.953, 1.052]	74	0.998 $\pm$ 0.020 [0.953, 1.052]	12	0.999 $\pm$ 0.021 [0.962, 1.047]	28	1.024 $\pm$ 0.025 [0.979, 1.064]	21
SL/CS	0.810 $\pm$ 0.024 [0.752, 0.893]	59	0.805 $\pm$ 0.019 [0.767, 0.846]	53	0.765 $\pm$ 0.029 [0.708, 0.823]	18	0.793 $\pm$ 0.021 [0.750, 0.857]	74	0.810 $\pm$ 0.019 [0.782, 0.839]	12	0.797 $\pm$ 0.030 [0.711, 0.839]	28	0.853 $\pm$ 0.020 [0.819, 0.905]	21
SL/Smax	8.32 $\pm$ 0.33 [7.54, 8.82]	29	7.97 $\pm$ 0.26 [7.44, 8.45]	31	7.85 $\pm$ 0.39 [7.12, 8.50]	18	8.21 $\pm$ 0.32 [7.43, 9.04]	38	8.30 $\pm$ 0.30 [7.91, 8.95]	11	8.41 $\pm$ 0.37 [7.51, 9.21]	28	9.75 $\pm$ 0.33 [9.19, 10.30]	21
ML/CS	1.681 $\pm$ 0.041 [1.550, 1.758]	29	1.662 $\pm$ 0.042 [1.591, 1.769]	31	1.653 $\pm$ 0.032 [1.593, 1.700]	18	1.691 $\pm$ 0.043 [1.617, 1.772]	38	1.714 $\pm$ 0.040 [1.657, 1.800]	11	1.719 $\pm$ 0.025 [1.682, 1.773]	28	1.698 $\pm$ 0.046 [1.631, 1.792]	20
PeW/CS	0.681 $\pm$ 0.041 [0.619, 0.788]	29	0.669 $\pm$ 0.026 [0.635, 0.734]	31	0.634 $\pm$ 0.028 [0.566, 0.673]	18	0.667 $\pm$ 0.032 [0.616, 0.755]	38	0.638 $\pm$ 0.031 [0.567, 0.673]	11	0.648 $\pm$ 0.031 [0.583, 0.704]	28	0.628 $\pm$ 0.033 [0.563, 0.699]	20
EyeHL	28.7 $\pm$ 4.3 [22, 37]	29	40.8 $\pm$ 4.8 [33, 53]	31	37.7 $\pm$ 4.4 [30, 45]	18	49.1 $\pm$ 12.8 [35, 96]	38	64.0 $\pm$ 34.0 [39, 151]	12	44.1 $\pm$ 5.9 [35, 56]	28	56.2 $\pm$ 10.6 [46, 86]	20
nSc	0.5 $\pm$ 1.0 [0.0, 3.5]	29	6.4 $\pm$ 5.1 [0.0, 20.0]	31	0.1 $\pm$ 0.3 [0.0, 1.0]	18	2.4 $\pm$ 2.7 [0.0, 9.5]	38	4.4 $\pm$ 6.5 [0.0, 21.0]	11	0.4 $\pm$ 0.8 [0.0, 4.0]	28	1.4 $\pm$ 2.3 [0.0, 9.0]	20
nCH	2.4 $\pm$ 2.9 [0, 10.0]	59	23.8 $\pm$ 6.2 [9.5, 39.0]	53	14.4 $\pm$ 2.4 [11.0, 19.0]	18	23.2 $\pm$ 5.7 [10.5, 38.0]	74	36.4 $\pm$ 13.9 [24.0, 65.0]	12	18.5 $\pm$ 4.1 [11.5, 30.0]	28	18.3 $\pm$ 12.5 [0.0, 38.0]	21
OccHL	29.8 $\pm$ 38.3 [0, 189]	29	116.8 $\pm$ 37.2 [62, 186]	31	52.1 $\pm$ 10.7 [40, 84]	18	199.6 $\pm$ 69.7 [60, 315]	38	182.8 $\pm$ 101.1 [74, 320]	11	178.6 $\pm$ 71.0 [50, 281]	28	152.1 $\pm$ 114.4 [0, 402]	20
nGu	3.1 $\pm$ 2.4 [0.0, 8.5]	29	16.7 $\pm$ 4.3 [6.0, 24.0]	31	12.7 $\pm$ 2.2 [8.5, 17.0]	18	19.9 $\pm$ 6.2 [8.0, 36.0]	38	21.7 $\pm$ 8.3 [9.0, 36.0]	11	17.2 $\pm$ 4.8 [11.0, 33.0]	28	14.4 $\pm$ 8.4 [2.5, 38.0]	20
GuHL	51.4 $\pm$ 23.8 [0, 107]	29	128.2 $\pm$ 63.9 [55, 267]	31	87.1 $\pm$ 20.9 [49, 129]	18	314.2 $\pm$ 58.3 [184, 425]	38	254.3 $\pm$ 73.7 [122, 338]	11	303.0 $\pm$ 54.3 [178, 418]	28	239.5 $\pm$ 122.6 [58, 404]	20
PnHL	42.3 $\pm$ 18.3 [0, 116]	59	88.2 $\pm$ 50.4 [33, 258]	53	56.5 $\pm$ 21.8 [34, 128]	18	245.9 $\pm$ 60.9 [113, 411]	74	214.7 $\pm$ 106.1 [83, 357]	12	236.5 $\pm$ 57.6 [116, 354]	28	245.6 $\pm$ 133.7 [30.405]	21
nMet	1.4 $\pm$ 2.0 [0.0, 6.5]	29	14.2 $\pm$ 3.9 [11.5, 17.0]	2	7.6 $\pm$ 2.4 [3.5, 11.5]	18	17.5 $\pm$ 4.4 [9.5, 26.0]	14	18.6 $\pm$ 6.1 [8.0, 27.0]	11	14.9 $\pm$ 3.2 [8.2, 22.0]	28	17.5 $\pm$ 6.9 [4.0, 34.0]	20
MetHL	31.5 $\pm$ 27.5 [0, 108]	59	109.9 $\pm$ 56.2 [32, 232]	53	76.7 $\pm$ 40.7 [40, 173]	18	309.8 $\pm$ 38.9 [159, 375]	74	228.9 $\pm$ 86.4 [96, 330]	12	286.9 $\pm$ 39.2 [214, 375]	28	224.1 $\pm$ 123.3 [43, 413]	21
nPe	3.9 $\pm$ 2.7 [0, 14.0]	59	9.2 $\pm$ 4.0 [3.0, 23.0]	53	5.5 $\pm$ 2.4 [2.0, 10.5]	18	18.6 $\pm$ 4.4 [9.0, 33.0]	74	10.6 $\pm$ 3.5 [7.0, 17.0]	12	13.7 $\pm$ 3.5 [7.0, 21.0]	28	10.1 $\pm$ 5.6 [0.0, 21.0]	21
sqPDG	9.23 $\pm$ 3.74 [4.16, 20.67]	29	4.62 $\pm$ 0.39 [3.92, 5.49]	31	3.97 $\pm$ 0.39 [3.39, 4.80]	18	5.01 $\pm$ 0.83 [3.88, 8.06]	38	6.21 $\pm$ 1.41 [4.11, 7.94]	11	4.84 $\pm$ 0.36 [4.00, 5.54]	28	4.03 $\pm$ 0.53 [3.09, 5.02]	20
FodG	27.7 $\pm$ 7.8 [19.0, 48.8]	29	21.8 $\pm$ 2.4 [18.9, 31.1]	31	21.1 $\pm$ 2.3 [17.9, 25.8]	18	27.4 $\pm$ 4.8 [20.5, 42.7]	38	25.5 $\pm$ 8.8 [19.4, 50.8]	11	26.1 $\pm$ 3.1 [20.3, 33.6]	28	26.2 $\pm$ 6.1 [20.9, 37.4]	7

Tab.8: Gynes of the *Formica truncorum* species complex; data given as arithmetic mean  $\pm$  standard deviation (lower extreme, upper extreme) number of individuals.

	<i>F. frontalis</i>	<i>F. truncorum</i>	<i>F. sinensis</i>
CS	2106 $\pm$ 32 [2070, 2149] 6	2002 $\pm$ 108 [1737, 2256] 22	2192 $\pm$ 34 [2145, 2241] 7
CL/CW	1.002 $\pm$ 0.017 [0.982, 1.028] 6	1.015 $\pm$ 0.024 [0.970, 1.065] 22	1.022 $\pm$ 0.019 [0.994, 1.048] 7
SL/CS	0.872 $\pm$ 0.019 [0.843, 0.892] 6	0.903 $\pm$ 0.030 [0.844, 0.961] 22	0.921 $\pm$ 0.040 [0.868, 0.966] 7
SL/Smax	9.30 $\pm$ 0.37 [8.89, 9.87] 6	9.63 $\pm$ 0.37 [8.98, 10.43] 22	10.30 $\pm$ 0.19 [10.11, 10.62] 7
ML/CS	1.735 $\pm$ 0.042 [1.675, 1.787] 6	1.734 $\pm$ 0.070 [1.541, 1.878] 22	1.702 $\pm$ 0.036 [1.636, 1.743] 7
PeW/CS	0.686 $\pm$ 0.054 [0.598, 0.745] 6	0.597 $\pm$ 0.041 [0.500, 0.693] 22	0.589 $\pm$ 0.027 [0.552, 0.625] 7
EyeHL	31.0 $\pm$ 17.3 [9, 62] 6	95.1 $\pm$ 26.0 [14, 130] 22	0.0 $\pm$ 0.0 [0.0, 0.0] 7
nSc	0.2 $\pm$ 0.3 [0.0, 0.5] 6	28.0 $\pm$ 17.2 [2.0, 82.0] 22	0.0 $\pm$ 0.0 [0.0, 0.0] 7
nCH	23.4 $\pm$ 7.6 [11.5, 30.5] 6	62.6 $\pm$ 18.1 [23.0, 95.0] 22	11.4 $\pm$ 4.4 [6.5, 18.0] 7
OccHL	201.7 $\pm$ 29.3 [169, 244] 6	214.9 $\pm$ 36.0 [166, 307] 22	163.4 $\pm$ 16.2 [148, 197] 7
nGu	34.8 $\pm$ 16.4 [20.0, 63.0] 6	65.1 $\pm$ 25.1 [22.5, 120.0] 22	33.0 $\pm$ 9.9 [22.0, 51.0] 7
GuHL	287.0 $\pm$ 32.0 [245, 330] 6	267.0 $\pm$ 44.8 [190, 352] 22	249.6 $\pm$ 17.3 [223, 275] 7
PnHL	255.3 $\pm$ 30.4 [201, 288] 6	241.6 $\pm$ 30.3 [181, 301] 22	193.6 $\pm$ 32.0 [170, 263] 7
nMet	26.3 $\pm$ 5.7 [20.0, 36.0] 6	38.0 $\pm$ 14.3 [16.0, 59.0] 22	22.3 $\pm$ 5.1 [16.0, 30.0] 7
MetHL	251.5 $\pm$ 40.8 [194, 305] 6	249.0 $\pm$ 45.0 [183, 349] 22	214.6 $\pm$ 31.4 [164, 247] 7
nPe	10.8 $\pm$ 3.0 [9.0, 16.0] 6	15.0 $\pm$ 7.0 [4.5, 28.0] 22	11.2 $\pm$ 3.6 [7.0, 16.5] 7
sqPDG	12.25 $\pm$ 1.41 [11.05, 14.94] 6	9.76 $\pm$ 3.41 [6.03, 22.10] 22	10.14 $\pm$ 1.22 [8.88, 11.71] 7
FodG	89.8 $\pm$ 23.8 [73.0, 106.6] 2	65.7 $\pm$ 18.9 [27.1, 119.2] 21	53.4 $\pm$ 4.6 [50.2, 56.7] 2

**Treatment by species:** The reasons for identification of a taxon are given in square brackets after the taxonomic name under which the taxon was introduced, author and year.

### ***Formica rufa* LINNAEUS, 1761**

*Formica rufa* LINNAEUS, 1761 [original description; YARROW (1954, 1955), photo of type specimen]

Each of the two first descriptions of this ant (LINNAEUS 1758, 1761) are contradictory within themselves. The morphological description of the worker states in 1758: "Thorace compresso toto ferrugineo, capite abdominique nigris." In 1761, the same statements are repeated and a supplementation is added: "Corpus fuscum. Thorax ferrugineus, compressus, squama intergerina ferruginea, acuminata." This agrees with the condition in *Camponotus herculeanus* or *Camponotus ligniperda*, which both occur in Sweden. In contradiction to the morphological description, LINNAEUS stated "habitat in Europae acervis-acerosis sylvaticis" (LINNAEUS 1758) and "Piss Myror. Suecis Stack-Myra...Habitat ubique in sylvis, acervos e foliolis acerosis exstruens." (LINNAEUS 1761). It is obvious from these data that Linnaeus in both publications more likely intended to give the name *F. rufa* to those most abundant ("Habitat ubique in sylvis"), needle-thatch building ("Stack-Myra...acervos e foliolis acerosis exstruens.") and acid squirting ("Piss Myror") woodland ants. The description of the gyne presented in 1761 reads as follows: "Corpus nigricans. Caput subtus ferrugineum. Thorax ferrugineus dorso fusco. Abdomen segmentis quatuor, primo antice ferrugineo." This description does not tell much but "Caput subtus ferrugineum" speaks against the two Swedish *Camponotus* species and is in agreement with the situation in ants of the *F. rufa* group. According to YARROW (1954), *F. rufa* group specimens were represented in the collection of the Linnaean Society London by a single worker bearing the label "rufa ex descr.", two unlabelled winged females, and three unlabelled males. YARROW (1954) published a lectotype fixation in the better preserved of the two winged *F. rufa* group gynes but he made no statements on its characters. The reasons why he did not fix a lectotype in the only specimen labelled "rufa ex descr." were not explained. I could not investigate the lectotype. As YARROW (1955) showed a rather good knowledge on the separation of the gynes of *F. rufa*, *Formica aquilonia*, *Formica lugubris*, and *Formica pratensis*, it appears most probable that he had a specimen at hand which indeed belonged to *F. rufa* as it is characterized here. Yet, as YARROW (1955) did not separate *F. rufa* and *Formica polycetena*, I inspected the picture of the lectotype (specimen number 2870) presented on the homepage of the Linnaean Society (<http://linnean-online.org/16186/>; retrieved on 31 October 2020). It shows a brilliantly shiny first gaster tergite, a shiny scutellum, and a massive, thick-set body. This overall impression corresponds to the gyne morph of monogynous *F. rufa* and likely precludes the specimen representing *F. polycetena*. In order to unambiguously dissolve the confusion with Linnaeus' descriptions, YARROW (1954) argued that "The Commission should use

their plenary power to place *F. rufa* L., 1758 on the list of permanently rejected names and to place instead *F. rufa* L., 1761 on the Official List of Specific Names in Zoology". This proposal was accepted by the International Commission of Zoological Nomenclature in an opinion published 2 October 1956.

### ***Formica piniphila* SCHENCK, 1852**

*Formica piniphila* SCHENCK, 1852 [description and zoogeography]

This taxon was described from Hessen-Nassau. Types were not available. SCHENCK (1852) reported for the worker "mesosoma always homogenously covered by setae, eyes bare, mesosoma with two small, pale blackish spots, the latter often missing" and for the gyne "scutellum and gaster brilliantly shiny." As SCHENCK (1852) correctly described differential characters of *Formica polycetena*, *Formica pratensis*, and *Formica truncorum* and because no other *Formica rufa* group species are expectable for Hessen-Nassau, the synonymy with *F. rufa* is obvious.

### ***Formica meridionalis* NASSONOV, 1889**

*Formica rufa* var. *meridionalis* NASSONOV, 1889 [identification by DLUSSKY (1967)]

This taxon was described from Kharkiv / E Ukraine and was synonymized by DLUSSKY (1967), who investigated types in the collection of ZMLU Moskva and stated these to be in all characters consistent with *F. rufa*. This is credible considering G.M. Dlussky's good knowledge of wood ants and the species spectrum present near Kharkiv.

### ***Formica rufotruncicola* WASMANN, 1891**

*Formica rufa* var. *rufotruncicola* WASMANN, 1891 [description of types by BETREM (1960)]

This taxon was described from Panheel near Roermond / Netherlands on the basis of workers collected from a nest in April 1889. WASMANN (1891a) gave no description of structural characters. However, as WASMANN (1891b) reported on the mixed colouration of the worker population of exactly this nest, *F. rufotruncicola* WASMANN, 1891 is no nomen nudum. The data reported by BETREM (1960) on seven investigated syntype workers from NHM Maastricht indicate that it is a red colour variant of *F. rufa*.

### ***Formica obscurata* SANTSCHI, 1925**

*Formica rufa* var. *obscurata* SANTSCHI, 1925 [type investigation]

This taxon was described from Vernon / France (49.09°N, 1.49° E, 19 m). Investigated were two type workers from NHM Basel labelled "type", "*F. rufa* L. v. *obscura* Sant type SANTSCHI det. 1925", "France Vernon (Eure) G. d. Kerville"; the specimen with CW = 1768 µm is additionally labelled with "ANTWEB CASENT 0912252". If run as wild-card in an LDA, the type sample is allocated with p = 0.8677 to *Formica rufa*, with p = 0.1321 to *Formica polycetena* × *rufa*, and with p = 0.0001 to *F. polycetena*.

### ***Formica rufa emeryi* STITZ, 1939**

*Formica rufa* ab. *emeryi* STITZ, 1939 [description and zoogeography]

STITZ (1939) made the first available use of *F. rufa* subsp. *rufa* ab. *emeryi* KRAUSSE, 1926. This taxon was described from near Eberswalde / Germany as specimens

found within the nests of *F. rufa* showing a colouration as in *Formica pratensis* but with missing setae on eyes and hind tibia. Considering the species spectrum occurring in the vicinity of Eberswalde, these statements make a synonymy with *F. rufa* most likely. Types are unknown.

All material examined. Numeric phenotypical data were recorded in 61 nest samples with 331 workers and 29 gynes; for details, see SI1, SI2, and SI3. The total number of mounted samples stored in SMN Görlitz and investigated either subjectively or by partial or complete numeric recording of the phenotypical characters used here was 103. These included 547 workers and 98 gynes and originated from Austria (two samples), Belgium (four), Bulgaria (six), Croatia (two), Finland (five), France (two), Germany (61), Greece (three), Italy (one), Norway (one), Poland (one), Russia (one), Slovenia (one), Spain (five), Sweden (four), and Switzerland (four). Character recording in ethanol-stored material according to the former investigation protocol of SEIFERT (1991) had been done until the year 1993 in further 196 nest samples with about 1600 workers, largely from Germany and Russia.

**Geographic range.** From Iberia east to Baikal region; probably a little more widely distributed than *Formica polyctena* due to the larger potency for long-range single-queen flight dispersal and socially parasitic colony foundation (SEIFERT 1991, 2018). In Europe between 40.5° N (Spain), 63.5° N (Sweden), and 64.8° N (Finland). A morphologically aberrant population exists in Asia Minor and Caucasus (here rare). The altitudinal distribution in European mountains is not well known. According to credible reports, it ascends in the Southern Alps (46° N) to 1500 m and in Asia Minor (40° N) to 1900 m.

**Diagnosis of worker (Tab. 1, key).** Large; mean and maximum CS over all social types 1891 and 2274 µm; Scape rather long and slender, SL / CS<sub>1750</sub> 0.939, SL / Smax 10.10. Setae on eyes short, EyeHL<sub>1750</sub> 22 µm. Setae on posterior margin of head usually missing and, if present, rather short, nCH<sub>1750</sub> 0.81, OccHL<sub>1750</sub> 23 µm (a population in the montane region of Blanský Les, S Bohemia – labelled “nespori” in the collection of SMN Görlitz – has above-average values of nCH and OccHL but does not form a cluster sufficiently separate from *Formica rufa* when all characters are considered). Gular, pronotal, mesopleural and propodeal setae always present and rather long, nGu<sub>1750</sub> 6.3, GuHL<sub>1750</sub> 188 µm, nPn<sub>1750</sub> 20.2, mPnHL<sub>1750</sub> 81 µm, nMes<sub>1750</sub> 15.4, nPr<sub>1750</sub> 12.9; setae on metapleuron few or absent and of medium length, nMet<sub>1750</sub> 1.9, MetHL<sub>1750</sub> 144 µm. Pigmentation: Head with genae and its ventral surfaces always light reddish, dorsal head caudad from about transverse level of eye centers, the area between frontal carinae and surface along the frontal carina usually blackish brown; mesosoma light reddish, often with a medium-sized dark brown patch on dorsal pronotum. Specimens with nearly all surfaces of head, the mesosoma, and frontal face of first gaster tergite reddish, reminiscent of the condition in *Formica truncorum*, may occur, most frequently in large workers of the most hairy phenotypes.

**Diagnosis of gyne (Tab. 6, Fig. 1).** Medium-sized, CS 2140 µm; scape rather long and slender, SL / CS 0.868, SL / Smax 9.13. Setae on eyes short, EyeHL 25 µm; setae on posterior margin of head always missing; gula without or with single setae of up to 280 µm length; pronotum without or single short setae of up to 44 µm length; meso- and metapleuron and frontal face of first gaster tergite without setae, if single setae are present these may have 200 - 244 µm length; ventral surface of first gaster sternite usually with numerous long setae, nSt 18.8, StHL 350 µm. Pubescence distance and distance of foveolae on paramedian dorsum of first gaster tergite rather high, sqPDG 9.00, FodG 57 µm. Large parts of median and paramedian scutellum perfectly smooth and brilliantly shiny. Dorsum of gaster viewed at lower magnification always shiny. Pigmentation of head similar to worker; mesonotum, scutellum, and metanotum blackish brown; gaster black.

