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A taxonomic revision of the Palaearctic ant subgenus *Coptoformica* Müller, 1923 (Hymenoptera, Formicidae)

With 40 figures and 7 tables and an electronic supplementary information SI1, SI2, SI3

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Abstract

A taxonomic revision of the Palaearctic ant subgenus *Coptoformica* Müller, 1923 is presented based on Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT). Indicated by five morphological and one morpho-ethological character, all species of the subgenus *Coptoformica* form a well-circumscribed group of undoubtedly monophyletic origin. 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 on 25 characters were recorded in a total of 944 samples (largely nest samples) with 3660 worker individuals and 402 gynes. Further 250 samples were investigated by subjective visual inspection. Comparative tables and keys to workers and gynes are presented. Intraspecific polymorphism is shown to represent a big challenge in *Coptoformica* taxonomy and is extremely developed in the Palaearctic population of *Formica exsecta* in which occurrence of distinct, most certainly genetically determined morphs within the same nest mound is no rare phenomenon. With the exception of *Formica brun*i x *pressilabris*, no conclusive indications on interspecific hybridization exist in *Coptoformica*. The complete absence of comparative studies on nuclear DNA and the abundance of cryptic species are probable explanations for this low level of hybrid identification. Considering 32 available names, the survey recognized 14 good species, 15 junior synonyms and 3 names not interpretable to species level (Incertae Sedis). Taxonomic changes relative to the revision of Seifert (2000) were as follows: Elevation to species rank was performed in *Formica longiceps* Dlussky, 1964 and *F. brunneonitida* Dlussky, 1964 whereas *F. caucasicola* spec. nov. was described as new Caucasian endemic species. *Formica fossilabris* Dlussky, 1965 has been recognized as junior synonym of *F. pisarskii* Dlussky, 1964.

Key words

cryptic species, polymorphism, morphometrics, hybridization

Nomenclatural acts

F. caucasicola spec. nov. – urn:lsid:zoobank.org:act: EFC74CC6-8FDA-4335-B902-E17C87AC8BB3

Zusammenfassung

Unter Anwendung von Numerischer Morphologie-Basierter Alpha-Taxonomie (NUMOBAT) wird eine taxonomische Revision des paläarktischen Ameisensubgenus *Coptoformica* MÜLLER, 1923 vorgestellt. Fünf morphologische und ein morpho-ethologisches Merkmal zeigen, dass alle Arten des Subgenus *Coptoformica* eine gut abgrenzbare Gruppe von zweifelsfrei monophyletischem Ursprung bilden. Standardisierte morphologische Merkmalssysteme wurden numerisch beschrieben, um eine objektive Hypothesenbildung mittels explorativer Datenanalysen und eine Testung dieser Hypothesen durch hypothesengetriebene Datenanalysen zu ermöglichen. NUMOBAT-Daten über 25 Merkmale wurden in insgesamt 944 Proben (überwiegend Nestproben) mit 3660 Arbeiterinnen und 402 Gynen erfasst. Weitere 250 Proben wurden durch subjektive Augenscheinbetrachtung untersucht. Es werden vergleichende morphologische Merkmalstabellen sowie Bestimmungsschlüssel für Arbeiterinnen und Gynen vorgestellt. Intraspezifischer Polymorphismus stellt eine große Herausforderung für die *Coptoformica*-Taxonomie dar und ist in der paläarktischen Population von *Formica exsecta* extrem ausgeprägt. Bei dieser Art ist das Auftreten verschiedener, sehr wahrscheinlich genetisch gesteuerter Morphen im gleichen Nesthügel kein seltenes Phänomen. Mit Ausnahme von *Formica bruni* X *pressilabris* gibt es bei *Coptoformica* bislang keine schlüssigen Indikationen für interspezifische Hybridisierung. Das Fehlen vergleichender Studien über nukleare DNA und die Häufigkeit kryptischer Arten werden als Ursache für diese geringe Identifikationsrate von Hybriden vermutet. Bei einer Gesamtzahl von 32 verfügbaren Namen werden 14 gute Arten und 15 jüngere Synonyme erkannt sowie drei Namen, die nicht bis zum Artniveau gedeutet werden konnten (Incertae Sedis). Taxonomische Veränderungen im Vergleich zur Revision von SEIFERT (2000) sind folgende: Eine Rangerhöhung zum Artniveau wurde bei *Formica longiceps* DLUSSKY, 1964 und *F. brunneonitida* DLUSSKY, 1964 durchgeführt, während *F. caucasicola* spec. nov. als neuer kaukasischer Endemit beschrieben wurde. *Formica fossilabris* DLUSSKY, 1965 wurde als jüngeres Synonym von *F. pisarskii* DLUSSKY, 1964 erkannt.

Schlüsselwörter

Kryptische Arten, Polymorphismus, Morphometrie, Hybridisierung

Content

1. Introduction

The members of the ant subgenus *Coptoformica* Mueller, 1923 are restricted to the Palaearctic region. They prefer open grassland habitats but some species also colonize bogs, fens and light woodland stands. In many parts of Europe they belong to the most endangered ant species due to human land use which affects the survival of oligotrophic, extensively managed grassland. *Coptoformica* ants are unique in a behavioral trait: facilitated by a special functional morphology of head and mandibles (Dietrich 1998), they cut grass leaves and stems into small pieces to serve as material for construction of mound cupolae with very smooth surfaces. In a former revision of *Coptoformica*, Seifert (2000) recognized the existence of eleven species, but he commented that this figure should be too low due to the fact that only 60 samples from Asia were available in that time. The revision presented here substantially cures this deficiency – 341 samples with 1300 specimens from various parts of Asia, or 36 % of the total, were investigated making use of Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT). Furthermore, some 100 additional Asian samples were classified by only subjective visual inspection. As result, the number of recognized species increased to fourteen, with one species described as new, and the knowledge on intraspecific variability grew considerably. The question whether differing phenotypes may be considered as different species or as intraspecific polymorphism represents a big challenge in *Coptoformica* taxonomy. Without extensive comparative studies on nuclear DNA being available so far, this problem may be tackled by a combination of exploratory and hypothesis-driven analyses of morphological data with careful evaluation of within-nest phenotype compositions (e.g., Seifert & al. 2013). Relating these empiric data to models of different social types and geographic distribution has been used as a criterion to distinguish between heterospecificity and polymorphism (Seifert 2016, 2019c).