**Taxonomic comments and clustering results.** The nomenclatorial separation of *Formica rufa* and *Formica polyctena* is maintained here for pragmatic reasons but this decision is problematic according to the data presented in the next paragraph. This pragmatism follows a functional argument: In their pure expression, *F. rufa* and *F. polyctena* represent most different morphologies, types of ecological adaptation, dispersal, and reproduction strategies, which call for a different naming. Several hundred papers have been published so far using the name *F. polyctena*. Giving up the name *F. polyctena* would mean a loss of information and would complicate communication about biological issues.

A broad study considering 432 nest samples with 6100 worker ants and eight NUMOBAT characters and integrating intranidal phenotype composition as well as

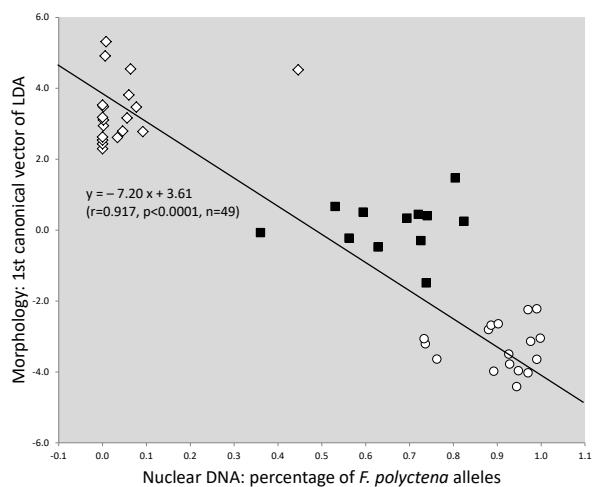


Fig. 21: Data of 49 samples from of E Saxony / Germany with *Formica rufa* (white rhombs), *Formica polyctena* × *rufa* (black squares), and *F. polyctena* (white dots). The first canonical vector of a three-class LDA, separating the parental species and considering 12 morphological characters, is plotted against the percentage of *F. polyctena* alleles determined by BAPS clustering (with K = 5) of 19 microsatellite markers (from SEIFERT & al. 2010, changed).

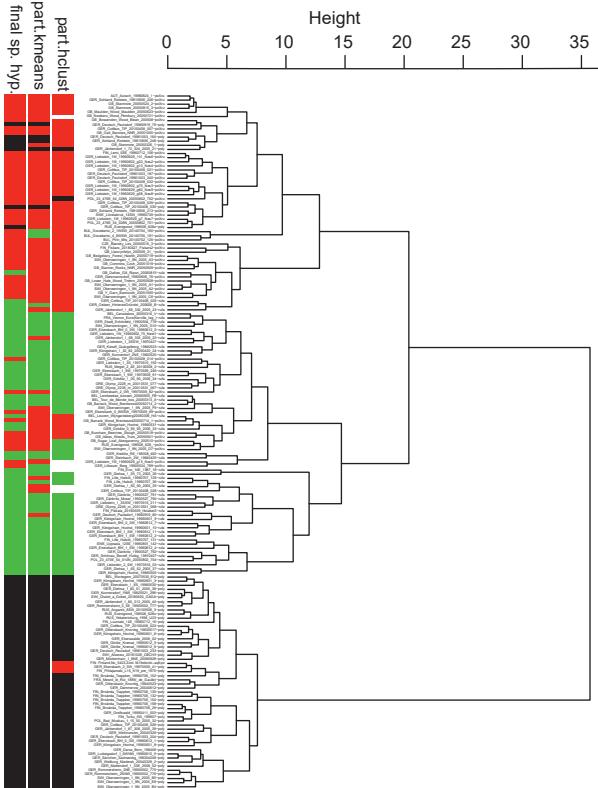


Fig. 22: Classification by the exploratory data analyses NC-Ward (dendrogram shown), NC-part.hclust and NC-part.kmeans and final species hypothesis formed by a controlling linear discriminant function (for details, see Material and Methods). Shown are 169 samples of workers of *Formica rufa* (red bars), *Formica polyctena* × *rufa* and backcrosses (green bars), and *F. polyctena* (black bars). White bars indicate outliers in NC-part.clust. The mean error of three analyses is 3.7% for  $K = 2$  (presence of hybrids ignored) but 13.2% for  $K = 3$  (presence of hybrids accepted), with 19% of the hybrid samples classified as either parental species. Accordingly, a hypothesis formation based on NC-clustering alone, neglecting any accessory information, would suggest two sufficiently separable species. Twelve phenotypic characters were considered.

topographic, ecological, and biological information (SEIFERT 1991) provided evidence for frequent hybridization of *Formica rufa* and *Formica polyctena*. The adaptive advantage of the hybrid for conditions of fragmented forest systems hypothesized by the same author was made credible through mathematic modelling by HÖFENER & al. (1996). The presence of the supposed hybrid cluster in East Germany was later convincingly confirmed by a study integrating NUMOBAT characters and nuclear DNA data (SEIFERT & al. 2010), with a high agreement of classifications provided by morphometrics and nuDNA (Fig. 21). Data on microsatellite DNA of GYLLENSTRAND & al. (2004) and SEIFERT & al. (2010) suggest that backcrossing of the hybrid and introgression occur mainly with the *F. polyctena* parent. This biased gene flow towards *F. polyctena* was also to be expected on the basis of differential queen acceptance and mating behaviour of the species (GÖSSWALD 1942, SEIFERT 1991).

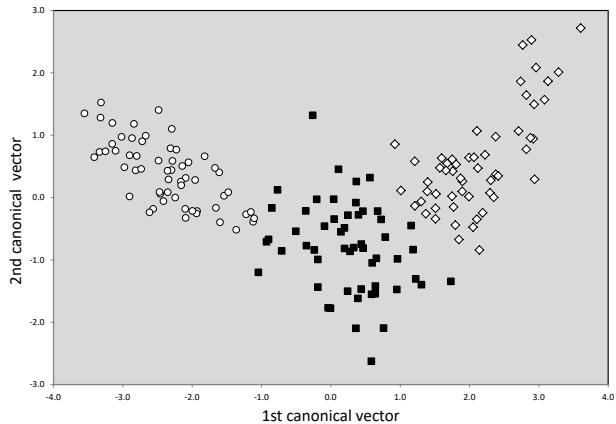


Fig. 23: Linear discriminant analysis of 169 samples of workers of *Formica rufa* (white rhombs), *Formica polyctena* × *rufa* and backcrosses (black squares), and *F. polyctena* (white dots) considering 12 morphological characters. The missing gaps between the clusters indicate introgression and prevent a clear discrimination of hybrids from parental species. Note that the frequency of hybrids in the analysis is about fivefold larger than expected for random sampling all over Europe.

Hybrid frequencies of up to 28% for particular regions sum up to 6 - 8% over the whole European range and cause a dilemma in taxonomic decision making. A blind NC-clustering study of morphological data, ignoring any other source of information and the possibility of hybrid occurrence, provided misleading results (Fig. 22). The figure considers 169 nest samples with 960 workers from entire Europe and the characters CS, CL / CW<sub>1750</sub>, SL / CS<sub>1750</sub>, nCH<sub>1750</sub>, OccHL<sub>1750</sub>, nGu<sub>1750</sub>, GuHL<sub>1750</sub>, nPn<sub>1750</sub>, mPnHL<sub>1750</sub>, nMes<sub>1750</sub>, nMet<sub>1750</sub>, MetHL<sub>1750</sub>, and nPr<sub>1750</sub>. Assuming  $K = 2$  (two species and no hybrids present), the disagreement of the exploratory data analyses with the controlling LDA was 4.1% in NC-Ward, 5.9% in NC-part.hclust, and 1.2% in NC-part.kmeans. This means an average error rate of 3.7% and suggests acceptance of heterospecificity of *Formica rufa* and *Formica polyctena* following the < 4% threshold recommended for NC-clustering by SEIFERT (2020a). Explicitly, NC-clustering confirms the *F. polyctena* cluster and a collective cluster formed by *F. rufa* and the hybrids. This clustering is largely explained by the high similarity of *F. rufa* and the hybrids in nGu<sub>1750</sub> and GuHL<sub>1750</sub> and a strong dissimilarity of *F. polyctena* regarding these characters. Assuming  $K = 3$  (two parental species and a hybrid cluster), the disagreement is 13.6% in NC-Ward, 15.4% in NC-part.hclust, and 10.6% in NC-part.kmeans. Out of 53 hybrid samples and as mean of the three methods, 16.4% were allocated to the *F. rufa* and 2.5% to the *F. polyctena* cluster. These data show that the different algorithms of NC clustering cannot clearly expose hybrid samples and are likely to suggest a stronger divergence of the parental clusters than really given. A clear demonstration of hybrids with gaps to the parental clusters may be achieved in a vectorial space, either by running a PCA of RAV-corrected data or checking suspicious samples as

wild-cards in an LDA. Yet, this proves only true when no or very few backcrosses are in the material (SEIFERT 1984, 1999, 2006, KULMUNI & al. 2010, BAGHERIAN YAZDI & al. 2012, SEIFERT 2019a, b). In the present case, the LDA of the 169 samples (Fig. 23) does not show obvious gaps separating the hybrid from the parental clusters, which may be explained by numerous backcrosses. The reader should be aware that the frequency of hybrids in this data set is about fivefold larger than the average figure expected for random sampling all over the European range. For hybridization with *Formica lugubris*, see section “Hybrids *Formica lugubris* × *rufa*” (p. 174).

**Bi ology.** See the condensed information in SEIFERT (2018).

### ***Formica polycتنا × rufa – hybrids and backcrosses***

All material examined. The full set of numeric phenotypical data was recorded in 55 nest samples with 345 workers and 16 gynes; for details, see SI1, SI2, and SI3. The total number of mounted samples stored in SMN Görlitz and investigated either subjectively or by partial or complete numeric recording of the phenotypical characters used here was 68. These included 453 workers and 18 gynes and originated from Austria (one sample), Bulgaria (three), Czechia (one), Finland (two), Germany (29), Great Britain (20), Poland (two), Russia (two), Sweden (one), and Switzerland (six). Character recording in ethanol-stored material according to the former investigation protocol of SEIFERT (1991) was done until the year 1993 in further 98 nest samples with about 2700 workers largely from Germany and Russia.

**Geographic range.** Hybrids are expected to occur wherever the parental species are in contact and hybrid frequency is estimated over the whole range as 6 - 8%. However, there are big regional differences in hybrid frequency. In Britain, where the typical *Formica polycتنا* and *Formica rufa* are absent, 95% of all samples are phenotypically intermediate and the whole population is supposed to consist of hybrids. The British hybrids are on average smaller and have longer gular setae than the continental hybrids (Tab. 1). Yet, describing them as a separate hybridogenous species is not justified as they cannot be separated from continental hybrids by any form of exploratory or hypothesis-driven data analysis. Anyway, it would be interesting to study their nuclear genome for genetic divergence during the time after the formation of the English Channel 7500 b.p.

**Diagnosis of worker** (Tab. 1, key). Both the continental and the British population are in nearly all characters intermediate between the parental species (Tab. 1). Identification is in most cases possible by discriminant functions if sufficiently large nest samples are considered.

**Diagnosis of gyne** (Tab. 6). Number and length of setae on average lower than in *Formica rufa* but on individual level often inseparable from either parental species.

**Taxonomic comments and clustering results.** This issue was thoroughly discussed in section “*Formica rufa* LINNAEUS, 1761” (p. 152).

**Bi ology.** A brief report on the relations between the hybrid and the parental genotypes as well as on the biological properties and the probable adaptive advantage of the hybrid is given in SEIFERT (2018).

### ***Formica polycتنا FOERSTER, 1850***

*Formica polycتنا* FOERSTER, 1850 [description, zoogeography]

This ant was described from Stolberg near Aachen / Germany where it formed a polydomous colony. FOERSTER (1850)'s description of setae condition and surface structures in the worker and gyne allows a clear differentiation from any *Formica rufa* group species present in this region.

### ***Formica gaullei* BONDROIT, 1917**

*Formica gaullei* BONDROIT, 1917 [type investigation]

This taxon was described using workers collected at Mesnil-le-Roi near St. Germain-en-Laye (48.925° N, 2.112° E, 65 m). Investigated were three worker syntypes collected in 1889 by de Gaulle at Mesnil-le-Roi and stored in MSNB Bruxelles. This sample showed the following posterior probabilities if run as wild-cards in an LDA: *Formica polycتنا* 0.9976, *F. polycتنا × rufa* 0.0024, *Formica rufa* 0.0002.

### ***Formica minor* GÖSSWALD, 1951**

*Formica minor* GÖSSWALD, 1951 [description]

This taxon was described from near Würzburg / Germany. GÖSSWALD (1951) apparently did not define type specimens but everything he reported in his lengthy treatise makes clear that he meant *Formica polycتنا*.

All material examined. The full set of numeric phenotypical data was recorded in 58 nest samples with 314 workers and 33 gynes; for details, see SI1, SI2, and SI3. The total number of mounted samples stored in SMN Görlitz and investigated either subjectively or by partial or complete numeric recording of the phenotypical characters used here was 69. These included 329 workers and 32 gynes and originated from Belgium (one), Finland (10), France (one), Germany (45), Poland (one), Russia (four), and Switzerland (seven). Character recording in ethanol-stored material according to the former investigation protocol of SEIFERT (1991) was done until the year 1993 in further 176 nest samples with about 1800 workers largely from Germany and the Moscow region.

**Geographic range.** Whole range apparently similar to that of *Formica rufa*: Iberia to Lake Baikal. The clearly confirmed occurrence in Europe extends between 42° N und 61° N; absent from British Isles, Asia Minor and Caucasus. The northern distributional border in Fennoscandia and Siberia and the upper altitudinal limit in Central European mountains are not exactly known because of frequent confusion with *Formica aquilonia* and occurrence of *F. aquilonia* × *polycتنا* hybrid populations. The putative northern limit in Finland is at 63° N or along the -10 °C January isotherm. Natural distribution in the Giant Mountains (Czechia) up to 800 m (here artificially

introduced at 1020 m), in the Alps ascending to 1200 m at least.

**Diagnosis of worker** (Tab. 1, key). Clearly smaller than *Formica rufa*, mean and maximum CS over all social types 1669 and 2067 µm. Scape rather long and slender, SL / CS<sub>1750</sub> 0.932, SL / Smax<sub>1750</sub> 9.97. Setae on eyes short, EyeHL<sub>1750</sub> 17 µm; on posterior margin of head nearly always missing and, if present, usually of minute size; gular, pronotal, mesopleural and propodeal setae sparse and rather short, nGu<sub>1750</sub> 1.46, GuHL<sub>1750</sub> 51 µm, nPn<sub>1750</sub> 2.5, mPnHL<sub>1750</sub> 30 µm, nMes<sub>1750</sub> 5.9, nPr<sub>1750</sub> 2.3; setae on metapleuron usually absent. Pigmentation as in *F. rufa* but percentage of dark pigmentation on mesosoma on average slightly higher due to smaller size and positive allometry of reddish pigmentation.

**Diagnosis of gyne** (Tab. 6, Fig. 2). Rather small; mean and maximum CS 2037 and 2165 µm; scape rather long and slender, SL / CS 0.864, SL / Smax 9.17. Setae on eyes short, EyeHL 21 µm; setae on posterior margin of head and gula always missing; pronotum bare, exceptionally without single short setae of up to 42 µm length; meso- and metapleuron and frontal face of first gaster tergite without setae, if single setae are present these may have 60 - 80 µm length; ventral surface of first gaster sternite with fewer setae than in *Formica rufa*, nSt 6.2, StHL 122 µm. Pubescence distance and distance of foveolae on paramedian dorsum of first gaster tergite high, sqPDG 12.2, FodG 58 µm. Shiny surface of scutellum usually restricted to a small median stripe. Dorsum of gaster viewed at lower magnification shiny but usually less than in *F. rufa*, which is caused by very faint transverse microripples. In some specimens the microripples may be stronger developed somewhat reminiscent of the situation in *Formica pratensis*. Colouration as in *F. rufa*.

**Taxonomic comments and clustering results.** For separation from *Formica rufa* and hybrids / backcrosses *Formica polyctena* × *rufa*, see section “*Formica rufa* LINNAEUS, 1761” (p. 152) and for separation from *Formica aquilonia* and hybrids / backcrosses *F. aquilonia* × *polyctena*, see section “*Formica aquilonia* × *polyctena* – hybrids and backcrosses” (p. 156).

**Biology.** See the condensed information in SEIFERT (2018).

### ***Formica aquilonia* × *polyctena* – hybrids and backcrosses**

Article 23.8 of ICZN regulates that a species-group name established for an animal later found to be a hybrid must not be used as the valid name for either of the parental species, even if it is older than all other available names for them. This excludes *Formica major* NYLANDER, 1849 and *Formica constricta* KARAVAJEV, 1926 to be considered as synonyms of *Formica polyctena* FOERSTER, 1850 or *F. aquilonia* YARROW, 1955.

#### ***Formica major* NYLANDER, 1849**

*Formica major* NYLANDER, 1849 [type investigation]

This taxon was described from the environs of Helsingfors (Helsinki). Three syntype workers on one pin labelled

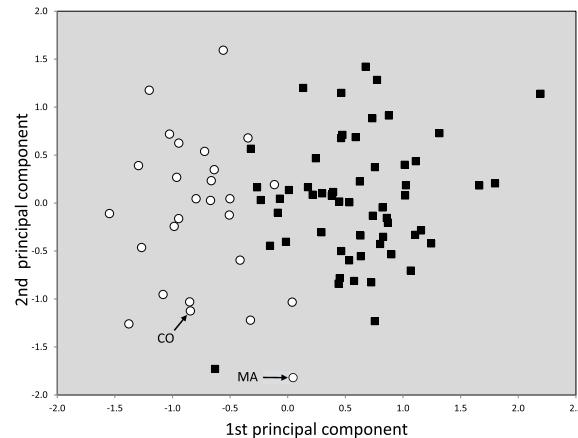


Fig. 24: Position of the type samples of *Formica major* NYLANDER, 1849 (MA) and *Formica constricta* KARAVAJEV, 1929 (CO) in a principal component analysis considering 58 nest samples of *Formica polyctena* (black squares) and 27 nest samples of *Formica aquilonia* × *polyctena* or backcrosses (white dots). The *F. polyctena* sample deeply placed within the hybrid cluster is aberrant and cannot be a hybrid for zoogeographical reasons. Seven phenotypic characters were considered.

“Zool. Mus. H:fors Spec. typ. No 5423 *Formica major* Nyl.”, “*major* Nyl piniphila Schenck rufa auctt nec Bondr.”, “Mus. Hels. N:o 2676” do not carry an information on the sampling locality but the specimens fully match the morphological description of NYLANDER (1849). Considering their numeric data and by subjective impression, the type series of *F. major* cannot be hybrids *Formica polyctena* × *rufa* but represents either *F. polyctena*, *Formica aquilonia* × *polyctena* hybrids or backcrosses. This morphology-based idea is fully in line with the existence of large hybridization and introgression zone in southern Finland shown by nuDNA data (BERESFORD & al. 2017). Run as wild-cards in a two-class LDA considering the characters CS, CL / CW<sub>1750</sub>, SL / CS<sub>1750</sub>, nCH<sub>1750</sub>, OccHL<sub>1750</sub>, nGu<sub>1750</sub>, GuHL<sub>1750</sub>, nPn<sub>1750</sub>, mPnHL<sub>1750</sub>, nMes<sub>1750</sub>, nMet<sub>1750</sub>, MetHL<sub>1750</sub>, nPr<sub>1750</sub>, SL / Smax<sub>1750</sub>, EyeHL<sub>1750</sub>, and nSc<sub>1750</sub>, the type sample is allocated with p = 0.4867 to *F. polyctena* and with p = 0.5133 to the hybrid cluster. The marginal position in the hybrid cluster suggests *F. major* to represent a backcross of a *F. aquilonia* × *polyctena* hybrid with *F. polyctena*. A PCA plot considering the characters CS, SL / CS<sub>1750</sub>, OccHL<sub>1750</sub>, GuHL<sub>1750</sub>, SL / Smax<sub>1750</sub>, EyeHL<sub>1750</sub>, and nSc<sub>1750</sub> provides the same impression (Fig. 24). These investigations considered 27 nest samples and 148 workers of *F. aquilonia* × *polyctena* hybrids or backcrosses and 57 nest samples with 217 workers of *F. polyctena*. See also section “*Formica aquilonia* YARROW, 1955” (p. 158) and Figure 25.

#### ***Formica constricta* KARAVAJEV, 1926**

*Formica rufa* var. *constricta* KARAVAJEV, 1926 [type investigation]

Investigated were two syntype workers on one pin labelled „Akmolin. ob. Kokchetav. g. bl. Borovoye.

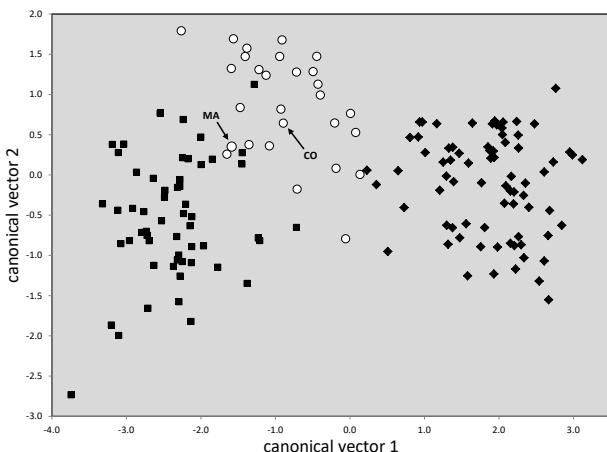


Fig. 25: Position of the type samples of *Formica major* NYLANDER, 1849 (MA) and *Formica constricta* KARAVAIEV, 1929 (CO) in a linear discriminant analysis considering 58 nest samples of *Formica polyctena* (black squares), 27 nest samples of *Formica aquilonia* × *polyctena* or backcrosses (white dots), and 75 nest samples of *F. aquilonia* (black rhombs). The type samples were run as wild-cards. Sixteen phenotypic characters were considered.

Bej-Bijenko”, “3269. coll Karavaiev”, “Form. (Form.) rufa v. constricta Karavaiev typ” (Karavaiev’s handwriting), “Syntypes *Formica rufa constricta* Karaw.” (label of Radchenko) and three syntype workers on another pin labelled “3269. coll Karavaiev”, “Syntypes *Formica rufa constricta* Karaw.” (label of Radchenko); depository SIZ Kiev. The type locality Borovoye is situated in the geographic zone (see below) where hybrids between *Formica aquilonia* and *Formica polyctena* do regularly occur. The status of the types was tested using the same 16 characters as in the analysis in the previous section. If run as wild-cards in a three-class LDA and comparing *F. aquilonia* (class 1), hybrids and backcrosses *F. aquilonia* × *polyctena* (class 2) and *F. polyctena* (class 3), the type series is allocated to these classes with  $p = 0.0152$ ,  $p = 0.8019$ , and  $p = 0.1829$ , respectively (Fig. 25). These investigations considered 75 nest samples with 345 workers of *F. aquilonia*, 27 nest samples and 148 workers of *F. aquilonia* × *polyctena* hybrids or backcrosses, and 57 nest samples with 217 workers of *F. polyctena*. Under this setting, the type series of *Formica major* was allocated in a wild-card run to the three classes with  $p = 0.0021$ ,  $p = 0.5244$ , and  $p = 0.4735$ , respectively.

All material examined. The full set of numeric phenotypical data was recorded in 27 nest samples with 148 workers and 18 gynes. These originated from Finland (13), Kazakhstan (one), Mongolia (one), and Russia (12). For details, see SI1, SI2, and SI3.

**Geographic range.** The geographic range where hybrids *Formica aquilonia* × *polyctena* are known to occur corresponds to the transition zone between temperate and boreal climate and ranges from 19.8° E (Aaland Isles / Finland) to 107° E (Baikal Region and Bogd Khan NP / Mongolia). With increasing continentality, this zone moves

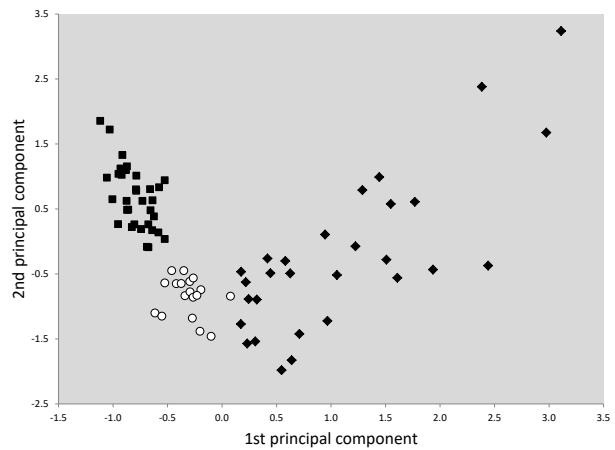


Fig. 26: Principal component analysis of gynes of *Formica polyctena* (black squares,  $n = 33$ ), *Formica aquilonia* × *polyctena* or backcrosses (white dots,  $n = 18$ ), and *F. aquilonia* (black rhombs,  $n = 29$ ). Twenty-four phenotypic characters were considered.

south: It extends in Finland between 59.8 and 63.3° N, in West Siberia (about 62° E) between 53.1 and 60.4° N, and in Central Siberia (about 104° E) between 47.8 and 53.2° N. Hybrid occurrence and introgression should also occur in the Alps somewhere in the submontane or montane zone.

**Diagnosis of worker (Tab. 2, key).** The hybrids are intermediate in all characters in which the parental species show notable differences (Tab. 2).

**Diagnosis of gyne (Tab. 6).** Except for one specimen, all examined gynes are from a single super-colony near Tärminne / Finland in which the genetic structure was thoroughly investigated by KULMUNI & al. (2010) and KULMUNI & PAMILO (2014). The data in Table 6 are thus biased to a local situation and probably not representative for the Palearctic hybrid population. Yet, the intermediate position of the hybrids becomes obvious in characters showing the most obvious differences of the parental species: SL / CS, SL / Smax, FodG, and GuHL.

**Taxonomic comments and clustering results.** The earliest indications of this hybridization came from a West Siberian sample (SaNo 156, Yekaterinburg-1998-U23) combining a clear *Formica polyctena* phenotype with a mtDNA of *Formica aquilonia* (GOROPASHNAYA & al. 2004) and observation of viable laboratory crosses (SORVARI 2006). In the time since then, hybridization of *F. aquilonia* and *F. polyctena* has been confirmed and thoroughly investigated by morphometric analyses and investigation of nuDNA (KULMUNI & al. 2010, BERESFORD & al. 2017). A nuDNA study of the latter authors in 17 sites within an area of 3000 km<sup>2</sup> in South Finland revealed extremely frequent hybridization and introgression between *F. aquilonia* and *F. polyctena*. This investigation showed that nest populations with a hybrid history but having developed their nuclear DNA close to the situation in the *F. aquilonia* parent preferentially had the mtDNA of *F. polyctena*, whereas a majority of those with a nuDNA approaching *F. polyctena* had the mtDNA of *F. aquilonia*.

Hybrids in the Irkutsk Region (Central Siberia) seem to form an own self-sustaining population – at least they are no result of a very recent hybridization because *Formica polyctena* is not confirmed so far to occur there and because its presence is unlikely for climatic reasons (mean January temperature -21 °C).

Results of clustering worker samples are commented above (Figs. 24, 25). Due to introgression, it is not possible to demonstrate three separate clusters. A PCA of the gynes, considering all 24 characters presented in Table 6, provided a rather good separation of the three entities (Fig. 26). However, there are no backcrosses in the gyne hybrid cluster in which 94% of specimens came from a single, isolated supercolony.

### ***Formica aquilonia* YARROW, 1955**

*Formica aquilonia* YARROW, 1955 [description, photo of holotype, zoogeography]

This taxon was described from Black Wood of Rannoch, Perthshire, Scotland (56.667° N, 4.347° W). YARROW (1955)'s description of gynes and workers, the pictures of the holotype gyne in AntWeb (ANTWEB 2021) (CASENT0903277), and the geographic position of the type locality unquestionably indicate the identity of this taxon.

All material examined. Numeric phenotypical data were recorded in 81 nest samples with 381 workers and 30 gynes. These originated from Austria (17 samples), Czechia (three), Finland (24), Scotland (one), Mongolia (five), Norway (three), Russia (19), Sweden (one), and Switzerland (eight). For details, see SI1, SI2, and SI3. The total number of samples numerically or subjectively investigated was 130.

Geographic range. Eurosiberian-boreomontane. Continuous range from Northern Ireland and Scotland to East Siberia (131° E), in Fennoscandia between 56.3 and 71° N, and in Siberia between 47.5 and 63° N. The montane range in Europe extends from SE to NW over the Rila Mountains, NW Carpathians, Bohemian Forest, and the Eastern Alps westward to 9° E. In the Alps ascending to 2400 m. Main distribution in the Alps within the autochthonous distributional area of *Larix* (EICHHORN 1964).

**Diagnosis of worker** (Tab. 2, key). Small; mean and maximum CS over all social types 1575 and 1902 µm. Scape short and rather thickset, SL / CS<sub>1750</sub> 0.908, SL / Smax<sub>1750</sub> 9.25. Setae on eyes rather short, EyeHL<sub>1750</sub> 24 µm; setae on dorsal plane of scape usually absent or few, nSc<sub>1750</sub> usually 0 - 2; head margin behind eyes with few short setae which usually concentrate at the occipital corners, nCH<sub>1750</sub> 5.1, OccHL<sub>1750</sub> 64 µm; gular, pronotal, and propodeal setae sparse and rather short, nPn<sub>1750</sub> 7.9, mPnHL<sub>1750</sub> 42 µm, nPr<sub>1750</sub> 5.8; seta on lateral mesopleuron more numerous but on lateral metapleuron absent or very few and of moderate length, nMes<sub>1750</sub> 14.7, nMet<sub>1750</sub> 1.8, MetHL<sub>1750</sub> 86 µm.

**Diagnosis of gyne** (Tab. 6, Fig. 8). Small; mean and maximum CS 2015 and 2173 µm. Scape short

and thickset, SL / CS 0.810, SL / Smax 8.32. Setae on eyes rather short, EyeHL 29 µm; head margin behind eyes with very few short setae which usually concentrate at the occipital corners, nCH 2.1, OccHL 30 µm; gular, pronotal, mesopleural, and metapleural setae and those on frontal face of first gaster tergite few and rather short, nGu 3.1, GuHL 51 µm, PnHL 43 µm, nMes 2.5, nMet 1.4, MetHL 30 µm, nGfr 8.1, GfrHL 64 µm. Margin of petiole scale above spiracle with few short setae. Pigmentation without peculiarities. Dorsum of gaster shiny but less than in *Formica rufa*; foveolae on first gaster tergite more dense, FodG 27.7 µm.

**Taxonomic comments and clustering results.** Results of clustering are shown and commented in section “*Formica aquilonia* × *polyctena* – hybrids and backcrosses” (p. 156). Frequent hybridization and introgression raise the question if *F. aquilonia* and *Formica polyctena* can be considered as separate species. One option would be to reduce them to subspecies with differing climatic adaptations – boreo-montane and frost-hardy in *F. aquilonia*, and temperate-planar-colline and less frost-hardy in *F. polyctena*. I advocate here, for operational and pragmatic reasons, to stay with a nomenclatorial treatment as different species. Reticulate evolution in the *Formica rufa* group as a whole already produces a difficult taxonomic situation which would be further complicated if we abandon the parsimonious binary naming. A third, radical solution, synonymizing *F. aquilonia* with *F. polyctena* and then, as a logical consequence (see section “*Formica rufa* LINNAEUS, 1761”, p. 152), synonymizing these two taxa also with *F. rufa*, causes more problems than it solves. Speaking only of *F. rufa* would cause a loss of information on the structure of biodiversity and on the natural history of its elements. For hybridization with *Formica lugubris* and *Formica paralugubris*, see sections “Hybrids *Formica aquilonia* × *lugubris*” (p. 152) and “Hybrids *Formica aquilonia* × *paralugubris*” (p. 156).

**Habitat and biology.** See the species profile in SEIFERT (2018).

### ***Formica ussuriensis* sp.n.**

**Etymology.** Referring to the region of the river Ussuri in which the species occurs.

**Type material.** Holotype worker plus four paratype workers labelled “RUS: Ussuri: 43.24N, 133.39E 770m, ober. Povarotnaja-Tal, lehmiger Hangschutt, Sandboden mit Pioniergebäude, 1999.09.14 -050 (L.Kanter)”; 5 paratype workers labelled “RUS: Ussuri: 43.01N, 133.21E, 850m; S-Mt. Lysaya Sopka, dunkle Fichten-Tannen-Taiga, 1999.09.03 -037 (L.Kanter)”; 5 paratype workers labelled “RUS: Ussuri: 43.24N, 133.39E, 555m; ober. Povaratnaya-Tal; sandige Flussterrasse, 1999.09.14 -051 (L.Kanter)”; depository SMN Görlitz.

All material examined. Numeric phenotypical data were recorded in 10 nest samples with 41 workers and three gynes. All these originated from Russian Far East. For details, see SI1, SI2, and SI3.

**Geographic range.** Known are eight sites in the Ussuri River / Sichote Alin region situated at altitudes between 270 and 850 m, and latitudes between 43.0 and 48.3° N.

**Diagnosis of worker** (Tab. 2, Figs. 5 and 6, key). Similar to *Formica aquilonia*; slightly smaller, mean and maximum CS over all social types 1537 and 1808 µm. Scape as short but less thickset than in *F. aquilonia*, SL / CS<sub>1750</sub> 0.903, SL / Smax<sub>1750</sub> 9.51. Petiole on average wider than in any other species, PeW / CS<sub>1750</sub> 0.519. Setae on eyes rather short, EyeHL<sub>1750</sub> 26 µm; setae on dorsal plane of scape much more numerous than in *F. aquilonia*, nSc<sub>1750</sub> 10.8; setae on head margin behind eyes more numerous than in *F. aquilonia* and slightly longer, nCH<sub>1750</sub> 10.9, OccHL<sub>1750</sub> 80 µm; gular, pronotal, propodeal, and metanotal setae sparse and short as in *F. aquilonia* with exception of clearly longer metanotal setae, nGu<sub>1750</sub> 5.6, GuHL<sub>1750</sub> 117 µm, nPn<sub>1750</sub> 7.1, mPnHL<sub>1750</sub> 47 µm, nPr<sub>1750</sub> 3.5; mMet<sub>1750</sub> 3.8, MetHL<sub>1750</sub> 141 µm; setae on lateral mesopleuron as numerous as in *F. aquilonia*, nMes<sub>1750</sub> 15.4. Pigmentation without specific characters.

**Diagnosis of gyne** (Tab. 6, Fig. 7). Clearly larger than *Formica aquilonia*, mean and maximum CS 2225 and 2357 µm. Hind margin and sides of head more linear, as result head shape more trapezoid. Scape short and thickset, SL / CS 0.806, SL / Smax 8.27. Setae on eyes rather short, EyeHL 33 µm; setae on head margin behind eyes much more numerous than in *F. aquilonia* and slightly longer, nCH 15.0, OccHL<sub>1750</sub> 65 µm; gular setae much more numerous and longer than in *F. aquilonia*, nGu 10.8, GuHL 107 µm; setae on metapleuron and frontal face of first gaster tergite much more numerous and much longer than in *F. aquilonia*, nMet 12.2, MetHL 167 µm, nGfr 26.3, GfrHL 257 µm. Distance of pubescence and of foveolae on paramedian surface of first gaster tergite as in *F. aquilonia*, sqPDG 10.12, FodG 25.3 µm. Pigmentation without diagnostic characters.

**Taxonomic comments and clustering results.** The species is similar to *Formica aquilonia* and probably closely related. The geographically closest finding of *F. aquilonia* in the south of Amur Oblast' (49.16° N, 130.67° E) is situated about 340 km west of the next known site of *Formica ussuriensis* at 48.22° N, 135.06° E. Accordingly, occurrence of hybridization and introgression has to be checked in the region of the lower course of river Amur. Yet, the data currently available provide clearly separate clusters in exploratory data analyses. Considering the characters CL / CW<sub>1750</sub>, SL / Smax<sub>1750</sub>, nSc<sub>1750</sub>, nCH<sub>1750</sub>, OccHL<sub>1750</sub>, nMet<sub>1750</sub>, MetHL<sub>1750</sub>, and nPr<sub>1750</sub>, 10 worker nest samples of *F. ussuriensis* were separated from 75 Panpalaearctic samples of *F. aquilonia* by NC-Ward, NC-part.kmeans, NC-NMDS-kmeans, and a PCA with an error rate of 0%, whereas NC-part.hclust misclassified 2.4% of the samples (Fig. 27). Using the same character system, an LDA classified 98.7% of 386 worker individuals in agreement with the classification provided by four exploratory data analyses. Regarding gynes, the first factor of PCA considering the characters CS, EyeHL, nCH, nMet,

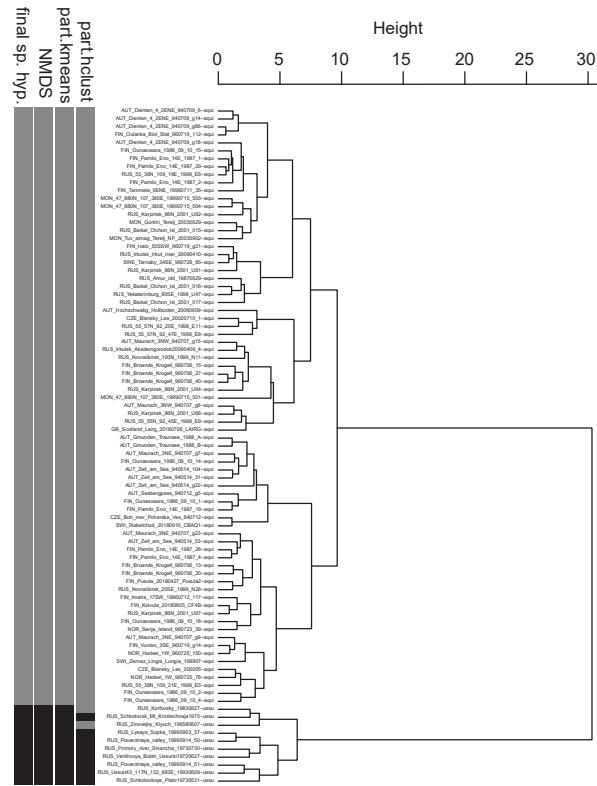


Fig. 27: Classification by four variants of NC-clustering of 75 nest samples of workers of *Formica aquilonia* (grey bars) and 10 nest samples of *Formica ussuriensis* sp.n. (black bars). The mean error of four exploratory data analyses is 0.6%. Eight phenotypic characters were considered.

and MetHL scored  $2.663 \pm 0.221$  (2.413, 2.832) in three gynes of *F. ussuriensis* but  $-0.275 \pm 0.515$  (-0.913, 0.784) in 29 gynes of *F. aquilonia*. A full separation by the PCA was also given when all 24 characters shown in Table 6 were considered unselectively.

**Habitat and biology.** It formed monodomous and polydomous colonies and was found in often very dark spruce (*Picea*), fir (*Abies*), and broadleaf forests. These biomes have a boreal to subboreal character due to the influence of cold waters of the Pacific Ocean. This leads to a shift of biomes to more southern latitudes and lower altitudes than observed in comparable biomes in Europe. The 10 known sites are situated at altitudes of  $622 \pm 213$  (270, 850) m.

### *Formica pratensis* RETZIUS, 1783

*Formica pratensis* RETZIUS, 1783 [concept of FOREL (1874), present neotype designation]

Type specimens are unknown and the original description of RETZIUS (1783), reporting only "rufa, capite abdomineque nigris, petiolo abdominis squamifero", does not allow an identification even of the genus. The tradition which ant has to be named as *F. pratensis* was founded by FOREL (1874) who reported for the worker a large extension of the dark patch on dorsal mesosoma, a longer pilosity compared with *Formica truncorum*, presence of setae on legs and eyes, and, for the gyne, a completely matt, densely

pubescent gaster. This character combination excludes any of the other seven species occurring in Switzerland. FOREL (1874) also reported as main habitat grassland and wood margins, which probably prompted him to assign A.J. Retzius' name to this ant. In order to stabilize the nomenclature, a neotype was fixed from a nest sample containing 18 workers, labelled "GER:51.4048° N, 14.8746° E, Daubitz-3.3 km ENE, 162 m, flacher Hügel, R.Schultz 1999.06.30-050" and "Neotype Formica pratensis Retzius 1783 des. B. Seifert 2020"; depository SMN Görlitz.

#### **Formica nigricans BONDROIT, 1912**

*Formica pratensis* var. *nigricans* BONDROIT, 1912 [photos of lectotype, zoogeography]

This is the first available use of *Formica rufa pratensis* var. *nigricans* EMERY, 1909. EMERY (1909) reported as collecting sites "eine südliche Form; aus den Seealpen und aus Spanien, auch im Apennin (Vallombrosa)". A lectotype was fixed in worker specimen stored in MHN Genève labelled "Cotypus", "Formica rufa pratensis var. nigricans Em Vallombrosa" (C. Emery's handwriting), "v. nigricans Em" (A. Forel's handwriting), and "MHNG ENTO 00085011". The characters revealed in the photos in combination with zoogeography clearly indicate that *F. pratensis* var. *nigricans* is a junior synonym of *F. pratensis* and not of *Formica lugubris*. The type locality Vallombrosa (43.73° N, 11.56° E, 950 m) is situated in a geographic region, as it is with the whole Apennine, where boreomontane species of the *F. lugubris* species complex did not occur in the times of C. Emery (BARONI URBANI 1971). All populations of boreomontane wood ants from the Apennine mountains known today go back to a massive artificial introduction performed during the years 1959 - 67 (e.g., PAVAN 1959).

#### **Formica cordieri BONDROIT, 1917**

*Formica cordieri* BONDROIT, 1917 [type investigation]

This taxon was described by BONDROIT (1917) as gyne in the key. No type locality, collector, nor date was given. Examined were three type specimens from MSNB Bruxelles: one gyne labelled "Orne-6-Longny Collection E.Cordier", "Formica cordieri Type Bondr."; one gyne labelled "Hte Savoie de Gaulle", "Formica v. cordieri Type Bondr.", and one gyne labelled "Sayat P. de D.", "Formica v. cordieri Type Bondr.". The synonymy with *Formica pratensis* is obvious: All three gynes belong to the hairy N-morph as defined by SEIFERT (1992). For separation of N- and P-morphs, see also below and Figure 29.

#### **Formica grouvellei BONDROIT, 1918**

*Formica grouvellei* BONDROIT, 1918 [type investigation]

Investigated was the type gyne from MSNB Bruxelles labelled "Digne Grouvelle", "F.rufa var. grouvellei Type Bondr.". The type belongs to the hairy N-morph as defined by SEIFERT (1992).