In any taxonomic revision considering a large zoogeographic region the problem of assessing allopatric populations is omnipresent. If two allopatric populations are shown to form separate clusters with a minimum of unclear samples, they may be treated as different species. This pragmatism, formulated in the GAGE species concept (Seifert 2020b), lead to the description of *Formica caucasicola* spec. nov. and the recognition of *Formica mesasiatica* Dlussky, 1964 as a species. The data available so far suggest that interspecific hybridization is less frequent in the subgenus *Coptoformica* than in ants of the *Formica rufa* group (for situation there see Seifert 2021). Hybrid identification by phenotypical characters requires sufficiently strong differences between the parental species. This may explain that *Formica bruni* x *pressilabris* remains the only credibly shown hybrid case in *Coptoformica* (Seifert 1999 and this paper). As hybrids between cryptic species are likely to remain undetected by morphology and because there is a complete absence of comparative studies on nuclear DNA in *Coptoformica*, it is likely that the frequency of hybridization is underestimated here.

2. Material

NUMOBAT data were recorded in a total of 944 samples (largely nest samples) with 3660 worker individuals and 402 gynes. Further 250 samples were investigated by simple visual inspection. 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 up in the **electronic supplementary information SI1, SI2 and SI3.** The abbreviations of depositories are as follows.

FMNH Helsinki	Finnish Museum of Natural History, Helsinki / Finland
ZIPAS Warszawa	Zoological Institute of the Polish Academy of Sciences, Warszawa / Poland
MCSN Genova	Museo Civico di Storia Naturale Genova, Genova / Italy
MCZ Cambridge	Museum of Comparative Zoology of the Harvard University, Cambridge / USA
MCZ Lausanne	Musée cantonal de zoologie, Lausanne / Switzerland
MHN Genève	Muséum d‘histoire naturelle de Genève, Genève / Switzerland
MSNB Bruxelles	Muséum des sciences naturelles de Belgique, Bruxelles / Belgium
NHM Wien	Naturhistorisches Museum Wien, Wien / Austria
RIFCAF Beijing	Research Institute of Forestry, Chinese Academy of Forestry, Beijing / China
SMN Görlitz	Senckenberg Museum für Naturkunde, Görlitz / Germany
ZM St. Petersburg	Zoological Museum of the St. Petersburg University, St. Petersburg / Russia
ZMLU Moskva	Zoological Museum of Moscow Lomonossov University, Moskva / Russia

Note that the statements on depositories in case of ZM St. Petersburg and ZMLU Moskva must not represent the current situation as Dlussky, who worked in both institutions, has transferred material to and fro.

3. Methods

3.1 The applied species concept

The GAGE species concept (Seifert 2020a) is used here. Formation of species hypotheses by exploratory data analyses of morphological data considered an error threshold <4 % for NUMOBAT analyses as it was proposed by Seifert (2020 a, b). The species hypotheses formed by NC-clustering were checked in the simple vectorial space (see section 3.3). Extensive future analyses of nuDNA have to show if significant interspecific hybridization and introgression occurs in the subgenus. According to the morphological data currently available, interspecific hybridization appears to be less frequent in *Coptoformica* than observed in the *Formica rufa* group (Seifert 2021).

3.2 Recording of morphological characters

A pin-holding stage, permitting full rotations around X, Y, and Z axes and a Leica M165C high-performance stereomicroscope equipped with a 2.0x planapochromatic objective (resolution 1050 lines/mm) was used for spatial adjustment of specimens at magnifications of 120–360x. A Schott KL 1500 cold–light source equipped with two flexible, focally mounted light–cables, providing 30°–inclined light from variable directions, allowed sufficient illumination over the full magnification range and a clear 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 ten different factors (Seifert 2002). Eighteen and nineteen numeric characters respectively were recorded in both workers and gynes. The character sets differed between workers and gynes. In workers, 6 shape, 8 setae and 3 pubescence characters plus absolute head size have been recorded. In gynes, 6 shape, 8 seta, 3 pubescence and one surface character plus absolute head size have been recorded. All bilateral characters were recorded as arithmetic mean of both sides. Setae, also called pilosity, are differentiated from pubescence hairs in having a significantly larger thickness than neighboring pubescence hairs – this is usually 4-8 µm in setae and 1-2 µm in pubescence. In problematic cases, a hair was classified as seta when it had at least twice the thickness of neighbored pubescence hairs; counts of 0.5 were applied in ambiguous cases. All seta counts (nMet, nCox, nHTfl, TERG, ClySet, nOce) are restricted to standing setae projecting >10 µm from cuticular surface. Scrutinizing cuticular surface for basal remnants of detached setae may be decisive for a determination!

CL – maximum cephalic length in median line; the head must be carefully tilted to the position with the true maximum. Excavations of hind vertex and/or clypeus reduce CL. Thus, in *Coptoformica*, CL is much smaller than the commonly used “overall head length in full face view” that includes the occipital corners and cannot be measured precisely without special devices.

ClyPub – unilateral number of pubescence hairs surpassing the frontolateral clypeal margin by more than 10 µm; counting begins at the sagittal level of the tentorial pit and ends at the lateralmost portion of the clypeus (Fig. 1); the number of both sides is halved.

ClySet – the presence of different setae positions on clypeus; look not only in profile view, but scrutinize the whole surface. The values 1 to 5 mean different distributional levels (Fig. 2):

- **1** – only apical setae based in the frontal clypeal margin and directed frontad are present or whole clypeus completely without setae
- **2** – single postapical clypeal setae present; the distance of the base points of these second level setae from anterior clypeal margin is less than 30 % of whole median clypeal length.
- **3** – single or several standing setae are found at central portions of clypeus; the distance of their base points from anterior clypeal margin is at least 30 % of whole median clypeal length.
- **4** – standing setae are found at posterior portions of clypeus; the distance of their base points from anterior clypeal margin is at least 60 % of whole median clypeal length.
- **5** – whole surface of clypeus with standing setae

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

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

EyeHL – the length of the longest hair on the eyes including microseta at magnifications of at least 150x. In case of curved hairs measure the chord length.

Fu2, Fu3 – median length of 2nd and 3rd segment of antennal funiculus measured with the swiveling plane of the 1st segment adjusted to visual plane. This spatial adjustment corresponds to standard viewing position SVPd as described in Seifert (2018). Because of frequently unequal length of left and right sides of a funiculus segment, of the 2nd in particular, it is important for reproducibility to really measure the median length.

GHL – length of longest hair on 1st gaster tergite; setae immediately before hind margin of the tergite are not considered.

GLANZ – only gynes; assessment of surface brilliancy of dorsal head ranging between extreme values 1 and 3;

score 1 = whole surface completely matt, score 3 = whole surface brilliantly shining; intermediate values 1.5, 2.0, 2.5 are determined by subjective estimate.

ML – only gynes; mesosoma length from caudalmost point of mesosoma to the most distant point of the steep anterior pronotal face.