#### **Formica thyssei STÄRCKE, 1942**

*Formica pratensis* ab. *thyssei* STÄRCKE, 1942 [type investigation]

This taxon was described from the Netherlands in a gyne collected at Eerbeek op de Veluwe, June 1916, leg. F.T. Valck Lucassen. This type from NBC Leiden was in-

vestigated and belongs to the less hairy P-morph as defined by SEIFERT (1992).

#### **Formica angusticeps STÄRCKE, 1947**

*Formica rufa* var. *angusticeps* STÄRCKE, 1947 [description, zoogeography]

The taxon was described from the Netherlands. BOLTON (1995) considered the name as available. The title of the paper "De boreale form van de rode boschnier (*Formica rufa rufa*)" suggests that STÄRCKE (1947) intended to introduce the new name at infrasubspecific rank. Yet, the main text did not make it clear what his intention was. If the name is available, we can assume a synonymy with *Formica pratensis* based on the following argumentation. The type locality is in Hoge Veluwe (51.08° N, 5.83° E, 38 m) – a sand dune area with interspersed moister parts. We have only four species of the *F. rufa* group potentially occurring in that region: *F. rufa*, *Formica polycetena*, *F. pratensis*, and *Formica truncorum*. *Formica truncorum* is extremely rare in the Netherlands and STÄRCKE (1947) would have noted the diagnostic pigmentation. Therefore, he would have referred to one of the other three species. The reported presence on extensor profile of tibiae of 5 - 11 setae which are erected by 30 - 45° clearly speaks against *F. rufa*, *F. polycetena*, or *F. polycetena* × *rufa*. STÄRCKE (1947) gave no data on pilosity on back of head but he compared his *F. angusticeps* with specimens of "*F. rufa rufa*" from the Norwegian coast near the Lofoten (68° N) and of "*F. rufa alpina* Santschi" from the high Alps. For zoogeographical and morphological reasons, his specimens from the Lofoten obviously belonged to *Formica lugubris* and those from the high Alps to either *F. lugubris* or *Formica paralugubris*. These data implicate *F. angusticeps* to have a rich overall pilosity as it is typical for *F. pratensis* and to be hairier than in the hairiest *F. rufa* phenotypes.

#### **Formica pratensoides GÖSSWALD, 1951**

*Formica minor* ssp. *pratensoides* GÖSSWALD, 1951 [description, zoogeography]

This taxon was described from near Würzburg (Germany): "Revierförsterei Irtenberg, Forstamt Waldbrunn". GÖSSWALD (1951) reported a large, clearly demarcated black patch on promesonotum of the workers and gynes having 110 - 115% of the size of *Formica rufa* and a completely matt gaster surface. It becomes obvious from his lengthy treatise that GÖSSWALD (1951) studied a polygynous-polydomous colony of *Formica pratensis*. Such colony types up to true supercolonial conditions have been repeatedly observed in forests of the planar and colline zone of Germany (SEIFERT 1992, 2018).

#### **Formica staerckeii BETREM, 1960**

*Formica nigricans* var. *staerckeii* BETREM, 1960 [description, zoogeography]

It was described from a gyne collected by E. Wasman on 30 May 1885 near Castle Exaten at Baexem (Netherlands). BETREM (1960), using low-resolution microscopes, mentioned hairy eyes, absence of long hairs on head, a "practically hairless" mesosoma, and a matt surface of scutellum and gaster. This corresponds to

the P-morph of *Formica pratensis*. The type specimen should exist in NHM Maastricht but was not available for investigation.

### ***Formica nigropratensis* BETREM, 1962**

*Formica nigropratensis* BETREM, 1962 [unnecessary replacement name]

This new name is an objective junior synonym as it was referred by BETREM (1962) simultaneously to the available names *Formica thyssei* STÄRCKE, 1947, *Formica pratensisoides* GÖSSWALD, 1951, and *Formica staerckei* BETREM, 1960.

All material examined. Numeric phenotypical data were recorded in 96 nest samples with 331 workers and 21 gynes. These originated from Bulgaria (seven samples), Czechia (one), Georgia (one), Finland (two), France (six), Germany (37), Hungary (two), Italy (one), Kazakhstan (four), Kyrgyzstan (three), Poland (one), Romania (two), Russia (21), Sweden (seven), and Switzerland (one). For details, see SI1, SI2, and SI3. Character recording in ethanol-stored material according to the former investigation protocol of SEIFERT (1992) had been done until the year 1991 in 224 nest samples with 1756 workers and 295 gynes originating from Europe.

**Geographic range.** Continuously distributed through the temperate and submeridional zones of the Palaearctic, from Spain ( $9^{\circ}$  W) to Irkutsk ( $104^{\circ}$  E) at least. In Europe from  $37^{\circ}$  N (S Spain) to  $63.9^{\circ}$  N (Fennoscandia). In the Alps ascending to 1500 m ( $46.0^{\circ}$  N), in the Pyrenees and Bulgaria to 1800 m ( $42^{\circ}$  N), and in the Tian Shan to 2100 m ( $42.2^{\circ}$  N). Reports from higher elevations in Europe should be checked for confusion with *Formica lugubris*.

**Diagnosis of worker** (Tabs. 3 and 4, Figs. 9 and 10, key). Dimorphic, with P and N morphs frequently occurring within the same nest. According to the data of SEIFERT (1992), then measured in ethanol-stored specimens, the less hairy P-morph had nCH  $17.9 \pm 5.7$ , OccHL  $103 \pm 25$  µm, nHT  $17.8 \pm 5.7$ , and CS  $1820 \pm 220$  (1050, 2250) µm in 962 workers, and the hairier N-morph nCH  $28.2 \pm 6.4$ , OccHL  $132 \pm 20$  µm, nHT  $25.1 \pm 5.1$  and CS  $1770 \pm 220$  (1040 - 2180) µm in 794 workers. Large species; mean and maximum CS over all social types and both morphs in dry mounted specimens (with slight bias to selecting larger specimens) 1819 and 2239 µm. Head elongated, CL / CW<sub>1750</sub> 1.111. Scape much longer and slender than in *Formica lugubris*, SL / CS<sub>1750</sub> 0.927, SL / Smax<sub>1750</sub> 10.66. Petiole scale clearly narrower than in *F. lugubris*, PeW / CS<sub>1750</sub> 0.453. Setae number and length extremely variable but even in the least hairy phenotypes larger than in *Formica rufa*; separation from *F. lugubris* by seta characters impossible due to extreme setae polymorphism also in this species; for variance of setae data, see Tables 3 and 4. All body surfaces except the frontal triangle matt due to developed microsculpture. The blackish patch on promesonotum is often larger than on average seen in other species and is often sharply demarcated from the reddish surface.

**Diagnosis of gyne** (Tab. 6; Figs. 4, 11, 12). Dimorphic, P- and N-morphs frequently occurring within the same nest, and more clearly separable than workers. According to the data of SEIFERT (1992), then measured in ethanol-stored specimens, the less hairy P-morph had nCH  $0.2 \pm 0.8$ , OccHL  $30 \pm 20$  µm, nHT  $0.6 \pm 1.0$ , and CS  $2290 \pm 80$  (2090, 2511) µm in 172 gynes, and the hairier N-morph nCH  $16.2 \pm 14.1$ , OccHL  $218 \pm 82$  µm, nHT  $8.4 \pm 4.3$ , and CS  $2250 \pm 70$  (2040 - 2400) µm in 123 gynes. Large; mean and maximum CS over all social types and both morphs in 21 mounted specimens 2296 and 2432 µm. Head moderately elongated, CL / CW 1.024. Scape much longer and more slender than in species related to *Formica rufa*, *Formica aquilonia*, or *Formica lugubris*, SL / CS 0.853, SL / Smax 9.75. Petiole scale relatively narrow, PeW / CS 0.628. Strong pilosity dimorphism: setae number, distribution, and length extremely variable (SEIFERT 1992). Setae on eyes always present and rather long to very long, EyeHL 46 - 86 µm. The least hairy gynes of the P-morph have no setae on posterior margin of head, scape, scutellum, propodeum, petiole scale above spiracle, frontal face of first gaster tergite, and extensor profile of hind tibiae. The hairiest gynes of the N-morph have an extremely rich pilosity on nearly all body surfaces with seta length reaching 453 µm on scutellum and 432 µm on frontal face of first gaster tergite. All body surfaces, with exception of the frontal triangle, matt due to developed microsculpture. At magnifications > 100x, the dorsum of gaster tergites shows strong transverse microripples and a dense pubescence; sqPDG  $4.0 \pm 0.5$ .

**Taxonomic comments and clustering results.** Combining big size, a long and slender scape, hairy eyes, and dense transverse microripples on gaster tergites, gynes are easily separable from any species except for the East Palaearctic sister species *Formica kupyanskayae* (for identification, see section “*Formica kupyanskayae* BOLTON, 1995”, p. 163). Separation of *Formica pratensis* workers from those of *Formica lugubris* is safely possible throughout the Palaearctic range using the characters CS, CL / CW<sub>1750</sub>, SL / CS<sub>1750</sub>, SL / Smax<sub>1750</sub>, PeW / CS<sub>1750</sub>, nSc<sub>1750</sub>, nCH<sub>1750</sub>, OccHL<sub>1750</sub>, mPnHL<sub>1750</sub>, nMet<sub>1750</sub>, and MetHL<sub>1750</sub>. Exploratory data analyses considering these characters could clearly distinguish 225 nest samples with 1059 workers of *F. lugubris* from 77 nest samples with 266 workers of *F. pratensis*. Classification errors were 0.6% in NC-part.hclust, 0% in both NC-part.kmeans and NC-Ward (Fig. 28), and 2% in a PCA. Separation on individual level by an LDA was also very strong with only 1.6% misclassification in 1325 worker individuals. Yet, the separation of the two clusters in two-dimensional plots of LDA and PCA was not strong enough to allow conclusions on recent hybrid samples. For repeated hybridization of the two species in the past, see section “Hybrids *Formica pratensis* × *lugubris*” (p. 174).

The strong dimorphism in *Formica pratensis* is most apparent in gynes. A re-analysis of the data of SEIFERT (1992) consisting of the 11 characters head width and number and maximum length of setae on posterior

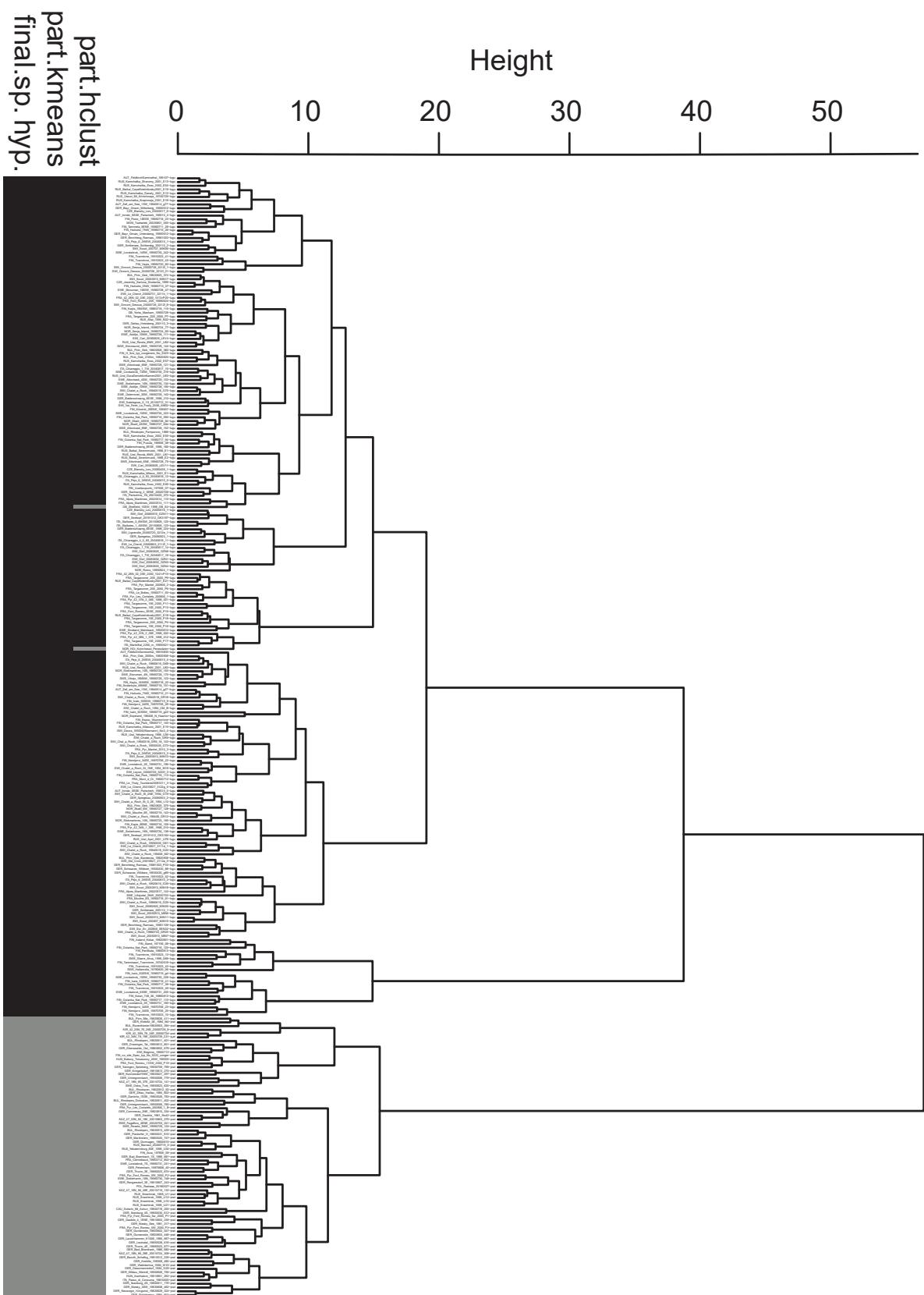


Fig. 28: Classification by three variants of NC-clustering of 225 nest samples of workers of *Formica lugubris* (black bars) and 76 nest samples of *Formica pratensis* (grey bars). The mean error of three analyses is 0.2%. Ten phenotypic characters were considered. The small, well separated sub-branch in the *F. lugubris* cluster represents Fennoscandian nest samples containing exclusively Hippie morph workers.

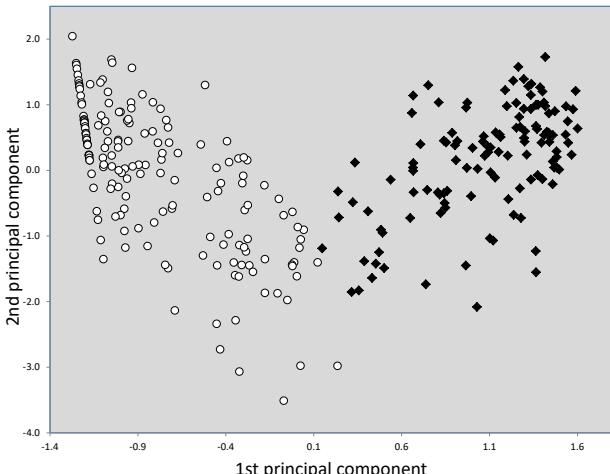


Fig. 29: Principal component analysis of polymorphism in 295 gynes of *Formica pratensis*. The P-morph with reduced setae (white dots) is clearly separated from the strongly haired N-morph (black rhombs). Eleven phenotypic characters were considered.

margin of head, scutellum, extensor part of hind tibia, propodeum, and frontal face of first gaster tergite was performed here. As result, the setae-reduced P-morph and the hairy N-morph can be clearly clustered in a PCA after logarithmic transformation of the raw data (Fig. 29). The low percentage of doubtful (or intermediate) specimens is also indicated by the LDA that classified only 2.4% of 295 gynes with posterior probabilities  $< 0.95$ . Clear arguments against considering the P-and N-morph as separate species are provided by the presence of both morphs in 21.6% of 37 nest samples and simultaneous observation of sexuals of both morphs at the same mating places (SEIFERT 1992). The same author also showed that phenotype dimorphism is correlated with ecological adaptations. He explained the demonstrated statistical differences in geographical distribution along a thermal gradient by selection of genotypes with differing climatic adaptations. According to SEIFERT (1992), the P-morph differs from the N-morph by the following traits: It constructs clearly flatter mounds for equal insolation conditions and goes to higher altitudes and latitudes. In Germany, the P-morph is rarer than the N-morph in dry habitats with typical Mediterranean elements but is more frequent than the N-morph on loamy soils.

**Biology.** See the species profile given by SEIFERT (2018).

### ***Formica kupyanskayae* BOLTON, 1995**

*Formica kupyanskayae* BOLTON, 1995 [type investigation]

Replacement name for *Formica opacus* KUPYANSKAYA, 1980 that is a junior primary homonym of *F. opaca* NYLANDER, 1856 (now in *Camponotus* MAYR, 1861).

**Type material.** Five paratype workers and two paratype gynes from the holotype sample labelled “Primorye, Anisimovka, 12.7.1975 Kupyanskaya”, “Paratypus *Formica opaca* Kupyanskaya”; depository SMN Görlitz.

All material examined. Numeric phenotypical data were recorded in 10 nest samples with 41 workers and two gynes plus one isolated gyne. All these originated from Russian Far East. For details, see SI1, SI2, and SI3.

**Geographic range.** Known are 10 sites in the Ussuri River / Sichote Alin region and one site in Sakhalin. These eleven sites are situated at altitudes of only  $180 \pm 150$  [40, 530] m which is clearly lower than in sympatric *Formica ussuriensis* sp.n. (ANOVA  $F_{1,19} = 30.6$ ,  $p < 0.001$ ).

**Diagnosis of worker** (Tab. 2, key). Large, mean and maximum CS over all social types 1745 and 2068  $\mu\text{m}$ . Scape rather long but less slender than in *Formica pratensis*, SL / CS<sub>1750</sub> 0.917, SL / Smax<sub>1750</sub> 9.78. Petiole width medium, PeW / CS<sub>1750</sub> 0.476. Setae on eyes long, EyeHL<sub>1750</sub> 35  $\mu\text{m}$ ; setae on dorsal plane of scape absent or very few, nSc<sub>1750</sub> 0.68; setae on head margin behind eyes less numerous than in *F. pratensis* but rather long, nCH<sub>1750</sub> 5.8, OccHL<sub>1750</sub> 118  $\mu\text{m}$ ; gular setae always present and long, nGu<sub>1750</sub> 7.0, GuHL<sub>1750</sub> 217  $\mu\text{m}$ ; pronotal setae moderately numerous and rather long, nPn<sub>1750</sub> 18.9, mPnHL<sub>1750</sub> 98  $\mu\text{m}$ , number of mesopleural, propodeal, and metanotal setae clearly smaller than in *F. pratensis* but of comparable length, nMes<sub>1750</sub> 6.6, nPr<sub>1750</sub> 9.0; mMet<sub>1750</sub> 3.4, Methl<sub>1750</sub> 198  $\mu\text{m}$ . Pigmentation without specific characters.

**Diagnosis of gyne** (Tab. 6, Fig. 13). In many characters similar to *Formica pratensis*. Very large, mean and maximum CS 2348 and 2386  $\mu\text{m}$ . Scape very long and slender, SL / CS 0.903, SL / Smax 9.66, absolute scape length  $> 2090 \mu\text{m}$ , exceeding data in other species. Setae on eyes long, EyeHL 44  $\mu\text{m}$ ; setae on head margin behind eyes much fewer and shorter than in *F. pratensis*, nCH 4.8, OccHL<sub>1750</sub> 87  $\mu\text{m}$ ; gular setae always present and long, nGu 9.3, GuHL 258  $\mu\text{m}$ ; setae on pronotum very few and short, PnHL 56  $\mu\text{m}$ ; setae number on mesopleuron, metapleuron, petiole above spiracle, frontal face of first gaster tergite, and flexor profile of hind tibia lower than in *F. pratensis*, nMes 2.7, nMet 4.8, nPe 0.2, nGfr 2.3, nHT 2.5; setae length on metapleuron and frontal face of first gaster tergite shorter than in *F. pratensis*, MetHL 125  $\mu\text{m}$ , GfrHL 44  $\mu\text{m}$ . All body surfaces matt; dorsum of first gaster tergite with dense pubescence, well-developed transverse microripples, and narrowly spaced foveolae as bases of pubescence hairs, sqPDG 3.6, FodG 20.5  $\mu\text{m}$ . Most surfaces light reddish brown; posterior dorsum of head and mesonotum dark reddish brown; scutellum, metanotum, and gaster blackish brown, except for light reddish brown frontal face of first gaster tergite.

**Taxonomic comments and clustering results.** *Formica kupyanskayae* is obviously the closest known relative of *Formica pratensis* but well separable. The 10 nest samples of *F. kupyanskayae* can be clearly separated from 76 nest samples of *F. pratensis* by all five exploratory data analyses considering the characters CS, CL / CW<sub>1750</sub>, SL / CS<sub>1750</sub>, nCH<sub>1750</sub>, OccHL<sub>1750</sub>, mPnHL<sub>1750</sub>, nMet<sub>1750</sub>, MetHL<sub>1750</sub>, PeW / CS<sub>1750</sub>, SL / Smax<sub>1750</sub>, and nSc<sub>1750</sub> (Fig. 30). The classification error by an LDA using the same character set was 0.7% in 301 worker individuals. Gynes of the two species can be strongly separated

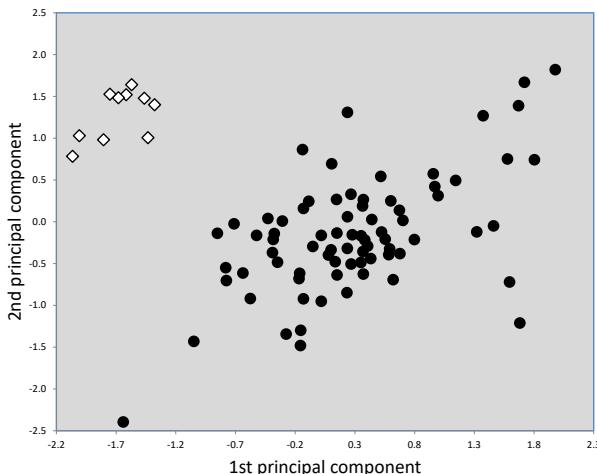


Fig. 30: Principal component analysis of 10 nest samples of *Formica kupyanskayae* (white rhombs) and of 76 nest samples of *Formica pratensis* (black dots). Ten phenotypic characters were considered.

by a PCA considering the characters SL / CS, GfrHL, nPe, nMet, and ML / CS.

**Habitat and biology.** There are no data on habitat selection available except for one record reporting a probably monogynous nest found in a bushy grassland with groups of trees. This selection of an open habitat and distribution at low altitudes suggests that it is a rather thermophilous species – another character it shares with *Formica pratensis*.

### ***Formica lugubris* ZETTERSTEDT, 1838**

*Formica lugubris* ZETTERSTEDT, 1838 [diagnosis of YARROW (1955)]

The taxon was described from a male from Ofotfjord (Norway, 68.43° N, 17.03° E). ZETTERSTEDT (1838)'s description matches all three species expected to occur at the Ofotfjord: *F. lugubris*, *Formica aquilonia*, and *Formica truncorum*. YARROW (1955), who was the first after 120 years to revive *F. lugubris* from synonymy and to give it a status of a good species, did not explain on which basis he identified J.W. Zetterstedt's male. All later authors (including me) followed YARROW (1955)'s diagnosis based on workers and gynes and kept silent regarding the male problem. J.W. Zetterstedt's type male is, according to YARROW (1955), stored in ZMLU Lund. If still present there, its identity can only be determined after a thorough, broad-based study on male characters at least in the Fennoscandian population of *F. lugubris*, *F. aquilonia* and *F. truncorum* – at least it remains to be investigated if the differential characters proposed in the keys of KUTTER (1977) and CZECHOWSKI & al. (2012) for the Central European population do apply to the boreal populations of these species.

### ***Formica congerens* NYLANDER, 1846**

*Formica congerens* NYLANDER, 1846 [type investigation]

NYLANDER (1846) described this species from the island Mjölon near Helsinki. Five syntypes from FMNH

Helsinki were investigated. These were two worker syntypes on the same pin labelled "H:Fors \ W. Nyland. \ Coll. Nyland \ congerens Nyl. \ Mus. Zool. H:fors Spec. typ. No 5023 Formica congerens Nyl.", ZM Helsinki. In the upper specimen, petiole and gaster are missing. The lower specimen with CS 2060 µm is designated herewith as lectotype and the upper one with CS 2152 µm is the paralectotype. When run as wild-cards in the two-class LDA described in section "*Formica pratensis* RETZIUS, 1783" (p. 159) and separating *Formica lugubris* and *F. pratensis*, the lectotype and paralectotype are classified as *F. lugubris* with posterior probabilities of p = 0.9921 and p = 1.0000. Three designated syntypes (now paralectotypes) on a second pin, with the lower specimen broken in two parts and badly glued on a card board, are labelled "Mus. Zool. H:fors Spec. typ. No 5022 Formica congerens Nyl.". There is no label indicating the sampling site. The two undamaged specimens were clearly classified as *F. pratensis* with posterior probabilities of 0.9998 and 0.9944.

### ***Formica nylanderi* BONDROIT, 1920**

*Formica nylanderi* BONDROIT, 1920 [type investigation]

Investigated were one syntype gyne labelled "Grindelwald Suisse Chabanaud coll. de Gaulle", "Type", "Formica v. nylanderi Type Bondr." and one syntype gyne labelled "Lautaret 15 VII", "Type", "Formica rufa v. Nylanderi Type Bondr."; depository MSNB Bruxelles.

Phenotypic variation in *Formica lugubris* gynes can be classified into several morphs the data of which are given in Table 7 (see also SEIFERT 2018). In both type gynes of *F. nylanderi*, data of OccHL, GuHL, PnHL, and MetHL are clearly above the upper extremes known from *Formica paralugubris* and morph A3 of Alpine *F. lugubris* but they may belong to *Formica helvetica* sp.n. or morph A1 of Alpine *F. lugubris*. Running the types as wild-cards against a sample of 28 gynes of *F. helvetica* and 36 gynes of morph A1, and considering the five characters ML / CS, PeW / CS, nCH, nMes, and nPe, the gyne from Grindelwald is allocated to morph A1 with p = 0.9928 and the gyne from Col de Lautaret with p = 0.9976. As the specimen from Grindelwald achieved a higher posterior probability in a wild-card run when all 20 characters were considered, it is designated herewith as lectotype.

### ***Formica rufopratensis* FOREL, 1874**

*Formica rufa* var. *rufopratensis* FOREL, 1874 [type investigation and zoogeography]

FOREL (1874) did not mention a type locality, and his description of worker and gyne may refer to *Formica lugubris*, *Formica paralugubris*, and *Formica helvetica* sp.n. A smaller set of morphological data available for two supposed type gynes in MNH Genève from the locality Barberine (France, 46.050° N, 6.943° E) allow to exclude *F. paralugubris* but cannot separate the other two species. As *F. helvetica* sp.n. is considered to be restricted to East Switzerland and unlikely to occur farther west, I synonymize *F. rufopratensis* with *F. lugubris*. Alternatively, if the Barberine specimens are not recognized as types, *F. rufopratensis* has to be listed up under incertae sedis.

### ***Formica santschii* WHEELER, 1913**

*Formica rufa* var. *santschii* WHEELER, 1913 [type investigation]

*Formica santschii* is WHEELER (1913)'s replacement name for *F. rufa* var. *alpina* SANTSCHI, 1911, which is a junior primary homonym of *Formica adamsi* var. *alpina* WHEELER, 1909. SANTSCHI (1911) described his *F. rufa* var. *alpina* from the Alps north of Sondrio. Investigated were two syntype workers on separate pins stored in NHM Basel and labelled in F. Santschi's handwriting. The larger specimen with CW 1754 µm is depicted in AntWeb (ANTWEB 2021) under CASENT0912249 and is labelled "Valteline. Galli-Valerio", "Formica alpina € Sant.", "type". The smaller, damaged specimen with CW = 1685 µm on the other pin is labelled "Valteline. Galli-Valerio", "Formica alpina € Sant." By morphology and geography, the *F. santschii* types could either belong to *Formica lugubris* or *Formica paralugubris*. The specimens were run as wild-cards in an LDA collecting 369 workers of the *F. lugubris* morphs A1 and A3 from the Alps in class 1, and 298 workers of *F. paralugubris* in class 2. The eleven characters available in the *F. santschii* types were CS, CL / CW<sub>1750</sub>, SL / CS<sub>1750</sub>, SL / Smax<sub>1750</sub>, PeW / CS<sub>1750</sub>, nSc<sub>1750</sub>, nCH<sub>1750</sub>, OccHL<sub>1750</sub>, mPnHL<sub>1750</sub>, nMet<sub>1750</sub>, and MetHL<sub>1750</sub>. With these data, the larger syntype worker was allocated to class 1 with p = 0.9674 but the smaller one with p = 0.9551 to class 2. It appears questionable if the two workers mounted on separate pins belong to the same nest sample. In order to save a stable nomenclature, a lectotype of *F. santschii* is fixed by present decision in the undamaged larger specimen labelled "CASENT0912249".

### ***Formica unicolor* Ruzsky, 1926**

*Formica pratensis* ssp. *unicolor* Ruzsky, 1926 [description, diagnosis of DLUSSKY (1967)]

This taxon was described on the basis of a single worker collected at Surgut (West Siberia, 62.25° N, 73.42° E) on 21 June 1913. A synonymy with *Formica lugubris* appears possible from description. DLUSSKY (1967), who might have seen the type specimen, interpreted this taxon as a light coloured *F. lugubris* without a dark patch on dorsal mesosoma. Such specimens are more frequent in Siberia than in Europe.

All material examined. Numeric phenotypical data were recorded in 224 nest samples with 1108 workers and 109 gynes. These originated from Austria (seven samples), Bulgaria (seven), Czechia (four), Finland (42), France (28), England (two), Germany (18), Italy (15), Mongolia (two), Norway (10), Russian West Siberia (seven) Russian East Siberia (15), Sweden (24), and Switzerland (44). For details, see SI1, SI2, and SI3.

Geographical range. Eurosiberian, boreo-montane. The huge boreal range extends from the British Isles east to Kamchatka. In Fennoscandia from S Sweden (55.5° N) to North Cape (71° N). The northern distribution in Siberia is limited by 65° N. Occurrence at low latitudes and altitudes in the Ussuri region (43.17° N, 132.79° E, 350 m) is explained by influence of cold water of the West Pacific. The montane-subalpine population in Europe extends over

the Pyrenees, Massif Central, Alps, Vosges, Schwarzwald, Bayrischer Wald, the whole Carpathians, Stara Planina, Vitosha, Rila, Pirin, and Rhodopes. In the Alps occurring at altitudes between 550 and 2510 m. Under influence of Atlantic climate descending to 250 m (Vosges, France) and 50 m (Ireland).

**Diagnosis of worker** (Tab. 3 and 4, Figs. 14 and 15, key). Extremely polymorphic, with regional differences shown in Table 3. Rather large, mean and maximum CS over all morphological and social types 1805 and 2184 µm. Scape shorter and much less slender than in *Formica pratensis*, SL / CS<sub>1750</sub> 0.894, SL / Smax<sub>1750</sub> 9.30. Petiole wider than in *F. pratensis*, PeW / CS<sub>1750</sub> 0.489. Setae on eyes long, EyeHL<sub>1750</sub> 33 µm; setae condition on dorsal plane of scape most variable, nSc<sub>1750</sub> usually 0 - 5 but in Fennoscandian Hippie-morph (SEIFERT 2003) up to 40. Setae on head margin behind eyes always numerous but most variable in length, nCH<sub>1750</sub> 25.0; average OccHL<sub>1750</sub> usually 115 µm but up to 235 µm in Fennoscandian Hippie-morph. Gular setae always numerous and long, nGu<sub>1750</sub> 15.1, GuHL<sub>1750</sub> 188 µm. Pronotal setae numerous but most variable in length, average mPnHL<sub>1750</sub> usually 84 - 112 µm but in Fennoscandian Hippie-morph up to 176 µm. Number and length of mesopleural, propodeal, and metanotal setae usually large, nMes<sub>1750</sub> 28.1, nPr<sub>1750</sub> 21.7; mMet<sub>1750</sub> 10.3, MetHL<sub>1750</sub> 182 µm. Pigmentation without specific characters. The dark patch on mesosoma is usually large with diffuse margins in European populations but may also be reduced.

**Diagnosis of gyne** (Tab. 7, Fig. 3, key). Extremely polymorphic. Mean number and length of setae is lowest in morph A3 from the Alps (SEIFERT 2018) and highest in the Fennoscandian Hippie-morph (SEIFERT 2003). The remaining morphs, such as the most abundant morphs A1 from the Central European mountains or morph N1 from Fennoscandia, are intermediate. The numeric data given in the following summarize data of 109 gynes from the whole geographic range and of any social and morphological type. Rather large, CS 2213 ± 80 (1996, 2382) µm. Head short, CL / CW 0.998 ± 0.020 (0.950, 1.052). Scape short and thickset, SL / CS 0.789 ± 0.026 (0.708, 0.857), SL / Smax 8.13 ± 0.37 (7.12, 9.04). Eyes always with setae, the longest occur in the Fennoscandian Hippie-morph, EyeHL 48 ± 18 (30, 151) µm. Dorsal plane of scape with most variable setae numbers, which are highest in Fennoscandian Hippie-morph, nSc 2.1 ± 3.5 (0, 21). Posterior margin of head always with setae, but these are most variable in length and number, nCH 23.2 ± 8.8 (10.5, 65.0), OccHL 156 ± 91 (40, 320) µm. Underside of head, all surfaces of mesosoma, and petiole scale always with setae of most variable length and number, nGu 18.3 ± 6.7 (8, 36), GuHL 244 ± 111 (49, 425) µm, PnHL 208 ± 93 (34 - 411), MethL 260 ± 97 µm (40, 375), nPe 15.5 ± 6.5 (2, 33). Dorsal surface of gaster appears at lower magnification more or less shiny. Transverse microripples on dorsum of first gaster tergite usually very weak or absent but occasionally more developed, then approaching the situation in *Formica pratensis*. Foveolae and pubescence on dorsum

of first gaster tergite on average more densely packed than in *Formica rufa* or *Formica polyctena*, FodG 25.2 ± 5.7 (17.9, 50.8) µm, sqPDG 4.84 ± 1.14 (3.13, 8.06) µm.

**Taxonomic comments and clustering results.** The European population is extremely polymorphic, being a mixture of (a) sympatrically occurring most different phenotypes, as for example observed in Fennoscandia (SEIFERT 2003) or in the Alps (SEIFERT 2018), and (b) of deviating but rather monomorphous regional populations, such as found in the Pyrenees or the Balkan mountains. Clustering of morphological data by exploratory data analyses and assessment of putative clusters by discriminant analyses did not allow to give one of these entities a taxonomic significance (for the special case of *Formica helvetica* sp.n., see section “*Formica helvetica* sp.n.”, p. 166). Considering this very complicated structure, it appears astonishing that the separation from *Formica pratensis* all over the Palaearctic range was such clear in workers and gynes (see section “*Formica pratensis* RETZIUS, 1783”, p. 159 or SEIFERT & GOROPASHNAYA 2004), and that also *Formica paralugubris* was sufficiently separable in both castes (see section “*Formica paralugubris* SEIFERT, 1996”, p. 167, and SEIFERT 2016a). Sections “Hybrids *Formica aquilonia* × *lugubris*” (p. 173), “Hybrids *Formica pratensis* × *lugubris*” (p. 174) and “Hybrids *Formica lugubris* × *rufa*” (p. 174) report on hybridization of *F. aquilonia* × *lugubris*, *F. pratensis* × *lugubris*, and *Formica rufa* × *lugubris*.

**Biology.** See the species profile given by SEIFERT (2018).

### ***Formica helvetica* sp.n.**

*Formica lugubris*-A2 (BERNASCONI & al. 2011)

*Formica lugubris*, morph A2 (SEIFERT 2018)

**Etymology.** Referring to Helvetia, the Latin name of Switzerland.

**Type material.** Holotype worker plus four paratype workers labelled “SWI: 46.7218° N, 10.2988° E, Scuol, Pinus forest, 1767 m, polydomous, Bernasconi 2005.05.13-MIN7”; another nine nest samples from the same supercolony with 47 paratype workers and 30 paratype gynes collected by C. Bernasconi in the years 2005 - 2008, sample numbers MIN8, MIN11, MIN13, MIN15, MIN17, MIN18, MIN20, MIN35, and MIN36; depository SMN Görlitz.

**All material examined.** Numeric phenotypical data were recorded in nine nest samples with 30 workers and 28 gynes. All originated from the supercolony of the type locality. For details, see SI1, SI2, and SI3.

**Geographic range.** Only known from the type locality in Mingèr Valley in the Eastern Swiss Alps at altitudes between 1700 and 2000 m.

**Diagnosis of worker** (Tab. 3, Figs. 16 and 17). Small, as it is expected for a supercolonial social phenotype, mean and maximum CS 1663 and 1966 µm. Scape as short as but on average less thickset than in Alpine *Formica lugubris*, SL / CS<sub>1750</sub> 0.904, SL / Smax<sub>1750</sub> 9.47. Petiole width and setae number as in Alpine *F. lugu-*

*bris* but setae length on average larger, EyeHL<sub>1750</sub> 37 µm, OccHL<sub>1750</sub> 132 µm, mPnHL<sub>1750</sub> 111 µm, MetHL<sub>1750</sub> 188 µm.

**Diagnosis of gyne** (Tab. 7). Size slightly smaller than in Alpine *Formica lugubris*, mean and maximum CS 2126 and 2278 µm. Head short, CL / CW 0.999. Scape on average longer and less thickset than in morph A3 of Alpine *F. lugubris*, SL / CS 0.797, SL / Smax 8.41. Eyes always with rather long setae, EyeHL 44 µm. Dorsal plane of scape usually without or very few setae, nSc 0.4. Posterior margin of head always with setae, these on average longer than in morph A3 of Alpine *F. lugubris*, nCH 18.5, OccHL 179 µm. Setae number comparable with morph A1 and A3 of Alpine *F. lugubris* but seta length larger than in morph A3, nGu 17.2, GuHL 303 µm, PnHL 236 µm, MetHL 287 µm, nPe 13.7. Dorsal surface of gaster appears at lower magnification more or less shiny. Dorsum of first gaster tergite usually with weak transverse microripples and with foveolae and pubescence being on average more densely packed than in *Formica rufa* or *Formica polyctena*, FodG 26.1 µm, sqPDG 4.84 µm.

**Taxonomic comments and clustering results.** *Formica helvetica* sp.n. is the first ant species I describe as new without having a sufficiently clear morphological diagnosis. This decision is certainly a risk, considering the patchwork situation in Alpine *Formica lugubris* populations. However, this taxonomic act is intended as a constructive, positively provocative hypothesis for future ant students to re-investigate the case with more advanced methods. The recognition as species here is largely based on an apparently clear clustering by nuclear DNA and moderate support by gyne morphology. BERNASCONI & al. (2011) investigated nine microsatellite markers in seven *Formica rufa* group species in and around the Swiss National Park in East Switzerland. They showed a clear difference between *F. helvetica* sp.n. and *F. lugubris* (in Mingèr Valley represented by morph A1) and five other *F. rufa* group species sympatrically occurring in the area. The genetic distance between *F. helvetica* sp.n. and *F. lugubris* ( $F_{st} = 0.101$ ) was comparable with those between *Formica aquilonia* and *Formica paralugubris* ( $F_{st} = 0.117$ ), or between *F. lugubris* and *F. aquilonia* ( $F_{st} = 0.130$ ) but lower than between monodomous and polydomous populations of *F. lugubris* in another area of the Swiss National Park (BERNASCONI & al. 2005). The mtDNA of *F. helvetica* sp.n. clustered with that of *F. paralugubris* and *F. aquilonia*, which may suggest a hybridogenous evolutionary history, but also that there was no influx of genes by immigration of *F. lugubris* gynes.

The morphological clustering of workers failed when the whole Alpine population from the French Jura to Eastern Austria was considered. Running an LDA with the characters CS, CL / CW<sub>1750</sub>, SL / CS<sub>1750</sub>, nSc<sub>1750</sub>, nCH<sub>1750</sub>, OccHL<sub>1750</sub>, mPnHL<sub>1750</sub>, and nMet<sub>1750</sub>, all nine worker nest samples of *Formica helvetica* were allocated to the same cluster, but this cluster was shared with nine *Formica lugubris* samples of the morph A1 from nine different localities. This meant a classification error of 9.3% in a total of 97 worker samples. The misplaced *F. lugubris* samples

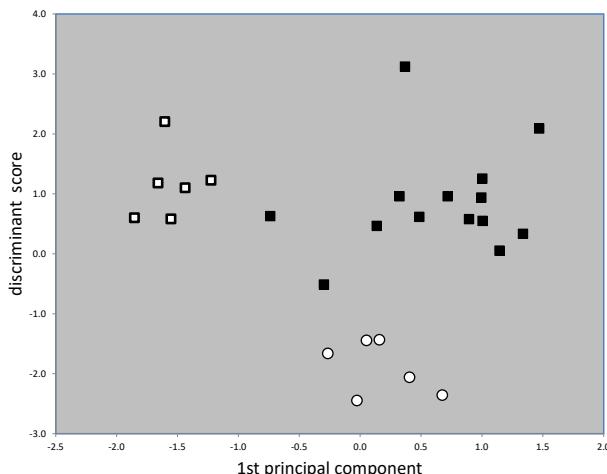


Fig. 31: Nest-sample means of a linear discriminant analysis and principal component analysis of *Formica lugubris* complex gynes considering eight phenotypic characters; *Formica helvetica* sp.n. (white dots), *F. lugubris* morph A1 (black squares), *F. lugubris* morph A3 (squares with white center). The means were calculated from 28, 38, and 18 individuals for each entity.

came from all over the Alps and included a population from Grande Rolat in Swiss Jura which had been intensively studied biologically, genetically and morphologically over many years.

The situation in gynes appears better, but the low sample size of only 28 specimens in *Formica helvetica* sp.n. required a strong character reduction, performed by a stepwise LDA. Using the eight characters SL / CS, SL / Smax, PeW / CS, ML / CS, nSc, nMes, GuHL, and nHT, the nest sample means of the LDA scores provide a rather good separation of *F. helvetica* sp.n. (Fig. 31), but the figure also shows that the first component of the PCA (calculated from the same eight characters as the LDA) does not expose *F. helvetica* but separates instead the *Formica lugubris* morphs A1 and A3.

**Habitat and biology.** The supercolony stretched along a transect of about 1.6 km length within a *Pinus* forest on limestone ground. The social structure is comparable with that of *Formica aquilonia*, with mating intranidally or within the colony borders and high genetic viscosity.