MnHL – only gynes, length of longest seta on mesonotum.

nCox – setae number on the **frontal** face of forecoxae. The number on both forecoxae is halved.

nHTfl – setae number on the outer edge of the hind tibial flexor side - i.e. the edge positioned laterally when the hind tibia is directed caudad. Not included in the count is the always existing strong hair on outer flexor apex representing a counterpart to the big spur on the inner flexor apex. If there is rich pilosity with different size classes of setae (*e.g.* in *exsecta*), only the 1st order setae are counted. These setae are significantly thicker than standing pubescence, they usually appear more yellowish-reddish instead of whitish as seen in second order setae and pubescence. The number of both tibiae is halved.

nMet – unilateral number of standing setae on lateral metapleuron and ventrolateral propodeum - i.e. the area below the level of propodeal spiracle but excluding those hairs fringing the metathoracal gland and those standing on the ventrolateral edge of metapleuron. The number of both sides is halved.

nOce – Sum of setae in ocellar triangle. The setae must be significantly thicker than neighboring pubescence hairs. One seta pit with no clearly visible remains of a seta scores 0.5, one seta of intermediate (indeterminate) thickness 0.5, one seta with clear thickness characteristics or a seta pit with a clear basal remnant of a detached seta scores 1. Examples of sums: two empty setae pits score 1.0, one seta + one empty seta pit score 1.5, two setae 2.0.

OccHD – seta shagginess in gynes: with head in full face view, longest distance of the tips of setae from cuticular surface in the region posterior of the eye and at occipital corners, measured perpendicular to cuticular surface.

OceD – distance between the inner margins of lateral ocellae.

OceSet – an older mode of assessing seta condition in the ocellar triangle applied in gynes. Only presence (score 1) and absence (score 0) of setae was recorded.

PeH – height of petiole scale from center of spiracle to top margin.

PeINC – depth of incision in upper margin of petiole scale.

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

sqPDO – square root of pubescence distance in the ocellar triangle. The number of pubescence hairs **n** crossing a transverse measuring line of length **L** is counted, hairs just touching the line are counted as 0.5. Pubescence distance PDO is then **L/n**. Four measuring lines equal in length to the distance between the inner margins of lateral ocellae are positioned at different transversal levels: the first line is between hind ocellae, the second line a short distance frontal to the hind ocellae, the third line between the hind and the frontal ocellus, and the forth a short distance caudal of the frontal ocellus. The four counts are averaged. Exact counting is only possible with clean surfaces, high-resolution stereomicroscopy at magnifications >= 280x and reflexion-reduced illumination visualizing the full length of hairs. Surface spots with torn-off pubescence were excluded from measuring. In order to normalize the positively skewed distributions, the square root of PDO is calculated.

sqPDG – square root of pubescence distance on the dorsomedian part of first gaster tergite. Principles of counting as in sqPDO. In case of surface damage or deformation, the second tergite may be used. To reduce accidental errors, 6 counts along 6 differently positioned, transverse measuring lines of 400 µm length are averaged. In order to normalize the positively skewed distributions, the square root of PDG is calculated.

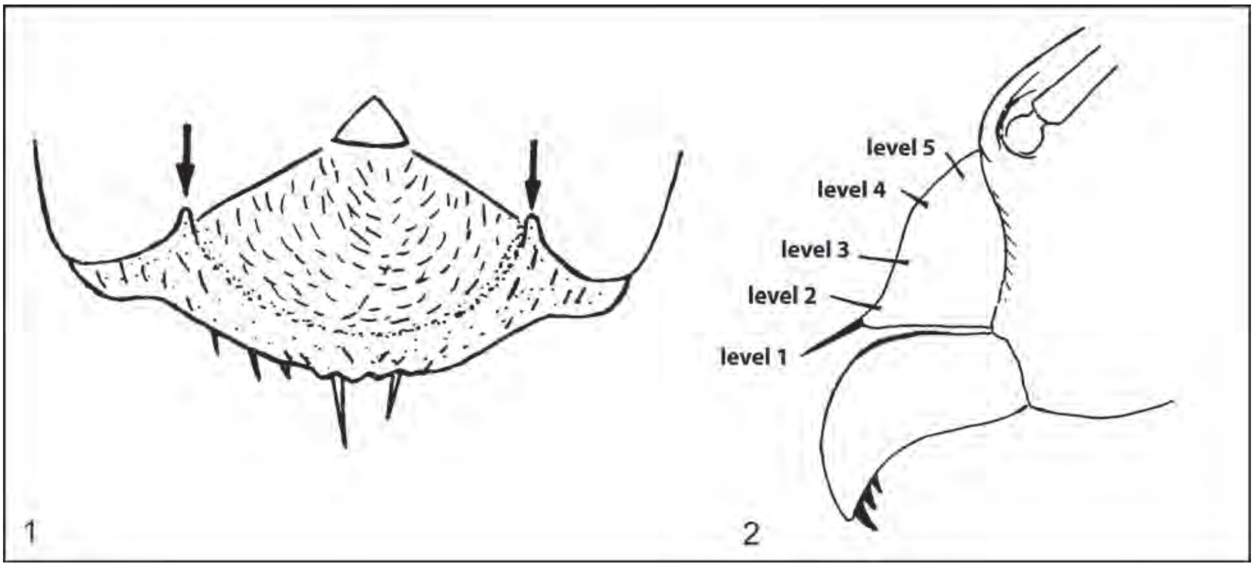

Fig. 1: Clypeal setae and pubescence condition as it is typical for *Formica foreli* and *F. pressilabris*. The arrows point to the tentorial pits. – **Fig. 2**: The levels of setae distribution on clypeus.

TERG – the ordinal number of the frontalmost gaster tergite with at least one standing seta. In species with reduced pilosity, the posterior tergite margins must be scrutinized carefully in search of a hair fitting the definition of seta. Intermediate scores may be applied when the classification of a particular hair is undecided. For instance, "3.5" means that there is a hair of doubtful classification on third tergite but clear seta on the fourth.

T3f – presence /absence (1/0) of setae placed at a clearly more frontal level than the subapical setae of 3rd gaster tergite.

3.3 Explorative and supervised data analyses, classification and statistical testing

Formation of species hypotheses was done by running five different forms of exploratory data analyses (EDA) considering the morphological standard characters specified in section 3.2. Four EDA methods using nest centroids as input data, named NC clustering, were applied. These were hierarchical NC-Ward clustering, 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 Csösz & Fisher 2015). Accessorily, as fourth method, nonmetric multidimensional scaling combined with iterative vector-quantization NC-NMDS.kmeans (Seifert & al. 2013) was applied. The first three methods were run as the standard working routine. All four methods of NC-clustering are excellent in formation of basal hypotheses but they tend to obscure intermediate morphologies possible generated by interspecific hybridization and introgression. Revealing such cases requires further analytical steps: checking the data sample by sample and analyzing them in the simple two-dimensional vectorial space. This was preferentially done by principle component analysis (PCA) with a maximum of three considered entities and often with character reduction. Alternatively, the position of suspicious samples was checked by wild-card runs in a LDA. 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. (2013). 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. PCA, LDA, ANOVA and X^2 tests were run with the SPSS 15.0 software package.