### ***Formica paralugubris* SEIFERT, 1996**

*Formica paralugubris* SEIFERT, 1996 [type investigation]

This taxon was described from the Swiss Jura Mountains ( $46.537^\circ$  N,  $6.192^\circ$  E, 1450 m). The holotype gyne is labelled "SWI: Jura: 1994.06, Le Brassus-5SSW, Challet a Roch Field Stat., nest G5" and depicted in AntWeb (ANTWEB 2021) under the unique specimen identifier FOCOL0762. Investigated was all type material, consisting of five gynes and 34 workers from the nests G1-G5 of the holotype supercolony, collected in the years 1993 and 1994. Depository SMN Görlitz.

All material examined. Numeric phenotypical data were recorded in 73 nest samples with 355 workers and in 53 gynes. These originated from Austria (six sam-

ples), Canada (two), France (two), Germany (four), Italy (three), and Switzerland (58).

**Geographical range.** Its natural range is rather small and extends over the montane-subalpine zone of the Jura Mountains and western Alps between  $6^\circ$  E and  $11.5^\circ$  E with a small enclave in the southern Schwarzwald / Germany. In the Alps, it ascends to 2300 m. A colony artificially introduced to Quebec / Canada in 1971 showed continuous growth to supercolonial size over 34 years (SEIFERT 2016a). Artificial introductions of wood ants to at least 42 localities over entire Italy south to Sicily and west to Sardinia were performed in the years 1959 - 1967 (e.g., PAVAN 1959). In that time, the transferred ants were classified as *Formica lugubris*. However, it is very likely that the vast majority of these introductions really involved *Formica paralugubris* as it was confirmed for five sites in the North Apennine (MASONI & al. 2019).

**Diagnosis of worker (Tab. 4, key).** Minimum size, mean and maximum CS 1680 and 2020 µm. Head rather short, CL / CW<sub>1750</sub> 1.091. Scape rather short and thickset, SL / CS<sub>1750</sub> 0.902, SL / Smax<sub>1750</sub> 9.22. Eyes always with long microsetae, EyeHL<sub>1750</sub> 34 µm. Setae number on dorsal plane of scape variable but on average higher than in Alpine *Formica lugubris*, nSc<sub>1750</sub> 5.2. Posterior margin and underside of head always with conspicuous setae, nCH<sub>1750</sub> 24.9, OccHL<sub>1750</sub> 108 µm, nGu<sub>1750</sub> 14.2, GuHL<sub>1750</sub> 164 µm. Mean length of pronotal setae, number and length of metapleural setae on average lower than in morph A1 of Alpine *F. lugubris*, mPnHL<sub>1750</sub> 78 µm, nMet<sub>1750</sub> 7.7, MetHL<sub>1750</sub> 154 µm. Workers of morph A3 of Alpine *F. lugubris* are similar in the pilosity condition but have a much larger size, a larger head length index, and a shorter scape.

**Diagnosis of gyne (Tab. 7).** On average smaller than morph A1 and A3 of Alpine *Formica lugubris*, mean and maximum CS 2095 and 2238 µm. Scape longer than in morph A3 of Alpine *F. lugubris* and very thickset, SL / CS 0.805, SL / Smax 7.97. Eyes always with conspicuous microsetae, EyeHL 41 µm. Setae number on dorsal plane of scape variable but on average higher than in morph A1 and A3 of Alpine *F. lugubris*, nSc 6.4. Posterior margin and underside of head always with conspicuous setae, the length of which is lower than in morph A1 but larger than in morph A3 of Alpine *F. lugubris*, nCH 23.8, OccHL 117 µm, nGu 16.7, GuHL 128 µm. Pronotal setae shorter than in morph A1 of Alpine *F. lugubris*, mPnHL 88 µm. Petiole setae fewer and metapleural setae shorter than in morph A1 of Alpine *F. lugubris* but more numerous and longer than in morph A3 of Alpine *F. lugubris*, nPe 9.2, MetHL 110 µm. Dorsal surface of gaster appears at lower magnification more or less shiny. Dorsum of first gaster tergite usually with weak transverse microripples and with foveolae and pubescence on average more densely packed than in *Formica rufa* or *Formica polyctena*, FodG 21.1 µm, sqPDG 4.62 µm.

**Taxonomic comments and clustering results.** Considering the extreme polymorphism in Alpine *Formica lugubris* and the presence of another similar sympatric species *Formica helvetica* sp.n., the separation

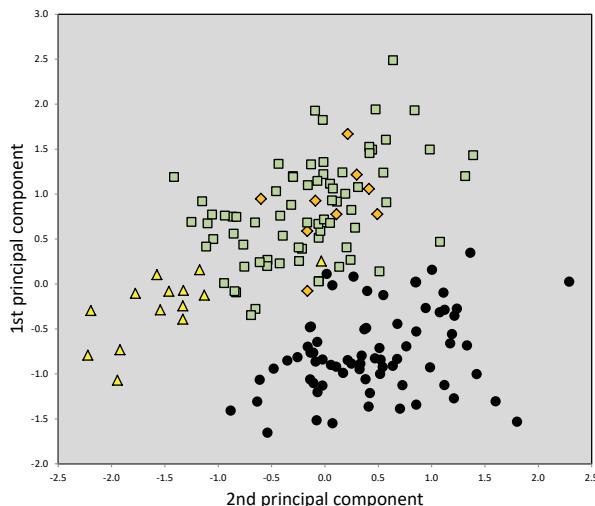


Fig. 32: Nest-sample means of the first and second principal component of workers of *Formica paralugubris* (black dots), *Formica lugubris* morph A1 (squares), *F. lugubris* morph A3 (triangles), and *Formica helvetica* sp.n. (rhombs). Eleven phenotypic characters were considered.

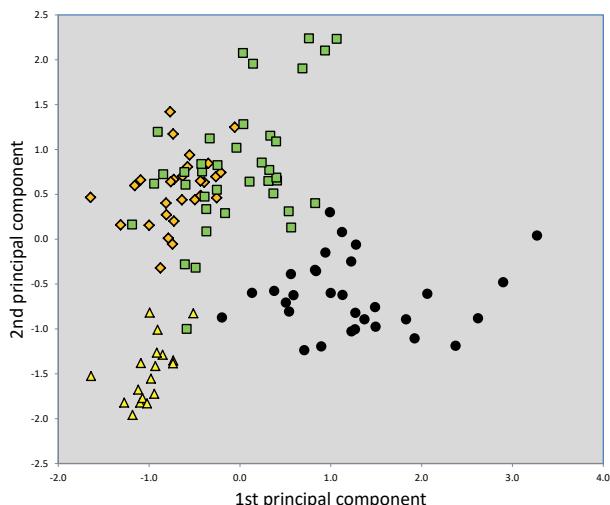


Fig. 33: Principal component analysis of gynes of *Formica paralugubris* (black dots), *Formica lugubris* morph A1 (squares), *F. lugubris* morph A3 (triangles), and *Formica helvetica* sp.n. (rhombs). Eight phenotypic characters were considered. The placement of the four entities within the plot is similar to that in workers (Fig. 32).

of *Formica paralugubris* in both workers and gynes should be problematic. I combined 98 nest samples with 409 workers of Alpine *F. lugubris* morphs A1 and A3 and of *F. helvetica* sp.n. in class 1, and 70 nest samples with 323 workers of *F. paralugubris* in class 2. A two-class LDA considering the characters CS, CL / CW<sub>1750</sub>, SL / CS<sub>1750</sub>, SL / Smax<sub>1750</sub>, PeW / CS<sub>1750</sub>, nSc<sub>1750</sub>, nCH<sub>1750</sub>, OccHL<sub>1750</sub>, mPnHL<sub>1750</sub>, nMet<sub>1750</sub>, and MetHL<sub>1750</sub> classified all samples of *F. paralugubris* and 96 samples of the collective cluster correctly. This means a classification error of 1.2% within a total of 168 nest samples. A plot of the first and second

factors of a PCA supported the existence of two main clusters class 1 and class 2, and disagreed in 3.0% of the samples with the LDA (Fig. 32). The exploratory data analyses NC-part.kmeans, NC-Ward, and NC-NMDS.kmeans suggested two clusters and disagreed with the final species hypothesis by 3.6, 4.1, and 3.0%. The clustering by NC-part.hclust was ignored as it splitted into seven clusters and exposed 8.9% indeterminate samples (outliers). As result, we have a sufficiently good separation of *F. paralugubris* workers by morphology. The distinction of *F. paralugubris* gynes from those of Alpine *F. lugubris* morphs A1 and A3, and of *F. helvetica* sp.n. by a principal component analysis appears also rather clear when the eight characters CS, SL / CS, SL / Smax, PeW / CS, ML / CS, nSc, nCH, and OccHL are considered (Fig. 33). Section “Hybrids *Formica aquilonia* × *paralugubris*” (p. 175) discusses the situation in hybrids *F. aquilonia* × *paralugubris*.

**Biology.** See the species profile given by SEIFERT (2018).

### ***Formica truncorum* FABRICIUS, 1804**

*Formica truncorum* FABRICIUS, 1804 [type investigation]

The taxon was described from Moravia / Czechia from a nest in a dead tree trunk. Investigated were two type specimens from ZM Copenhagen: one worker labelled “*Formica truncorum* 403.31 Kiel” (a permanent loan from ZM Kiel) and with a handwritten fragmentary label “*trunca fusca*”, and a strongly damaged alate gyne labelled “*Formica truncorum* 403.31 Kiel” but without a second label. Both specimens are fully consistent with the established conception of *F. truncorum*. A synonymy with *Formica frontalis* is excluded by zoogeography and the higher setae numbers on scape and metapleuron. Data of the worker are: CS 1957 µm, CL / CW 1.046, SL / CS 0.978, PeW / CS 0.483; nGu 29, OccHL 124 µm, GuHL 220 µm, mPnHL 81.6 µm, nPr 44.5, nMet 24.5, MetHL 170 µm (setae data of damaged body parts were estimated and are not given here). The gyne fragment, consisting of the dorsal mesosoma with wings, petiole, both hindlegs, and one foreleg, is a typical reddish *F. truncorum* with all surfaces covered by a profuse, thin, and very long pilosity. The wings are notably infuscated, matching the original description.

### ***Formica truncicola* NYLANDER, 1846**

*Formica truncicola* NYLANDER, 1846 [type investigation]

Investigated were four type specimens from ZM Helsinki: one worker syntype pinned together with an alate gyne, both with detached heads glued on a separate cardboard, labelled “Kuusamo \ W. Nyland. \ Coll. Nyland \ Mus. Zool. H:fors Spec. typ. No 5026 *Formica truncicola* Nyl.”; one alate gyne on another pin with same labels but “...Spec. typ. No 5024”; one male on a third pin with same labels but “...Spec. typ. No 5025”. All specimens fully match the established conception *Formica truncorum*.

### ***Formica truncicolopratensis* FOREL, 1874**

*Formica rufa* var. *truncicolopratensis* FOREL, 1874 [photo of type]

Forel described the worker and gyne but did not mention a type locality. The taxon was synonymized by all

previous authors with *Formica truncorum*. If a worker specimen in MHN Genève, labelled “Typus”, “F. truncicolo-pratensis Mt Ce..ere” and “ANTWEB CASENT 0911086” can be recognized as true type, the synonymy with *F. truncorum* appears likely after inspecting the z-stack photos shown in AntWeb (ANTWEB 2021) under the specimen identifier CASENT0911086. The photos suggest shiny circular lateral clypeal depressions and the length of the second funiculus segment to be more than twice its width as it is typical for *F. truncorum*. The more developed dark pigmentation is not contradictory as such specimens do occasionally occur over the whole range of the species.

***Formica yessensis* WHEELER, 1913**

*Formica truncorum* var. *yessensis* WHEELER, 1913 [type investigation]

The taxon was described by FOREL (1901) under the infrasubspecific name *Formica rufa* r. *truncorum* var. *yessensis* FOREL, 1901 from Sorachi, some 100km ENE of Sapporo, Hokaido. Investigated was one type worker from MHN Genève labelled by A. Forel “*Formica truncicola* v. *yessensis* For Type” and carrying a printed label “Sorachi Prov. Ishikari Yesso V. 1899. Mus.em.24.XI.1899”. The specimen shows below average setae length on eyes and no setae on dorsum of scape, and extensor profile of hind tibia but is in any character within the range of variation known from the Palaearctic population of *F. truncorum*. For a more detailed argumentation in favor of this synonymization, see below under taxonomic comments.

***Formica approximans* WHEELER, 1933**

*Formica truncorum* var. *approximans* WHEELER, 1933 [type investigation]

The taxon was described from Eastern Tomb / China. Investigated were six worker syntypes from MCZ Harvard, labelled “Eastern Tomb July 16, 30 Chi Ho”, “Gift of W.M.Wheeler”, “M.C.Z. CoType 1.-6 21720”, and “Syntypes *Formica truncorum* var. *approximans* Wheeler” (upper side) “S P Cover IX-2006” (underside). The specimens fully correspond to the East Palaearctic population of *F. truncorum*. For a more detailed argumentation in favor of this synonymization, see below under taxonomic comments.

***Formica finzii* STITZ, 1939**

*Formica truncorum* var. *finzii* STITZ, 1939 [description and zoogeography]

This taxon was described in a gyne from near Eberswalde (Germany) under the unavailable name *Formica rufa* ssp. *truncicola* var. *finzii* KRAUSSE, 1926. Types are unknown. Within the four species known to occur in the vicinity of Eberswalde, the description matches the situation in *F. truncorum*.

***Formica menozzii* STITZ, 1939**

*Formica truncorum* var. *menzzii* STITZ, 1939 [description and zoogeography]

This taxon was described from near Eberswalde (Germany) under the unavailable name *Formica rufa* ssp. *truncicola* var. *menzzii* KRAUSSE, 1926. Types are unknown. Within the four species known to occur in the vicinity of

Eberswalde, the description matches the situation in *F. truncorum*.

***Formica staegeri* STITZ, 1939**

*Formica truncorum* var. *staegeri* STITZ, 1939 [description and zoogeography]

This taxon was described from near Eberswalde (Germany) under the unavailable name *Formica rufa* ssp. *truncicola* var. *staegeri* KRAUSSE, 1926. Types are unknown. Within the four species known to occur in the vicinity of Eberswalde, the description matches the situation in *F. truncorum*.

***Formica stitzi* STITZ, 1939**

*Formica truncorum* var. *stitzi* STITZ, 1939 [description and zoogeography]

This taxon was described from near Eberswalde (Germany) under the unavailable name *Formica rufa* ssp. *truncicola* var. *stitzi* KRAUSSE, 1926. Types are unknown. Within the four species known to occur in the vicinity of Eberswalde, the description matches the situation in *F. truncorum*.

All material examined. Numeric phenotypical data were recorded in 50 samples with 92 workers and in 22 gynes. These originated from Belarus (one sample), China (seven), Czechia (one), Denmark (one), Finland (two), France (three), Germany (12), Japan (two), Kazakhstan (seven), Kyrgyzstan (11), Norway (one), Russia (two), and Ukraine (one). For details, see SI1, SI2, and SI3. The total of samples investigated either numerically or subjectively was 136.

Geographical range. Eurosiberian, temperate to boreal; from Netherlands and E France ( $5^{\circ}$  E) to Yakutsk at least ( $62^{\circ}$  N,  $130^{\circ}$  E). In NE China, the Ussuri region, Sakhalin, Hokkaido, the northern half of Honshu, and the Western Kurils ( $148^{\circ}$  E), it is replaced by the weakly deviating East Asian population. The southern and northern distributional limits in Europe are  $42^{\circ}$  N (Bulgaria) and  $71^{\circ}$  N (North Cape). These are in Central Siberia, along the  $100^{\text{th}}$  degree of longitude,  $46^{\circ}$  N and  $67^{\circ}$  N. In Europe occurring from the planar to montane zone, in the Alps ascending to 1800 m. Rare in the Crimea and Caucasus (DLUSSKY 1967). A population isolated from the Eurosiberian one is found in the Central Asian mountains – in Dzungarian Alatau, Tian Shan (here at  $43^{\circ}$  N up to 2700 m), and Pamir south to Karakoram ( $35^{\circ}$  N).

Diagnosis of worker (Tab. 5, Fig. 18, key). Polymorphic, with regional differences shown in Table 5. Medium-sized, mean and maximum CS over all morphological and social phenotypes 1754 and 2177  $\mu\text{m}$ . Head moderately elongated, CL / CW<sub>1750</sub> 1.099. Middle part of lateral clypeus more deeply depressed than in the *Formica rufa* species complex, anterolateral clypeus as a result forming a bead; median clypeal carina blunt or absent. Scape long and very slender, SL / CS<sub>1750</sub> 0.985, SL / Smax<sub>1750</sub> 10.87. Second and third segment of antennal funiculus more slender than in the species treated above, IF2 2.15  $\pm$  0.09 (n = 70). Petiole scale narrow, PeW / CS<sub>1750</sub> 0.442. Eyes always with microsetae, EyeHL<sub>1750</sub> 40  $\mu\text{m}$ . Dorsal plane of scape usually with more setae than in

other species,  $nSc_{1750}$  10.3. Except for the Hippie-morph of *Formica lugubris*, setae number on each place of the body larger than in any species of the *F. rufa* group,  $nCH_{1750}$  42.5,  $nGu_{1750}$  40.5,  $nPn_{1750}$  81.6,  $nMes_{1750}$  35.8,  $nPr_{1750}$  46.5,  $nMet_{1750}$  17.6. Hind margin of head usually with very long setae, but setae length on other body parts lower than in the most hairy morphs of *Formica pratensis* and *F. lugubris*,  $OccHL_{1750}$  136 µm,  $GuHL_{1750}$  187 µm,  $mPnHL_{1750}$  91 µm,  $MetHL_{1750}$  142 µm. Dorsum of head, in addition to the other elements of microsculpture, with deeper and broader microfoveolae which are usually the base of setae. Typical pigmentation in medium-sized to large workers: whole head, mesosoma, petiole, and frontal part of first gaster segment light orange brown; dark brown or blackish brown patches on vertex and dorsal mesosoma may occur in some samples.

**Diagnosis of gyne** (Tab. 8, Fig. 19, key). On average rather small but extremely size-polymorphic; minimum, mean, and maximum CS over all social phenotypes 1737, 2002, and 2256 µm. Head capsule in dorsal view appears trapezoidal, with more or less linear, frontad converging sides. Middle part of lateral clypeus more deeply depressed than in the *Formica rufa* species complex, anterolateral clypeus as a result forming a bead; median clypeal carina absent. Scape long and slender, SL / CS 0.903, SL / Smax 9.63. Petiole scale relatively narrow, PeW / CS 0.597. Setae on whole body very numerous, very thin, and usually very long. EyeHL 95 µm,  $nSc$  28.0,  $nCH$  62.6,  $OccHL$  215 µm,  $nGu$  65.1,  $GuHL$  267 µm,  $PnHL$  242 µm,  $nMet$  38.0,  $MetHL$  249 µm,  $nPe$  15.0. Dorsum of first gaster tergite moderately shiny, with dense transverse microripples, rather dilute pubescence (sqPDG 9.76 µm), and rather large, deep, and widely spaced microfoveolae. The latter may be occasionally absent. Light reddish pigmentation component on all body surfaces more developed than in the *F. rufa* species complex.

**Taxonomic comments and clustering results.** *Formica truncorum*, as any species of the *F. truncorum* species complex, is rarely confused with other species of the *Formica rufa* group. Occasional confusion with *Formica pratensis* is possible due to high similarity in pilosity data and most of the body shape data and due to variation in pigmentation in both species. However, the separation by exploratory and hypothesis-driven data analyses shows an error < 1% on the nest sample level in material from the whole Palaearctic range. Furthermore, the shape of clypeus and funiculus segments is usually diagnostic. In gynes, the separation from any species of the *F. rufa* species complex is also clear in both exploratory and hypothesis-driven data analyses. Less hirsute specimens from Kyrgyzstan, formerly identified as „*Formica cf. frontalis*“ (SCHULTZ & al. 2006), were re-classified in this study as *F. truncorum*. The current data give no indication that *F. frontalis* does occur outside of Iberia.

The Panpalaearctic population of *Formica truncorum* cannot reasonably be subdivided into clusters of separate taxonomic identity based on the morphological data available at present. On worker individual level, the West

and Central Palaearctic population differs from the East Palaearctic one by smaller SL / CS<sub>1750</sub>,  $nPn_{1750}$ , and  $nMet_{1750}$  (Tab. 5; ANOVA  $F_{1,90} > 15$ ,  $p < 0.001$ ). Yet, it was not possible by any tested exploratory data analysis to cluster the East Palaearctic population separately – neither on individual nor on nest sample level. As a consequence, *Formica yessensis* WHEELER, 1913 and *Formica approximans* WHEELER, 1933 are synonymized here with *F. truncorum*. A subdivision within the East Palaearctic population is also not possible. Using nuDNA (microsatellites), IMAI & al. (2016) investigated the Japanese-Korean population. They could not show genetic differences between populations they had pre-determined as “*F. yessensis*” and “*F. truncorum*” based on subjective assessment of setae numbers on hind tibia. IMAI & al. (2016) reported a “robust” genetic indication for the presence of only a single Japanese-Korean population and a “fragile” morphological classification. For separation from *Formica frontalis* and *Formica sinensis*, see section “*Formica frontalis* SANTSCHI, 1919” (p. 171) and “*Formica sinensis* WHEELER, 1913” (p. 172).

**Biology.** See the species profile given by SEIFERT (2018). Gyne size polymorphism with large disperser gynes having more fat and glycogen and larger flight muscles than smaller inbreeding gynes is more strongly expressed in *Formica truncorum* than in any other species of the *Formica rufa* group.

### ***Formica dusmeti* EMERY, 1909**

*Formica rufa* ssp. *dusmeti* EMERY, 1909 [conception of TINAUT & MARTINEZ-IBANEZ (1998)]

The original description reports as type locality and collector: “Peñalosa in Spanien; 3 Exemplare wurden mir von Herrn Dusmet mitgeteilt.” According to TINAUT & MARTINEZ-IBANEZ (1998), there is obviously a misspelling of the site as the two worker specimens in the Dusmet collection in MNCN Madrid bear labels indicating “Peñalara” as the collecting site. Furthermore, TINAUT & MARTINEZ-IBANEZ (1998) quoted *F. dusmeti* to be frequent at Peñalara (Sierra de Peñalara) but to be absent from Peñalosa and surrounding areas in the province of Cordoba.

**All material examined.** Numeric phenotypical data were recorded in three samples with seven workers from Spain. For details, see SI1, SI2, and SI3.

**Geographical range.** According to TINAUT & MARTINEZ-IBANEZ (1998) and ESPADALER & GOMEZ (2000) restricted to Iberia with main occurrence in the northern part of the Peninsula. The altitude of seven sites was 1573 ± 261 m, which is higher than in *Formica frontalis*.

**Diagnosis of worker** (Tab. 5, key). Medium-sized, mean and maximum CS 1706 and 2074 µm. Head elongated, CL / CW<sub>1750</sub> 1.113. Clypeal structure as in *Formica truncorum*. Scape very long and slender, SL / CS<sub>1750</sub> 1.001, SL / Smax<sub>1750</sub> 11.08. Petiole scale narrow, PeW / CS<sub>1750</sub> 0.438. Eyes without or with only short microsetae, EyeHL<sub>1750</sub> 14 µm. Dorsal plane of scape completely without setae,  $nSc_{1750}$  0.0. Setae number on each place of the body strongly reduced, clearly smaller than in *Formica frontalis*,  $nCH_{1750}$  0.0,  $nGu_{1750}$  0.0,  $nPn_{1750}$

0.3, nMes<sub>1750</sub> 2.4, nPr<sub>1750</sub> 0.8, nMet<sub>1750</sub> 0.4; when present, setae are short or of medium length, GuHL<sub>1750</sub> 156 µm, mPnHL<sub>1750</sub> 18 µm, MetHL<sub>1750</sub> 28 µm. Typical pigmentation in medium-sized to large workers: whole head, mesosoma, petiole, and frontal part of first gaster segment light orange brown.

**Diagnosis of gyne.** Unknown to me.

**Taxonomic comments and clustering results.** I maintain here the concept of TINAUT & MARTINEZ-IBANEZ (1998), who separated *Formica dusmeti* and *Formica frontalis* workers based on strong differences in setae numbers on pronotum, hind margin, and underside of head. This is basically confirmed by the data given in Table 5. Using these data, the first principal component provided a clear separation of seven *F. dusmeti* and 25 *F. frontalis* workers. However, the sample size is low, and considering the extreme intraspecific variation of pilosity data known in several species of the *Formica rufa* group, a thorough morphometric and genetic study is desired. Xavier Espadaler (pers. comm. July 2020) commented that some Portuguese and West Spanish populations of *F. dusmeti* and *F. frontalis* appeared to be intermediate in pilosity data.

**Biology.** TINAUT & MARTINEZ-IBANEZ (1998) report as main habitat conifer woodland, but it has also been found in open situations under large rocks and stone plates. Alates were observed between 14 June and 4 August.

### ***Formica frontalis* SANTSCHI, 1919**

*Formica truncorum* var. *frontalis* SANTSCHI, 1919 [type investigation]

Investigated was the lectotype worker (by present designation), labelled in Santschi's handwriting "Formica truncorum F. v. frontalis type Sants", "Espagne Pozuelo de Calatrava (de la Fuente)", depository NHM Basel. The original description reports as type locality nothing but "Pozuelo de Calatrava (De la Fuente)". Accordingly, a worker specimen depicted in AntWeb (ANTWEB 2021) under CASENT0912253, labelled "SIERRA DE QUADARRAMA Dusmet" and "type" has no type status.

All material examined. Numeric phenotypical data were recorded in 11 samples with 26 workers and six gynes from Spain. For details, see SI1, SI2, and SI3.

**Geographical range.** According to TINAUT & MARTINEZ-IBANEZ (1998) and ESPADALER & GOMEZ (2000) rather homogenously distributed over entire Iberia with the altitude of 15 sites being 1160 ± 450 m, which is lower than in *Formica dusmeti*.

**Diagnosis of worker (Tab. 5, key).** Medium-sized, mean and maximum CS over all morphological and social phenotypes 1792 and 2045 µm. Head moderately elongated, CL / CW<sub>1750</sub> 1.102. Clypeal morphology as in *Formica truncorum*. Scape long and slender, SL / CS<sub>1750</sub> 0.993, SL / Smax<sub>1750</sub> 10.60. Petiole scale narrow, PeW / CS<sub>1750</sub> 0.450. Eyes without or with short microsetae, EyeHL<sub>1750</sub> 16 µm. Dorsal plane of scape without or with only single setae, nSc<sub>1750</sub> 0.7. Setae number on each place

of the body smaller than in *F. truncorum* but setae length equal or even larger, nCH<sub>1750</sub> 14.5, nGu<sub>1750</sub> 19.5, nPn<sub>1750</sub> 59.5, nMes<sub>1750</sub> 26.1, nPr<sub>1750</sub> 29.2, nMet<sub>1750</sub> 10.2, OccHL<sub>1750</sub> 114 µm, GuHL<sub>1750</sub> 204 µm, mPnHL<sub>1750</sub> 97 µm, MetHL<sub>1750</sub> 161 µm. Dorsal surface of head usually without the deep and broad microfoveolae characteristic for *F. truncorum*. Pigmentation as in the latter.

**Diagnosis of gyne (Tab. 8).** Only specimens from a single supercolony were available. These were much larger than *Formica truncorum* gynes of the polygynous to supercolonial social form, CS 2106 µm. Head capsule in dorsal view less trapezoidal than in *F. truncorum*, clypeal shape as in that species. Scape rather long and slender, SL / CS 0.872, SL / Smax 9.30. Petiole wider than in *F. truncorum*, PeW / CS 0.686. Setae on eyes short, EyeHL 31 µm. Setae on dorsum of scape usually absent, nSc 0.2. Setae on remaining parts of body present, less numerous than in *F. truncorum* but of similar length, nCH 23.4, OccHL 202 µm, nGu 34.8, GuHL 287 µm, PnHL 255 µm, nMet 26.3, MetHL 252 µm, nPe 10.8. Dorsum of first gaster tergite moderately shiny, with dense transverse microripples and dilute pubescence (sqPDG 12.25 µm), microfoveolae often absent. Pigmentation as in *F. truncorum*.

**Taxonomic comments and clustering results.** The geographic ranges of *Formica frontalis* and *Formica truncorum* are disjunct, and the morphological distinctness of the two species is strong enough to consider them as heterospecific. The eleven Iberian nest samples of *F. frontalis* can be separated from 37 Panpalaearctic nest samples of *F. truncorum* using the characters SL / CS<sub>1750</sub>, PeW / CS<sub>1750</sub>, EyeHL<sub>1750</sub>, nCH<sub>1750</sub>, nMet<sub>1750</sub>, and MetHL<sub>1750</sub> (Fig. 34). The classification error by an LDA was 4.2% in 118 worker specimens. It is worth mentioning that gynes from highly polygynous or supercolonial

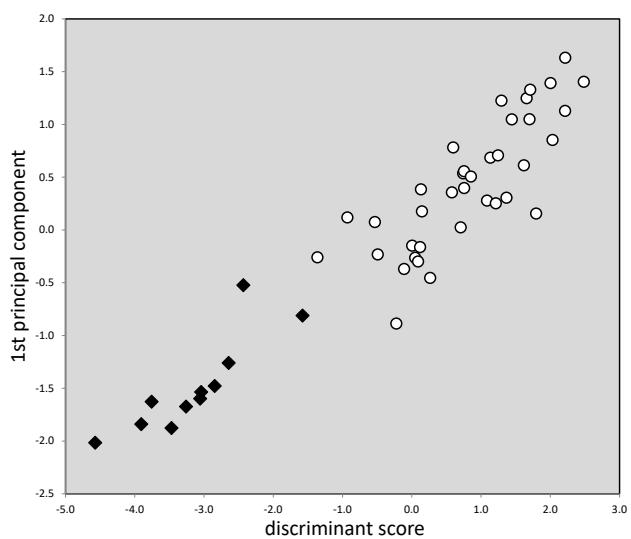


Fig. 34: Nest-sample means of a linear discriminant analysis and principal component analysis of workers of *Formica frontalis* (black rhombs) and *Formica truncorum* (white dots). Six phenotypic characters were considered.

*F. truncorum* populations have a much smaller size than the investigated gynes from the *F. frontalis* supercolony at Puerto de Navacerrado (SaNo. 149 and 150), which provides additional support for heterospecificity.

**Biology.** Compared with *Formica dusmeti*, TINAUT & MARTINEZ-IBANEZ (1998) reported a more frequent occurrence in *Quercus* than in conifer forests, which is probably not due to a preference of broad-leaved woodland but rather a consequence of the lower altitudinal range. The species is also found in open treeless habitats with low shrubs. Nest construction is similar to *Formica truncorum*, not showing the large regular mounds seen in the *Formica rufa* species complex. The above-ground part is usually a rather flat accumulation of plant material, or the nests are completely under stones around which some plant material is deposited.

### ***Formica sinensis* WHEELER, 1913**

*Formica truncicola* var. *sinensis* WHEELER, 1913 [type investigation]

This taxon was described from the vicinity of Chongqing (W China, 29.53° N, 106.52° E). Investigated were 32 syntype workers on 10 pins which were probably from the same sample as concluded from the consistent morphology. A lectotype plus two paralectotype workers on the same pin are labelled "Lectotype (top specimen) *Formica truncicola* var. *sinensis* Wheeler 1913 desig. B.Seifert 2006", "Chun King, China, 1909", "Am. Mus. Nat. Hist. Dept. Invert. Zool. No. 22594" and "Formica truncicola var. *sinensis* Whlr."; depository AMNH New York. 26 paralectotype workers on eight pins in AMNH New York and three paralectotype workers in SMN Görlitz are all labelled "Chun King, China, 1909" and "Am. Mus. Nat. Hist. Dept. Invert. Zool. No. 22594". In the key of the original description (p. 391) and on the syntype labels, WHEELER (1913) used *F. sinensis* as trinomen but later in the heading of the main text (p. 437) as quadrinomen. Herewith, by majority indication, I suppose that WHEELER (1913) did not intend to introduce this taxon in infrasubspecific rank. Otherwise, WU (1990) would be the first who made the name available.

### ***Formica wongi* WU, 1990**

*Formica wongi* WU, 1990 [type investigation]

This taxon was described from near Yongji, province Jilin (NE China, 43.70° N, 126.34° E) in material collected 6 October 1983. Investigated were five paratype workers from the holotype sample from RIFCAF Beijing (now in SMN Görlitz) labelled in handwritten Chinese. The label was confirmed by different native Chinese speakers to name the type locality and it contained the sequence "1983.X.6" and "*Formica wongi* Wu". The type series consists of unusually small workers of apparently a colony in foundation and its higher SL / CS of 1.018, and reduction of reddish pigment is explained by the normal allometric trends we observe in all *Formica rufa* group ants. For investigation results of the type series, see below under taxonomic comments and clustering results.

### ***Formica delinghaensis* CHANG & HE, 2002**

*Formica delinghaensis* CHANG & HE, 2002 [zoogeography and description]

This taxon was described from Delingha, Qinghai Province / China (37.32° N, 97.22° E, 2750 m). CHANG & HE (2002) separated *F. delinghaensis* from *Formica wongi* by a brighter colour and a shorter scape (SL / CL 0.89 - 1.00). This scape length ratio is just the typical situation in *Formica sinensis* (SL / CL in 70 specimens 0.944 ± 0.027). Furthermore, only a single *Formica rufa* group species was discovered in E Tibet, Sichuan, and Gansu during seven collecting trips performed by A. Gebauer, D. Wräse, M. Schülke, I. Kabak, B. Seifert, R. Schultz, V. Assing, and A. Pütz in the years 1990 - 2012, and this species was *F. sinensis*.

All material examined. Numeric phenotypical data were recorded in 29 samples with 70 workers and seven gynes from China. For details, see SI1, SI2, and SI3.

**Geographical range.** *Formica sinensis* is found in the Chinese provinces Qinghai, Gansu, Sichuan, Chongqing, and, as a seemingly disjunct population, in the province Jilin. Eleven samples from Qinghai and Gansu, from latitudes of 33 - 38° N, were found at elevations of 2480 ± 276 [2080, 2862] m and 11 samples from Sichuan, from latitudes between 28 - 32° N, at elevations of 3334 ± 542 [2700, 4130] m. This indication of high-altitude distribution may be partially misleading as the entomologists were not much motivated to sample in anthropogenically affected landscapes at lower elevations. A much lower altitudinal limit is indicated by the findings from Chongqing (29.53° N, 106.52° E, 1500 m), Chincheng Shan (30.90° N, 103.55° E, 975 m), and Yongji (43.7° N, 126.3° E, 560 m).

**Diagnosis of worker** (Tab. 5, Fig. 20, key). Medium-sized, mean and maximum CS over all morphological and social phenotypes 1783 and 2134 µm. Head elongated CL / CW<sub>1750</sub> 1.113. Clypeal morphology as in *Formica truncorum*. Scape very long and slender, SL / CS<sub>1750</sub> 0.997, SL / Smax<sub>1750</sub> 11.18. Petiole scale very narrow, PeW / CS<sub>1750</sub> 0.430. Eyes with no or only short microsetae, EyeHL<sub>1750</sub> 5 µm. Dorsal plane of scape always without setae, nSc<sub>1750</sub> 0.0. Setae number on each place of the body smaller than in *F. truncorum* but setae length on underside of head and metapleuron comparable: nCH<sub>1750</sub> 8.2, nGu<sub>1750</sub> 26.1, nPn<sub>1750</sub> 26.6, nMes<sub>1750</sub> 24.2, nPr<sub>1750</sub> 20.5, nMet<sub>1750</sub> 7.7, OccHL<sub>1750</sub> 114 µm, GuHL<sub>1750</sub> 184 µm, mPnHL<sub>1750</sub> 70 µm, MethL<sub>1750</sub> 140 µm. Dorsal surface of head without the deep and broad microfoveolae characteristic for *F. truncorum*. Pigmentation as in the latter.

**Diagnosis of gyne** (Tab. 8). Rather large, mean CS 2192 µm. Head capsule in dorsal view less trapzoidal than in *Formica truncorum*, clypeal shape as in that species. Scape length and slenderness largest in all species considered here, SL / CS 0.921, SL / Smax 10.30. Petiole width as in *F. truncorum*, PeW / CS 0.589. Setae on eyes fully absent, EyeHL 0 µm. Setae on dorsum of scape always absent, nSc 0.0. Setae on hind margin of head much less numerous and shorter than in *F. truncorum*, nCH 11.4, OccHL 163 µm. Gular setae less numerous than in *F.*

*truncorum* but of similar length, nGu 33.0, GuHL 250 µm. Setae on pronotum, metapleuron and petiole scale less numerous and shorter than in *F. truncorum*, PnHL 194 µm, nMet 22.3, MetHL 215 µm, nPe 11.2. Cuticular surface of head very homogenous, without pits or foveolae. Dorsum of first gaster tergite weakly shiny, with dense transverse microripples and dilute pubescence (sqPDG 10.14 µm) but very homogenous microsculpture, microfoveolae often absent. Pigmentation as in *F. truncorum*.

**Taxonomic comments and clustering results.** Wu (1990) separated his new taxon *Formica wongi* from *Formica sinensis* because of absence of setae from pronotum and from the first three gaster tergites and the “rather dull body”. As there are always setae on the first three gaster tergites even in the least hairy species of the Palaearctic *Formica rufa* group, it appeared unclear if Wu’s material really belonged to this species group. The investigation of five syntypes had the following results:

Very small body size for a species of the *Formica truncorum* species complex (CS = 1214, 1251, 1326, 1490, 1563 µm) – this suggests a colony shortly after foundation. Ablation of pilosity on many areas of surface is confirmed by presence of numerous basal pits of setae. Anterior face of first tergite with numerous standing setae; most setae on exposed dorsal surfaces of first three tergites torn off, the few remaining are pasted flat to surface; in sheltered surface dints numerous and long setae are present. Large parts of cuticular surface are polluted (“rather dull body”) and setae ablations are possibly due to attempts of mechanical cleaning prior preparation. Standard setae numbers and lengths were estimated in the three largest workers by scrutinizing the cuticular surface at magnifications of 360 × for basal pits of setae and measuring the

length of both standing setae and those glued flat to the surface. The sample means of the three largest workers are: CS 1460 µm, CL / CW<sub>1750</sub> 1.119, SL / CS<sub>1750</sub> 1.067, SL / Smax<sub>1750</sub> 11.67, PeW / CS<sub>1750</sub> 0.397, EyeHL<sub>1750</sub> 7.3 µm, nSc<sub>1750</sub> 0.0, nCH<sub>1750</sub> 5.1, OccHL<sub>1750</sub> 105.6 µm, nGu<sub>1750</sub> 31.1, GuHL<sub>1750</sub> 130.0 µm, nPn<sub>1750</sub> 5.4, mPnHL<sub>1750</sub> 57.1 µm, nMes<sub>1750</sub> 22.5, nPr<sub>1750</sub> 24.8, nMet<sub>1750</sub> 11.4, and MethL<sub>1750</sub> 114.0 µm. All these data indicate a typical series of *F. sinensis*.

The separation of *Formica sinensis* and *Formica truncorum* was very clear in any exploratory and hypothesis-driven data analysis considering the 17 characters mentioned above (Fig. 35). The classification error in an LDA was 0% in 70 and 92 individual workers of *F. sinensis* and *F. truncorum*, respectively. Wild-card runs allocated all type specimens of *F. truncorum*, *Formica truncicola*, *Formica approximans*, and *Formica yessensis* to the *F. truncorum* cluster and all type specimens of *F. sinensis* and *Formica wongi* to the *F. sinensis* cluster. The classification errors in NC-Ward and NC-part.hclust were 0% and 1.6% in NC-part.kmeans.

**Biology.** The data collected for this revision show the following aspects: *Formica sinensis* is the only *Formica rufa* group species present in large areas of China and thus without direct competitors in a rather broad niche space. It occurs in coniferous, mixed, and broad-leaved woodland of natural or anthropogenic origin – at higher elevations preferentially in woodland with low canopy closure or on clearings. Social types vary from monodomous colonies to true supercolonies with large mounds. Six observations of alates occurred between 26 June and 5 August.

### Rarer hybrids

The situation in the frequent and geographically widely spread hybrids *Formica polyctena* × *rufa* and *Formica aquilonia* × *polyctena* and their backcrosses has already been discussed in sections “*Formica polyctena* × *rufa* – hybrids and backcrosses” (p. 155) and “*Formica aquilonia* × *polyctena* – hybrids and backcrosses” (p. 156). The sections below consider other hybrid combinations which are obviously rare and of regional occurrence or hybrid combinations which are traced as ancestral.

**Hybrids *Formica aquilonia* × *lugubris*.** Indication of ancient hybridization of *F. aquilonia* with *F. lugubris* is provided by a sample from the Baikal region (SaNo 166, Severobaikalsk-1998-E5) which had a clear *F. aquilonia* phenotype but a mtDNA clustering with that of *F. lugubris* from the same locality (GOROPASHNAYA & al. 2004). Considering the 10 thoroughly recorded characters CS, CL / CW<sub>1750</sub>, SL / CS<sub>1750</sub>, SL / Smax<sub>1750</sub>, nSc<sub>1750</sub>, nCH<sub>1750</sub>, OccHL<sub>1750</sub>, mPnHL<sub>1750</sub>, nMet<sub>1750</sub>, and MethL<sub>1750</sub>, the sample is placed by a PCA in the center of the *F. aquilonia* cluster (Fig. 36) and is confirmed as this phenotype in a wild-card run of an LDA with p = 1.000. The interpretation of this case is mating of a *F. lugubris* gyne by a *F. aquilonia* male in the past with gradual removal of *F. lugubris* genes from the nuclear genome by repeated backcrossing with only *F. aquilonia* males.

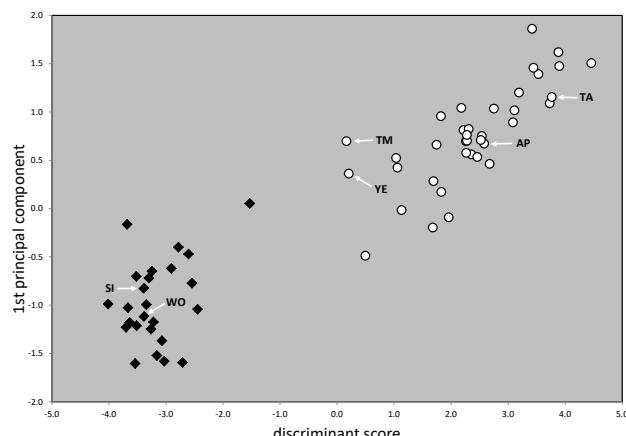


Fig. 35: Nest-sample means of the discriminant score and the first factor of principal component analysis of workers of *Formica truncorum* (white dots) and of *Formica sinensis* (black rhombs) considering seven phenotypic characters. The positions of the single type specimens of *F. truncorum* FABRICIUS, 1804 (abbreviation TM), *Formica truncicola* NYLANDER, 1846 (TA), and *Formica yessensis* WHEELER, 1913 (YE) and of the type series of *Formica approximans* WHEELER, 1933 (AP), *F. sinensis* WHEELER, 1913 (SI), and *Formica wongi* WU, 1990 (WO) are indicated by arrows.