4 Results

4.1 Diagnosis of the subgenus *Coptoformica* Müller, 1923

All *Coptoformica* species constantly share the following character combination:

(a) Occipital margin of head both in big and small specimens deeply excavated; depth of excavation 4.9-9.6 % of overall cephalic width (CW).

(b) mandibles always with 1-3 prebasal denticles - i.e., denticles positioned caudolateral of the true masticatory border.

(c) Petiole scale with straight, parallel to subparallel sides (roughly rectangular in frontal view); its dorsal crest is always excavated with the depth of excavation being 2.2–5.7 % of head size CS.

(d) In contrast to members of the congeneric subgenera *Serviformica*, *Formica* s.str. and *Raptiformica* which show negative allometries in the indices CL/CW and SL/CW in all 50 tested species, *Coptoformica* species are nearly isometric or slightly positively allometric (Tab. 1, p. 215). The reasons for this peculiarity are explained below.

(e) Clypeal profile discontinuous: its caudal portion straight to slightly convex, changing into anterior portion with a break. Anterior portion often concave ("pressilabris" condition), sometimes straight, but never convex.

(f) The hull of nest mounds is constructed with finely cut pieces of herbs (preferentially grasses). This special behavior is also observed in *Formica suecica*, although this species uses this technology only under certain conditions.

Character combination (a) to (f) is not found in any other species of the tribe Formicini. The genus *Rossomyrmex* shows character (a) but has a very thick petiole scale and no prebasal mandibular denticles. Members of the Nearctic *Formica exsectoides* group occasionally show prebasal denticles, but have a weakly or not excavated occiput (0–3.5 % of CW), differ in clypeal shape, and do not show character (f). As result, all species of the subgenus *Coptoformica* form a well-circumscribed group of undoubtedly monophyletic origin which has already been suggested by Agosti (1989). This could justify elevating *Coptoformica* to genus rank. However, as the weight of pragmatic arguments in favor of this taxonomic act is not much larger than that of the counter-arguments, we do not change the traditional use.

The effective cutting of grasses and the painful biting of *Coptoformica* ants is known to every field observer and can be explained by an altered system of mandible and adductor muscle mechanics which is considered as autapomorphy (Dietrich 1998). This may be considered a special adaptation to nest construction and furthermore enables a very effective decapitation of enemy ants and powerful disintegration of food items as, e.g., large Lumbricidae. Dietrich compared mechanical parameters of the mandible adductor system in *Coptoformica exsecta* and *Formica pratensis*. An elongated lever between the mandibular condyles and the attachment point of the adductor muscle in combination with a shortened lever between the mandibular condyles and the effective biting point at basal masticatory border leads to a significantly increased biting power in *Coptoformica*. This is outstanding for ants of such moderate body size. This system, however, needs a longer adductor contraction length. The necessary elongation of the whole muscle has led to a posterior extension of occipital corners in *Coptoformica*. The consequence is an isometry of scape and head length indices. In contrast, in the subgenera *Serviformica*, *Formica* s. str. and *Raptiformica*, an increase of biting power is mainly generated by enlarging the cross-section area of the adductor muscle. This requires a disproportionate increase of head width with growing body size, leading to negative allometries in SL/CW and CL/CW.

All gynes of *Coptoformica* cannot found new nests independently in a claustral or semiclaustral way. The initial step of colonizing a new site is single queen (flight) dispersal with subsequent socially parasitic colony foundation in host species of the subgenus *Serviformica*. Except for *Formica* (*Coptoformica*) *forsslundi* that seems to have *Formica* (*Serviformica*) *picea* as exclusive host in all parts of its geographic range, distributional data demand that most *Coptoformica* species are not strictly host specific. Very little is known on behavior and conditions of socially parasitic colony foundation. Pisarski (1982) claimed that gynes of *Formica exsecta* can only perform colony foundation in queenless host colonies. A report of Kutter (1969), attributed by him without further explanations to *Formica* (*Coptoformica*) *pressilabris,* indicates one way of colony foundation: a mated dealate gyne went to a nest entrance of a *Serviformica* species, adopted a nymphal posture, and was carried by a host worker into the nest without being attacked or mutilated. It appears also likely that gynes may actively penetrate a host nest during cool morning hours when host worker aggression is low and could use the favorable situation to decapitate the host queen.

4.2 Comments on the taxonomic significance of character systems

Inspection of Tabs. 2–7 reveals which numerically described characters are important for species discrimination. Considering the thirteen characters thoroughly recorded in the workers and running all species and morphs in a single stepwise LDA, the ranking in falling order of importance appears as follows: ClySet, EyeHL, TERG, nCox, sqPDO, ClyPub, SL/CS, nHTfl, CL/CW, CS, nMet, nOce and sqPDG. This illustrates the dominance of setae and pubescence characters and the requirement of meticulously considering the conditions of their recording. Controversial opinions on the taxonomic value of pubescence characters of authors in the past (Dlussky 1967, Dlussky & Pisarski 1971, Collingwood 1979, Agosti 1989) are largely explained by their subjective mode of assessment (no recording and testing of data) and to a lesser extent by inadequate equipment. The data presented here prove that pubescence density on gaster tergites and in the ocellar triangle may have considerable discriminative power in particular species pairs. As general rule in *Coptoformica*, the number of pubescence hairs per unit square of body surface shows a strong negative correlation with the mean length of pubescence hairs whereas pubescence distance, as defined here, shows a weakly positive correlation (Seifert 2000). This is important in the context of frequently used key termini such as “distance between pubescence hairs smaller than their length”. Seifert (2000) further argued that the square-root-transformed data sqPDG and sqPDO have an improved discriminative power compared to simple pubescence density numbers. More difficult to assess is the overall value of characters which have been rarely or inconsistently recorded in this study (Fu2, Fu3, OceD, PeINC and T3f). A more general value of OceD is proven here whereas the other four characters appear to be of use in only few particular cases.

We comment in the following on characters that have been supposed by several authors in the past as diagnostic.

Clypeal depression. The intraspecific variation of the depth and shape of this structure is according to my (BS) subjective perception too large to have discriminative value but this needs to be tested by numeric description.

Maxillary and labial palps. These structures appear to be of low use for species discrimination. The basic palp formula in *Coptoformica* is 6,4. Due to fusion of terminal maxillary palp segments, this formula may vary intranidally: 6,4 – 5,4 in *F. bruni*, *F. forsslundi* and *F. pisarskii* or 6,4 – 5,4 – 4,4 in *F. foreli*. The intranidal variation in other species is not investigated. Similarly, maxillary palp length shows high intranidal variation and, without having tested this, we assume a low discriminative value. Another argument against using this character is the difficult or impossible examination in many mounted specimens.