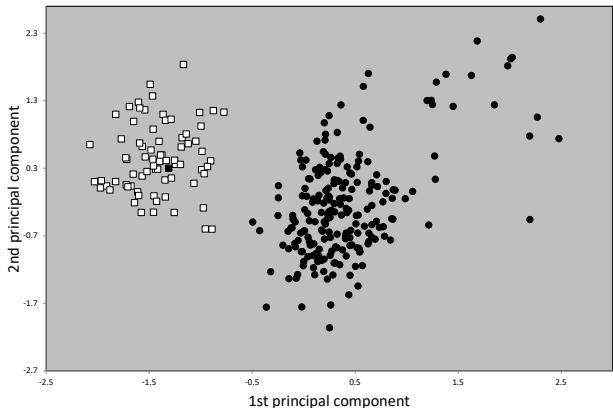


Fig. 36: Worker nest-sample means of principal component analysis of *Formica aquilonia* (white squares, 75 nest samples) and of *Formica lugubris* (black dots, 217 nest samples) from the whole Palaearctic range considering 10 phenotypic characters. The black square marks the *F. aquilonia* sample from Severobaikalsk with a mtDNA haplotype clustering with that of syntopic *F. lugubris*. *Formica lugubris* samples with very large scores of first principal component do mainly or fully contain workers of the Fennoscandian Hippie morph.

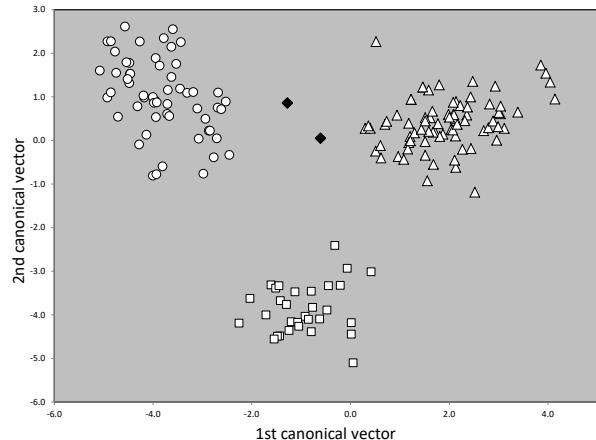


Fig. 37: Worker nest-sample means of a linear discriminant analysis separating *Formica aquilonia* (squares), *Formica lugubris* (triangles), and *Formica rufa* (discs). The 10 and nine worker individuals of the hybrid samples *F. lugubris* × *rufa* (black rhombs) were run as wild-cards. Ten phenotypic characters and a total of 165 nest samples with 794 individuals of the three species compared were considered.

**Hybrids *Formica pratensis* × *lugubris*.** Evidence for ancient hybridization of *F. pratensis* with *F. lugubris* is provided by four samples from two localities in the Pyrenees (SaNo 514-P1, 613-P2, 614-P3, 624-P19) and five samples from two sites in West Siberia (SaNo 625-U1, 626-U10, 627-U12, 628-U21, 631-U30). All these nine samples were morphometrically clearly *F. pratensis* but showed mtDNA haplotypes of regional *F. lugubris* (SEIFERT & GOROPASHNAYA 2004). These samples were checked in wild-card runs in an LDA considering the characters CS, CL / CW<sub>1750</sub>, SL / CS<sub>1750</sub>, SL / Smax<sub>1750</sub>, PeW / CS<sub>1750</sub>, nCH<sub>1750</sub>, OccHL<sub>1750</sub>, mPnHL<sub>1750</sub>, nMet<sub>1750</sub>, MethL<sub>1750</sub>, and nSc<sub>1750</sub>. All were clearly classified as *F. pratensis* – eight samples with posterior probabilities p > 0.998 and one sample (SaNo 631-U30) with p = 0.946. The used classification system appears very safe with an error of 1.6% in 1322 worker individuals belonging to 225 nest samples of *F. lugubris* and 76 nest samples of *F. pratensis*. The interpretation of these cases is mating of *F. lugubris* gynes by *F. pratensis* males in the past with gradual removal of *F. lugubris* genes from the nuclear genome by repeated backcrossing with only *F. pratensis* males.

**Hybrids *Formica lugubris* × *rufa*.** The first indication for occurrence of this hybridization provides a nest sample from Heathersage Peak District National Park (England, SaNo 645, GB: Sheffield-15SW-1999-GB-S4 in SI1 and SI2). It shows the mtDNA of *Formica rufa* (A. Goropashnaya, pers. comm. 2004) but is by phenotype a perfect *F. lugubris*. It is allocated in the nest sample mean to the center of *F. lugubris* cluster (p = 1.0000) if checked by a wild-card run in a three-class LDA against the candidate species occurring in the area. These were *Formica aquilonia* (31 nest samples, 102 individuals), *F. lugubris* (226, 1065), and *F. rufa* (57, 215). *Formica pratensis* is

not present in the area and considered extinct all over the British Isles. The check was done computing 10 thoroughly available characters (CS, CL / CW<sub>1750</sub>, SL / CS<sub>1750</sub>, SL / Smax<sub>1750</sub>, PeW / CS<sub>1750</sub>, nCH<sub>1750</sub>, OccHL<sub>1750</sub>, mPnHL<sub>1750</sub>, nMet<sub>1750</sub>, MethL<sub>1750</sub>, and nSc<sub>1750</sub>) with a classification error of 2.1% in 1384 individuals – a very discriminative system. The case suggests ancient hybridization of a *F. rufa* gyne with a *F. lugubris* male with subsequent purging of the nuclear genome towards *F. lugubris*. Yet, incomplete lineage sorting of ancient mtDNA cannot be fully excluded as a source for the mismatch.

Evidence for recent hybridization *Formica lugubris* × *rufa* is provided by a sample from Sweden (SaNo 401, SWE: Hallamölla 1978.07.27-05 in SI2, 10 workers examined) and another one from Finland (SaNo 475, FIN: Tärminne 1991.05.23-12 in SI2, nine workers examined). The position of these samples in the vectorial space of morphological data was checked as above with the exception that only Fennoscandian material was considered in *F. lugubris* (77 nest samples, 476 individuals). The wild card-run placed the nest means of the Hallamölla and Tärminne samples intermediate between *F. lugubris* and *F. rufa* and clearly distant from *Formica aquilonia* (Fig. 37). This classification system was also safe with a determination error of 0.9% in 794 individuals. The supposed parental species do occur in the Hallamölla and Tärminne area and the swarming periods of both species overlap considerably (SEIFERT 2018). However, *Formica pratensis* is also present in Fennoscandia and clustering with the 10-character system could not exclude it as a parental species. Yet, in SaNo 475, *F. pratensis* appears unlikely due to its rarity near to the collecting site and variation in the allozyme locus Pgk which was not observed in *F. pratensis* (Pekka Pamilo, pers. comm. 2021). Anyway, we need here a thorough investigation through nuDNA markers.

**Hybrids *Formica aquilonia* × *paralugubris*.** BERNASCONI & al. (2011), analyzing nine microsatellite markers, indicated hybridization of *F. aquilonia* and *F. paralugubris* in a small area near Zernez in the Swiss Alps. This material (SaNo 698-700, Zernez 2007.08.16, cra8, cra12, cra15) was investigated both by a linear discriminant analysis and a principal component analysis considering the characters CS, CL / CW<sub>1750</sub>, SL / CS<sub>1750</sub>, nCH<sub>1750</sub>, OccHL<sub>1750</sub>, mPnHL<sub>1750</sub>, nMet<sub>1750</sub>, MetHL<sub>1750</sub>, EyeHL<sub>1750</sub>, nSc<sub>1750</sub>, and SL / Smax<sub>1750</sub>. Both analyses did not expose the hybrid samples as intermediate, but the placement at the margin of the *F. paralugubris* cluster suggested backcrossing of hybrids with *F. paralugubris*.

### Summary account of hybridization and reticulate evolution in *Formica rufa* group ants

Figure 38 gives a schematic overview about what has been reported in this treatise on hybridization and reticulate evolution in Palaearctic *F. rufa* group ants. There has been little target-aimed investigation of this issue so far. Genetic investigations of these ants are only beginning, with very few and only local investigations of nuclear gene sequences. Generally, there is no whole-genome sequencing over a wide set of species in a comparative context – the papers of PURCELL & al. (2014) and DHAYGUDE & al. (2019), though both dealing with a single-species issue, might serve as template for future genomic investigation. Furthermore, the phenetic methods, though executed extensively here, are not able to detect each hybridization. F<sub>1</sub>-Hybrids do not always exhibit clearly intermediate phenotypes, and backcrosses are usually placed in the twilight area. In addition to publications on *F. rufa* group ants, there are seven published cases of ant hybrids in which thorough morphometric studies comparable with those presented here were done: *Formica bruni* × *pressilabris* (SEIFERT 1999), *Lasius meridionalis* × *umbratus*, *Lasius jensi* × *umbratus* (both SEIFERT 2006), *Messor wasmanni* × *minor* (STEINER & al. 2011), *Myrmica scabrinodis* × *vandeli* (BAGHERIAN YAZDI & al. 2012), *Lasius niger* × *emarginatus* (SEIFERT 2019a), and *Camponotus herculeanus* × *ligniperda* (SEIFERT 2019b). Considering all these cases and only those characters in which the parental species showed clear differences, the hybrids were intermediate in 32 characters (50%), approached to one of the parental species in 29 characters (45%) but exceeded character expression in both parents in three characters (5%) – the latter might possibly be a heterosis effect. When characters approached in a hybrid the situation in a parental species, this was usually not unidirectionally biased: Approaches to parent A in a number of characters were accompanied by approaches to parent B in other characters. This explains why placement of hybrids in the morphometric space considering all characters was intermediate in the majority of cases. Only in *Lasius jensi* × *umbratus*, the hybrid cluster was placed very close to that of *L. umbratus* without a clear demarcation.

Despite the expectable failure of morphological hybrid identification in cryptic species and the scarcity of nuDNA

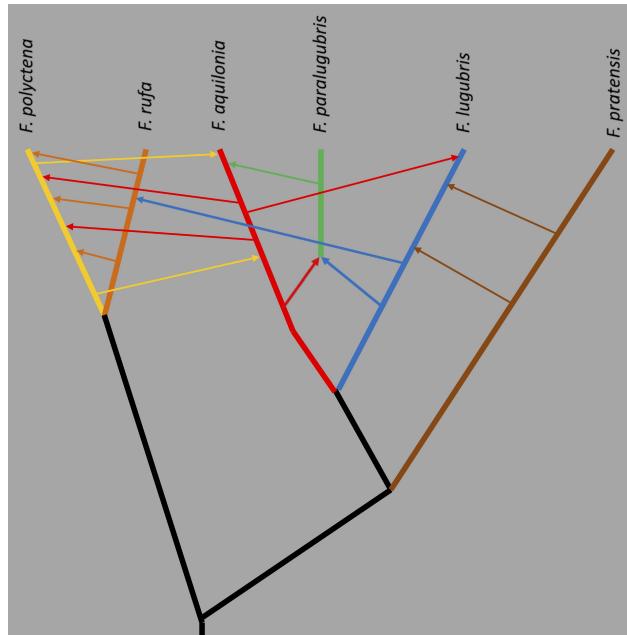


Fig. 38: Schematic presentation of hybridization and reticulate evolution in Palaearctic *Formica rufa* group ants as it is apparent in the younger evolutionary history. The arrows connecting the main branches indicate the direction of gene flow after backcrossing of hybrids – for example, brown arrows directed from *Formica pratensis* to *Formica lugubris* indicate that *Formica pratensis* × *lugubris* hybrids have backcrossed with *F. pratensis*. Examples of both uni- and bidirectional gene flow are shown. The number of arrows is proportional to the supposed frequency of hybridization or backcrossing. *Formica paralugubris* is likely to be of hybridogenous origin. For details, see the main text.

studies, the contours of a most reticulate scenario became already visible. Six species, or 46% of the total, have hybridized. *Formica aquilonia* hybridized with *Formica polyctena*, *Formica paralugubris*, and *Formica lugubris*. *Formica lugubris* hybridized with *Formica rufa*, *F. aquilonia*, and *Formica pratensis*. *Formica polyctena* hybridized with *F. rufa* and *F. aquilonia*, *F. rufa* with *F. polyctena* and *F. lugubris*, *F. paralugubris* with *F. aquilonia*, and *F. pratensis* with *F. lugubris*. It appears to be no risk predicting that the evolutionary history of Palaearctic *F. rufa* group ants as a whole will turn out as extremely reticulate once whole genome analyses are available for many species over a wide geographical range. Future work should aim to study reticulate evolution in *Formica* in a manner similar to that carried out in *Heliconius* butterflies by EDELMAN & al. (2019). Reticulate evolution is a nightmare for taxonomists but an evolutionary biologist's delight. In the wake of ongoing massive ecosystem change due to human land use and anthropogenic climate warming, repeated introgression of genes may provide an adaptive advantage for long-term survival and prosperity of *F. rufa* group ants. The species present in the 22<sup>nd</sup> century, however, will differ in their genomic composition from those we have today, and the geographic distribution will shift.

## Comments on incertae sedis and unavailable names

This chapter comments on taxa which cannot be interpreted to species level due to missing or insufficient descriptions and unavailability of type specimens. There are two ways to treat this misery. The first is placing these names in a speculative way in synonymic lists under a certain species following the rationale that nobody can present counter-arguments. Such solutions were chosen for example by BOLTON (1995) and have the advantage that all names are listed in a single system. The alternative is listing these names under incertae sedis. I prefer the latter solution and recommend future revisers not to synonymize these names as long as no reliably identified type specimens have been discovered. Taxonomy needs clear arguments and not speculative assertions. I express here a particular appeal to responsible behavior of future taxonomists in dealing with unexploded bomb shells hidden in the ground. This refers in particular to the collection of M. Ruzsky in St. Petersburg, which could not be checked. There are repeated bitter experiences in the past regarding losses of type material during mailing between Germany and Russia, and restrictions during the COVID19 pandemic prevented a personal visit of the Ruzsky collection. If a future taxonomist has the opportunity for scrutinizing this collection and discovers ants reliably identifiable as types and if their data can reliably document a senior synonymy with *Formica aquilonia*, he / she has to consider if destroying a long naming tradition is a good service to the community of wood ant researchers. Below, I present the incertae sedis and unavailable names in alphabetic order.

### ***Formica rufa* ssp. *polyctena* ab. *bondroiti* STÄRCKE, 1942**

Unavailable infrasubspecific name.

### ***Formica pratensis* var. *ciliata* RUZSKY, 1926**

Unavailable name; junior primary homonym of Nearctic *Formica ciliata* MAYR, 1886; described from village Jamynsk near Tomsk; probably belonging to *F. pratensis*.

### ***Formica dorsata* PANZER, 1798**

*Formica* incertae sedis; described from Austria, probably a gyne of *Formica rufa* group with shiny, weakly pubescent gaster.

### ***Formica ferruginea* CHRIST, 1791**

*Formica* incertae sedis; an unidentified species of the *Formica rufa* group: "black, mesosoma and petiole rusty red ... prefers fir and spruce forests, builds its home often at cut tree stumps, erects there mounds of 60 - 90 cm height, to which a lot of resin is retrieved".

### ***Formica rufa* ssp. *pratensis* var. *foreli* KRAUSSE, 1926**

Unavailable name, quadrinomen and homonym of *Formica foreli* BONDROIT, 1918.

### ***Formica rufa* ssp. *pratensis* var. *incisa* KRAUSSE, 1922**

Unavailable infrasubspecific name.

### ***Formica rufa* ssp. *pratensis* var. *major* GöSSWALD, 1942**

Unavailable name, quadrinomen and homonym of *Formica major* NYLANDER, 1849.

### ***Formica rufa* var. *montana* SADIL, 1953**

Unavailable name; junior primary homonym of the Nearctic *Formica montana* WHEELER, 1910; belongs to *Formica lugubris*.

### ***Formica pratensis* ssp. *nuda* RUZSKY, 1926**

*Formica* incertae sedis; described from Semipalatinsk; eyes, head, and mesosoma without setae; few on underside of head; might possibly belong to *Formica aquilonia* which may occur there. According to Dmitri Dubovikoff (pers. comm. September 2020), there is no specimen in the Ruzsky collection in St. Petersburg which could be recognized as a type specimen.

### ***Formica rufa* var. *nuda* KARAVAJEV, 1930**

Unavailable name; junior primary homonym of *Formica nuda* RUZSKY, 1926; described from the Swedish islands Öland and Gotland. DLUSSKY (1967) investigated type specimens in the collection of SIZ Kiev and stated these to be in all characters consistent with *Formica polyctena*. This is credible considering Dlussky's knowledge of wood ants and the species spectrum present in the terra typica.

### ***Formica rufa* r. *pratensis* var. *rufoides* FOREL, 1874**

Unavailable infrasubspecific name.

### ***Formica rufa* var. *rufopratensisoides* FOREL, 1874**

*Formica* incertae sedis. BOLTON (1995) formally treated *F. rufopratensisoides* as a good species. However, the only text referring to this name, hidden in a chapter on life habits, is: "The forms *rufo-pratensisoides* are in general of small size and have more the life habits of *F. rufa* (*polyctena*, *piniphila*)."  
 (FOREL 1874, p. 368). This tells nothing and figures or data on collecting sites were not found elsewhere in this bulky publication including the keys on workers, gynes, and males.

### ***Formica rufa* var. *rufotruncicola* RUZSKY, 1896**

Unavailable name, junior primary homonym of *Formica rufotruncicola* WASMANN, 1891.

### ***Formica rufa* ssp. *pratensis* var. *santschii* KRAUSSE, 1926**

Unavailable name, quadrinomen and junior primary homonym of *Formica santschii* WHEELER, 1913.

### ***Formica rufa* var. *schmidti* RUZSKY, 1920**

*Formica* incertae sedis; described from Kamchatka, village Kozyrevka. According to article 23.9.5. of the ICZN, there is no need to select a replacement name for *Formica schmidti* RUZSKY, 1920 because *Formica* (*Liometopum*) *schmidti* HEER, 1850 is allocated to another subfamily since 1867 and will never return to *Formica*. According to the description and type locality, there is some probability that *F. schmidti* RUZSKY, 1920 may represent a junior synonym of *Formica lugubris*.

### ***Formica simulata* SMITH, 1878**

*Formica* incertae sedis; this taxon was described from Hindu Kush Mountains and was synonymized by FOREL (1894) with *Formica truncorum*. However, the sharp

clypeal carina and densely pubescent gaster reported by SMITH (1878) speak against *F. truncorum* and suggest a proximity to a species of the subgenus *Serviformica* with a reddish mesosoma.

***Formica pratensis* var. *superba* WHEELER, 1933**

*Formica* incertae sedis; described from Eastern Tombs near Beijing. The description seems to exclude an allocation to the *Formica rufa* group but suggests a junior synonymy with *Formica uralensis* Ruzsky, 1895.

***Formica rufa* ssp. *dusmeti* var. *suzukii* TERANISHI, 1940**

Unavailable infrasubspecific name; described from Korea, probably belonging to poorly haired *Formica truncorum*.

***Formica rufa* ssp. *rufa* ab. *tir* STÄRCKE, 1942**

Unavailable infrasubspecific name; described in a gyne from Stockmarkness (Norway). The type specimen was investigated and belongs to a weakly haired morph of *Formica lugubris*.

***Formica rufa* var. *tshugunovi* Ruzsky, 1914**

*Formica* incertae sedis; described from near Yuganskoe (Russia, 61.09° N, 72.61° E). The description is based on a single small worker. Zoogeography and description suggest a synonymy with either *Formica lugubris* or *Formica pratensis*.

***Formica villiscapa* CHANG & HE, 2002**

*Formica* incertae sedis; described from Hezuo, Gansu Province (China, 34.92° N, 102.87° E, 3100 m). The poor description suggests that it may belong to another subgenus.

### Acknowledgements

The picture of wood ant taxonomy and evolution presented here would have been unthinkable without the contribution of skilled geneticists from the universities of Lausanne, Uppsala, and Helsinki who provided a lot of genetically characterized samples over the last 25 years. I am deeply grateful to all of them. Without being complete and in chronological order of the onset of mutual cooperation, I acknowledge in particular the contribution of Michel Chapuisat, Pekka Pamilo, Anya Goropashnaya, Jonna Kulmuni, and Christian Bernasconi. In 1994, Michel and Pekka prompted me to have a closer look at these many different phenotypes collected in that time under *Formica lugubris*. In 2003, it were Anya and Pekka who opened my eyes on the genetic connections between *Formica pratensis* and *F. lugubris*, which would have remained undetected using morphology alone. In 2009, Jonna and Pekka provided the final genetic proof of my old argumentation on hybridization between *Formica polyctena* and *Formica rufa*. In about the same time, Jonna and Pekka directed my attention to hybridization between *F. polyctena* and *Formica aquilonia* – I would not have touched this diffuse issue without parallel genetic information. Also in about 2009, Christian and Pekka provided me the unpleasant experience that advanced methods of phenotyping may fail to corroborate a genetically demonstrated cluster. Such challenges are a good remedy against developing simple-mindedness and carelessness. I am furthermore indebted

to Sándor Csósz for his important contributions to the development of NC-clustering methods, which are indispensable first steps in formation of taxonomic hypotheses based on morphology. I acknowledge with many thanks the major support by Roland Schultz, who produced and processed fine z-stack photos. Thanks are also given to some 50 persons who provided wood ant samples over now 40 years of my professional activity as ant researcher in Görlitz. The publication of this article was funded by the Open Access Fund of the Leibniz Association.

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