Mesosomal shape. We agree with Agosti (1989) that intraspecific variation of mesosomal shape is much larger than interspecific differences. Kutter (1977) has used a ‘thoracic index’ (ML / mesosoma width before the tegulae) for species separation in gynes. Yet, this index is without taxonomic value. Our own investigations in several *Lasius* and *Formica* species have shown gyne mesosomal width to have much higher coefficients of variation than mesosomal length and other body measures. This could be the expression for selection to a functional polymorphism – i.e. wide-breasted gynes with strong wing muscles might perform a long-range flight while the narrow-breasted queens stay in the vicinity of their mother colonies. In *Coptoformica*, this gyne polymorphism might be a functional analogy to the well-known male size polymorphism. Wide- and narrow-breasted gynes are known in *F. foreli*, *F. bruni* and *F. forsslundi*.

Color. The workers of nearly all species show a very similar color pattern both in the mean situation and in variance. Similar to other *Formica* species (see Lange 1956, Dlussky 1967, Pisarski 1981; Seifert 1997, Seifert & Schultz 2009), the ratio of red vs. blackish pigmentation increases with growing body size (i.e. better larval nutrition) and growing xerothermy of the nest spot. Workers with the whole dorsum of head showing reddish pigmentation ("suecica condition") are known in nearly all species. Genetic factors are very likely to contribute to color variation. In gynes, color is useless for separation of just the most similar species. However, the gynes of *F. pressilabris*, *F. forsslundi*, *F. brunneonitida*, *F. caucasicola* spec. nov. and *F. suecica* differ from all other species by absence of any red pigmentation component. As the gynes of these five species also share a very low body size and very shining cuticular surfaces, they can probably be grouped into a species complex.

4.3 Key to the workers and gynes of the subgenus *Coptoformica*

This key may solve a big part of determination problems in a comparably simple way. Yet, the user should be aware that worker separation in species with longer eye setae (Tab. 2 and 5) is strongly complicated by intraspecific polymorphism in *Formica exsecta*. Notwithstanding strong regional differences in morph frequency, nests of *F. exsecta* may contain both pure samples of the three morphs as well as any thinkable mixture of them. The best determination results are undoubtedly achieved when users run their own discriminant functions by using the data of supplementary information SI1 as species standards. Saying this, we repeat the demand of meticulously considering the conditions for data recording in setae and pubescence characters. Overlooking basal residues of detached setae in ClySet or TERG, avoidance of intermediate scores for hairs which cannot be classified in clear Yes/No decisions, as well as using inadequate illumination and a low-resolution optics in sqPDO and sqPDG will lead to frequent misidentifications.

Workers

1a Palaearctic west of 88°E. **2**

1b Palaearctic east of 88°E. **13**

2a Use magnifications >= 120x: microsetae on eyes at least in a fraction of colony members clearly protruding above ommatidiae. Length of longest seta on eyes in the nest mean 8–34 µm. **3**

2b Use magnifications >= 120x: eyes completely hairless or with microsetae only slightly protruding above ommatidiae (Fig. 3). Length of longest seta on eyes in the nest mean < 8 µm. **8**

3a Middle Asian Mountains (Tian Shan, Tarbagatai, Dzungarian Alatau, Bogda Shan). **4**

3b Outside this area. **5**

4a Pubescence distance in ocellar triangle and on gaster tergites extremely low, frontal face of forecoxae with few setae, setae on rear margin of gaster tergites always beginning with the 1st tergite, clypeal setae usually in four levels present; means of 40 nest samples: sqPDO 4.07 ± 0.45, sqPDG 4.73 ± 0.53, nCox 4.13 ± 1.49, TERG 1.0 ± 0.0, ClySet 4.00 ± 0.64. .... ***mesasiatica***

4b Pubescence distance in ocellar triangle and on gaster tergites larger, frontal face of forecoxae with many setae, setae on rear margin of gaster tergites usually beginning with the 1st tergite, clypeal setae usually in four levels present; means of 137 nest samples with mainly Normal morph individuals: sqPDO 5.42 ± 0.83, sqPDG 6.95 ± 1.00, nCox 9.43 ± 2.64, TERG 1.03 ± 0.17, ClySet 3.99 ± 0.54. .... ***exscecta*, Normal morph**

4c Pubescence distance in ocellar triangle and on gaster tergites larger, frontal face of forecoxae with few setae, setae on rear margin of gaster tergites beginning with the 2nd tergite, clypeal setae usually only in two levels present; means of 61 nest samples with mainly Rubens morph individuals: sqPDO 6.75 ± 1.25, sqPDG 7.56 ± 1.06, nCox 3.68 ± 1.84, TERG 2.32 ± 0.84, ClySet 2.21 ± 0.37. .... ***exsecta*, Rubens morph**

5a Setae on rear margin of gaster tergites usually beginning with the 1st tergite (scrutinize areas near posterior segment borders!): nest means of TERG 1.03 ± 0.17. Clypeus usually from anterior margin to center with scattered setae: nest means of ClySet 3.99 ± 0.54. Frontal face of forecoxae usually with numerous semierect setae: nest means of nCox 9.43 ± 2.64. .... ***exsecta*, Normal morph**

5b Setae on rear margin usually absent from 1st tergite: nest means of TERG > 1.7. Clypeus usually only with setae on anterior margin and few setae set back a little: nest means of ClySet 1.0–2.7. Frontal face of forecoxae without or very few semierect setae: nest means of nCox < 3.8. .... **6**

6a Pubescence distance in ocellar triangle and on dorsal plane of 1st gaster tergite very low (consider the required investigation standard!), nest means of sqPDO < 5.0 and of sqPDG < 6.9. Setae on outer edge of flexor side of hind tibia sparse, usually restricted to the distal half: nest means of nHTfl < 5.5. Head often shorter: nest means of CL/CW 1.049 ± 0.011. Dry to fresh-dry grasslands from Spain to E Kazakhstan (86°E). North to south Sweden (56°N) .... ***bruni***

6b Pubescence distance in ocellar triangle and on dorsal plane of 1st gaster tergite high, nest means of sqPDO > 5.7 and of sqPDG > 6.9. Setae on outer edge of flexor side of hind tibia more numerous and usually distributed from apex to the beginning of the proximal third: nest means of nHTfl > 5.5. Head often longer, nest means of CL/CW 1.061 ± 0.015. .... **7**

7a Setae in ocellar triangle and on frontal area of 3rd gaster tergite nearly always absent, frontal face of forecoxae with occasional small setae; nest means: nOce 0.35 ± 0.42, T3f 0.16 ± 0.25, nCox 1.00 ± 0.68. With CS in mm and using nest sample means, discriminant 13.482*CS – 41.77*CL/CW +1.154*nOce +1.171*T3f + 0.45*sqPDG + 21.63 < 0 [error 0 % in 25 nest samples]. Subboreal and subalpine semidry to fresh-dry grassland. Finland and Caucasus. .... ***fennica***

7b Setae in ocellar triangle and on frontal area of 3rd gaster tergite often present, frontal face of forecoxae usually with few setae; nest means: nOce 1.39 ± 0.53, T3f 0.69 ± 0.36, nCox 3.7 ± 1.8. Discriminant > 0 [error 0 % in 59 nest samples]. .... ***exsecta*, Rubens morph**

8a Clypeal setae restricted to anterior margin, single additional setae set back a little may be present; nest means of ClySet 1.0–2.0 .... **9**

8b Setae present from anterior margin to caudal part of clypeus, ClySet always > 3. Frontal face of forecoxae with few semierect setae, nest means of nCox > 1.5. Head short, its sides and caudolateral corners more rounded (Fig. 23), nest means of CL/CW 0.979–1.047. Ocellar triangle and dorsum of 1st gaster tergite with very dense pubescence, nest means of sqPDO 4.1–4.6 and of sqPDG 4.8–5.6. Outer edge of flexor side of hind tibia with several setae, nest means of nHTfl 5.8–7.2. Fennoscandia and Alps (Ötztal). .... ***suecica***

9a Setae on rear margin of gaster tergites beginning much more frontal: nest means of TERG 1.14 ± 0.25 [1.0–1.67]. **10**

9b Setae on rear margin of gaster tergites beginning much more caudal: nest means of TERG 3.50 ± 0.49 [2.0–4.33]. **11**

10a Caucasian endemite. Scape short, setae in ocellar triangle and on frontal face of forecoxae nearly always absent, pubescence hairs protruding the anterolateral clypeal border by more than 10 µm nearly always absent; nest means: SL/CS 0.972 ± 0.12, nOce 0.20 ± 0.16, nCox 0.06 ± 0.08, ClyPub 0.10 ± 0.11. .... ***caucasicola***

10b Unknown from Caucasus. Scape longer, setae in ocellar triangle (Fig. 4) and on frontal face of forecoxae frequently present. Pubescence hairs protruding the anterolateral clypeal border by more than 10 µm often present; nest means: SL/CS 1.008 ± 0.14, nOce 1.56 ± 0.83, nCox 1.80 ± 1.25, ClyPub 1.91 ± 1.07. Boreal and subboreal, in Western Alps in submontane peat bogs. .... ***forsslundi***

11a Pubescence hairs protruding the clypeal border lateral of the level of tentorial pits by more than 10 µm usually absent, nest means of ClyPub 0–1.3. Standing setae restricted to anterior clypeal margin, single small setae set back from the margin in only 1 % of the individuals present. **12**

11b Pubescence hairs protruding the anterolateral clypeal border by more than 10 µm always present (Fig. 5), nest means of ClyPub 1.6–6.4. Clypeus frequently with single 2nd-level setae in addition to setae on anterior margin, nest means of ClySet 1.3–2.0. Pubescence distance in ocellar triangle and on dorsum of 1st gaster tergite very low; nest means sqPDO<5.0 µm and of sqPDG<6.9. From Spain to E Kazakhstan (86°E). North to south Sweden (56°N). ... ***bruni***

12a Pubescence distance in ocellar triangle small: nest means of sqPDO in 98 % of the cases < 5.2 (consider measuring conditions, incomplete visualization of pubescence hairs may cause confusion with *pressilabris*). With CS in mm, discriminant 4.089*CS – 17.87*SL/CS + 1.089*sqPDO + 0.503*sqPDG – 0.732*TERG +6.303 < 0 [error 4.4 % in 468 individuals and 1.5 % in 130 nest samples]. Submediterranean. Xerothermous grasslands. Westpalaearctic from N Iberia to SE Kazakhstan (85°E), north to S Scandinavia (56°N). .... ***foreli***

12b Pubescence distance in ocellar triangle large: nest means of sqPDO in 98 % of the cases > 5.2. Discriminant > 0 [error 4.6 % in 458 individuals and 0.9 % in 112 nest samples]. Westpalaearctic, from the Netherlands (6°E) and the W Alps east to W Siberia (61°E), in Fennoscandia north to 64°N. .... ***pressilabris***

13a Use magnifications >= 120x: microsetae on eyes at least in a fraction of colony members clearly protruding above ommatidiae. Longest hair on eyes in the nest mean > 13 µm. **14**

13b Use magnifications >= 120x: eyes completely hairless or with microsetae only slightly protruding above ommatidiae (Fig. 3). Longest hair on eyes in the nest mean < 13 µm. **18**

14a Pubescence distance in ocellar triangle and on gaster tergites extremely low (mean sqPDO and sqPDG < 4.2), setae beginning caudal of 1st gaster tergite (mean TERG always > 1.5) and restricted to anterior part of clypeus (mean ClySet < 2.5). Only Japan. .... ***fukaii***

14b Pubescence distance in ocellar triangle and on gaster tergites not extremely low (sqPDO and sqPDG usually > 4.2); if very low (*mesasiatica*), then setae always beginning on 1st gaster tergite (mean TERG always < 1.5) and clypeal setae also present caudal of the 2nd level (mean ClySet > 2.5). **15**

15a Pubescence distance on 1st gaster tergite low (nest means of sqPDG < 5.6), setae always beginning on 1st gaster tergite, frontal face of forecoxae with only few setae (mean nCox < 2.5). Isolated population in mountains of South Sichuan above 3500 m. .... ***mesasiatica***

15b Character combination in at least one character clearly differing. **16**

16a Setae in ocellar triangle frequently absent (nOce 0.42 ± 0.58), setae on rear margin of gaster tergites usually beginning with the 3rd tergite (TERG 2.91 ± 0.33), distance of lateral ocellae small (OceD/CS 0.167 ± 0.010), outer edge of hind tibia's flexor side with fewer setae (nHTfl 5.16 ± 1.07). Discriminant 44.87*OceD/CS–13.905*CL/CW+0.634*nOce–0.538*TERG–0.102*nCox+0.275*nHTfl +6.034 < 0 [error 0 % in 96 nest samples and 2.9 % in 315 individuals]. .... ***manchu***

16b Setae in ocellar triangle usually present (nOce 1.81 ± 0.73), setae on rear margin of gaster tergites usually beginning before 3rd tergite (TERG 1.55 ± 0.87), distance of lateral ocellae often larger (OceD/CS 0.185 ± 0.012), outer edge of hind tibia's flexor side with more numerous setae (nHTfl 8.56 ± 1.85). Discriminant 44.87*OceD/CS–13.905*CL/CW+0.634*nOce–0.538*TERG–0.102*nCox +0.275*nHTfl +6.034 > 0 [error 1.5 % in 198 nest samples and 7.0 % in 597 individuals] **17**

17a Head and scape elongated (CL/CW 1.076 ± 0.017, SL/CS 1.089 ± 0.20), depth of excision of petiole scale lower (PeINC/CS 3.0 ± 1.0 %). With CS and EyeHL in mm, discriminant 14.68*CL/CW+29.09*SL/CS–5.58*CS–0.252*ClySet+0.226*ClyPub–55*EyeHL–37.758 > 0 [error 0 % in 15 nest samples and 1.8 % in 55 individuals]. Not in Tibet. .... ***longiceps***

17b Head and scape less elongated (CL/CW 1.048 ± 0.021, SL/CS 1.030 ± 0.26), depth of excision of petiole scale larger (PeINC/CS 5.2 ± 1.6 %). Discriminant < 0 [error 1.6 % in 183 nest samples and 5.2 % in 541 individuals, the three misclassified samples belong to the Beishan morph] .... ***exsecta***

18a Head and scape more elongated (CL/CW 1.069 ± 0.018, SL/CS 1.044 ± 0.020), clypeal setae also found on posterior surface (ClySet 3.92 ± 0.67). Members of the Siberian population with single setae on promesonotum. Discriminant 11.155*CL/CW+15.323*SL/CS+1.392*ClySet–0.201*ClyPub +0.229*nOce –31.853 > 0 [error 0 % in 35 nest samples and 7.6 % in 92 individuals]. .... ***pisarskii***

18b Head and scape less elongated (CL/CW 1.050 ± 0.020, SL/CS 1.017 ± 0.022), clypeal setae only exceptionally found on posterior surface (ClySet 1.62 ± 0.64). Never with setae on promesonotum. Discriminant < 0 [error 0 % in 80 nest samples and 3.1 % in 255 individuals]. **19**

19a Pubescence hairs protruding the anterolateral clypeal border frequently present (ClyPub 1.87 ± 2.36), frontal face of forecoxae and area of ocellar triangle frequently with single setae (nCox 1.82 ± 1.39, nOce 1.48 ± 1.04). Discriminant 0.602*ClyPub +0.351*ClySet +0.24*nOce +0.579*nCox –18.088*SL/CS +16.84 > 0 [error 0 % in 39 nest samples, 14.3 % in 112 individuals]. .... ***forsslundi***

19b Pubescence hairs protruding the anterolateral clypeal border almost always absent (ClyPub 0.08 ± 0.39), frontal face of forecoxae and area of ocellar triangle frequently without setae (nCox 0.10 ± 0.36, nOce 0.28 ± 0.54). Discriminant < 0 [error 0 % in 41 nest samples and 2.8 % in 143 individuals]. .... ***brunneonitida***

Gynes

1a Palaearctic west of 88°E. **2**

1b Palaearctic east of 88°E. **10**

2a Large, CS >1535 µm. If CS 1470-1535 µm, then sqPDG > 7.0 .... **3**

2b Smaller, CS <1535 µm. **5**

3a Discriminant 13.171*CS–25.35*CL/CW +4.728 < 0 [error 0 % in 19 individuals]. Only Finland and Caucasus. .... ***fennica***

3b Discriminant >0 [error 0 % in 97 gynes]. **4**

4a Pubescence distance on 1st gaster tergite very low (sqPDG 4.48 ± 0.51), area in ocellar triangle always with setae (nOce 5.67 ± 2.11). Discriminant 0.639*sqPDG–0.678*nOce+0.163*nCox+0.130*nHTfl–12.028*ML/CS + 17.168 < 0 [error 0 % in 19 gynes]. Only Middle Asian mountains (Tian Shan, Tarbagatai, Dzungarian Alatau, Bogda Shan) .... ***mesasiatica***

4b Pubescence distance on 1st gaster tergite higher (sqPDG 6.97 ± 1.61), area in ocellar triangle always with fewer setae (nOce 2.02 ± 0.87). Discriminant > 0 [error 0 % in 78 gynes]. .... ***exsecta***

5a Clypeal setae present in four levels, ClySet 3.97 ± 0.26. Anterior face of forecoxae always with setae, nCox 5–10. Setae near posterior margin of gaster tergites always beginning on the 1st tergite. Pubescence distance in ocellar tringle and on gaster tergites very low, sqPDO 3.97 ± 0.29, sqPDG 4.75 ± 0.41. Fennoscandia and Alps (W Siberia?) .... ***suecica***

5b Character combination in at least one character strongly deviating. **6**

6a Pubescence protruding over lateral clypeus present, ClyPub 5.14 ± 1.18. All body surfaces with a dense pubescence bent up by 20–35°. Eyes hairy, EyeHL 16–34 µm. Pubescence in ocellar triangle and on dorsum of gaster extremely dense, sqPDO < 4.1, sqPDG < 5.4. Mesonotal setae always present. .... ***bruni***

6b Character combination strongly deviating. **7**

7a Setae near posterior margin of gaster tergites usually beginning on the 1st, rarely on the 2nd tergite, TERG 1.21 ± 0.41. .... **8**

7b Setae near posterior margin of gaster tergites almost always beginning after the 2nd tergite, TERG 4.24 ± 0.70.. .... **9**

8a Not in Caucasus. Scape longer, SL/CS 0.853 ± 0.023. Single setae in ocellar triangle and on anterior face of forecoxae frequently present, nOce 1.00 ± 0.71, nCox 1.88 ± 1.26. Pubescence protruding over lateral clypeus often present, ClyPub 1.59 ± 1.22. .... ***forsslundi***

8b Only Caucasus. Scape shorter. Setae in ocellar triangle and on anterior face of forecoxae always absent. Pubescence protruding over lateral clypeus absent. .... ***caucasicola***

9a Pubescence distance in ocellar triangle and on 1st gaster tergite high: sqPDO 4.5–7.8, sqPDG 5.5–8.6. Smaller: ML 1.843–2.192 mm. Scape shorter, SL/CL 0.822–0.892. Dorsal surface of head frequently strongly shining. Discriminant 20.72*CL–12.01*SL–11.70*ML+0.695*sqPDO +0.762*sqPDG+3.936 > 0 [error 0 % in 67 specimens] ... . ***pressilabris***

9b Pubescence in ocellar triangle and on 1st gaster tergite dense, sqPDO 3.4–4.8, sqPDG 4.5–6.7. Larger: ML 2.107–2.415 mm. Scape longer, SL/CL 0.857–0.962. Dorsal surface of head usually rather matt. Discriminant <0 [error 0 % in 70 specimens] .... ***foreli***

10a Large, CW > 1.52 mm. **11**

10b Smaller, CW < 1.52 mm. **14**

11a Pubescence distance extremely low, sqPDG <3.67, anterior face of forecoxae without setae. Setae near posterior margin of gaster tergites beginning at the 3rd tergite. Only Japan. .... ***fukaii***

11b Pubescence distance larger, sqPDG > 3.66, anterior face of forecoxae with few to many setae. Setae near posterior margin of gaster tergites beginning before the 2nd tergite; if beginning more caudal, then sqPDG > 5.7. .... **12**

12a Data predicted: pubescence distance on 1st gaster tergite low (nest means of sqPDG < 5), setae always beginning on 1st gaster tergite, frontal face of forecoxae with only few setae (mean nCox < 3.5). Setae in ocellar triangle always present. Isolated population in mountains of South Sichuan above 3500 m. .... ***mesasiatica***

12b Character combination in at least one character strongly deviating. **13**

13a Outer flexor margin of hind tibia with few setae, nHTfl 3.7 ± 1.2; setae in ocellar triangle nearly always absent, nOce 0.07 ± 0.24; distance between lateral ocellae small, OceD/CS 0.176 ± 0.009. With CS and EyeHL in mm, discriminant 0.385*nHTfl+0.908*nOce−12.102*CS−59*EyeHL +42.845*OceD/CS+0.492*sqPDG+8.584 < 0 [error 0 % in 21 gynes]. .... ***manchu***

13b Outer flexor margin of hind tibia with more setae, nHTfl 9.3 ± 2.2; setae in ocellar triangle frequently present, nOce 1.79 ± 0.94; distance between lateral ocellae larger, OceD/CS 0.196 ± 0.011. Discriminant > 0 [error 0 % in 50 gynes of all three morphs]. .... ***exsecta***

14a Scape much longer, SL > 1.28 mm. .... ***longiceps***

14b Scape much shorter, SL < 1.28 mm. **15**

15a Setae near posterior margin of gaster tergites usually beginning on the 1st, rarely on the 2nd tergite, TERG 1.15 ± 0.37. Anterior face of forecoxae frequently with few setae, nCox 1.94 ± 1.19. Single setae in ocellar triangle often present, nOce 1.19 ± 0.75. Setae on mesonotum frequently present. With MnHL in mm, discriminant 0.848*nOce+0.895*nCox+26*MnHL−0.549−0.735 > 0 [error 0 % in 26 gynes]. **16**

15b Setae near posterior margin almost always beginning after the 2nd tergite, TERG 3.68 ± 0.72. Anterior face of forecoxae always without setae, nCox 0.0 ± 0.0. Setae in ocellar triangle and on mesonotum almost always absent, nOce 0.05 ± 0.25. Discriminant < 0 [error 1.2 % in 80 gynes] **17**

16a Clypeal setae usually reaching caudad to the 3rd or 4th level, ClySet 3.5 ± 1.1. Pubescence distance in ocellar triangle and on gaster tergites very large, sqPDO 7.10 ± 0.56, sqPDG 8.29 ± 0.80. Discriminant 1.119*ClySet+3.843*SL/CS+0.833*sqPDO+1.049*sqPDG−19.886 > 0 [error 0 % in 5 gynes]. .... ***pisarskii***

16b Clypeal setae mainly restricted to the 1st and 2nd level, ClySet 1.83 ± 0.58. Pubescence distance in ocellar triangle and on gaster tergites lower, sqPDO 5.91 ± 0.40, sqPDG 6.72 ± 0.66. Discriminant < 0 [error 0 % in 21 gynes]. .... ***forsslundi***

17a Scape longer, SL/CS 0.871 ± 0.020; setae condition on hind tibia and gaster tergites less strongly reduced, nHTfl 2.97 ± 1.41, TERG 2.92 ± 0.95. With EyeHL in mm, discriminant 21.106*SL/CS +288*Eyehl+0.609*nHTfl−0.828*TERG−18.845 > 0 [error 7.7 % in 13 gynes]. .... ***brunneonitida***

17b Scape shorter, SL/CS 0.845 ± 0.020; setae condition on hind tibia and gaster tergites strongly reduced, nHTfl 1.31 ± 0.67, TERG 3.82 ± 0.57. Discriminant < 0 [error 0 % in 67 gynes]. Not known from east of 88°E but potentially occurring. .... ***pressilabris***

Fig. 3: Eye of a *Formica foreli* worker as example for strongly reduced hairiness. The shown microsetae are 3–5 µm long. – **Fig. 4**: Typical pubescence and setae condition in the ocellar triangle in the worker of *Formica forsslundi*. The position of the two setae indicates the surface spots which have to be scrutinized for basal pits of setae or basal remains of detached setae. – **Fig. 5**: Well-developed eye setae in a worker of *Formica* exsecta. The shown setae are 26-30 µm long. – **Fig. 6**: Typical clypeal setae and pubescence condition in a worker of *Formica bruni*. The shown setae are 26-30 µm long. – **Fig. 7**: Head of a gyne of the Rubens morph of *Formica exsecta*. – **Fig. 8**: Head of a *Formica mesasiatica* worker. – **Fig. 9**: Lateral aspect of a *Formica mesasiatica* worker. – **Fig. 10**: Head of a *Formica manchu* worker. – **Fig. 11**: Lateral aspect of a *Formica manchu* worker.

Fig. 12: Head of a *Formica longiceps* worker. – **Fig. 13**: Lateral aspect of a *Formica longiceps* worker. – **Fig. 14**: Head of a *Formica fennica* worker. – **Fig. 15**: Lateral aspect of a *Formica fennica* worker. – **Fig. 16**: Head of a *Formica fennica* gyne. – **Fig. 17**: Head of the *Formica forsslundi* neotype worker. – **Fig. 18**: Lateral aspect of the *Formica forsslundi* neotype worker.

Fig. 19: Head of the *Formica caucasicola* spec. nov. holotype worker. – **Fig. 20**: Lateral aspect of the *Formica caucasicola* spec. nov. holotype worker. – **Fig. 21**: Head of the *Formica pressilabris* worker; syntype of *F. rufomaculata* Ruzsky (CASENT0911092 in www.antweb.org, photo Zach Lieberman). – **Fig. 22**: Lateral aspect of the *Formica pressilabris* worker; syntype of *F. rufomaculata* Ruzsky (CASENT0911092 in www.antweb.org, photo Zach Lieberman). – **Fig. 23**: Head of the *Formica suecica* worker. – **Fig. 24**: Lateral aspect of the *Formica suecica* worker. – **Fig. 25**: Head of the *Formica pisarskii* worker. – **Fig. 26**: Lateral aspect of the *Formica pisarskii* worker.

4.4 Treatment by species

The reasons for identification of a taxon are given in square brackets after taxonomic name, author and year. Figures 27–40 are presented coherently after section 4.7 and Tables 1–7 coherently at the very end of this paper.

4.4.1 *Formica exsecta* Nylander, 1846

Formica exsecta Nylander, 1846 [type investigation]

This taxon has been described from Finland. Investigated were three syntype workers on one pin labelled “H: fors”, “W. Nyland.”, “Coll. Nyland.”, “Mus. Zool. H: fors Spec. typ. No. 5028 *Formica picea* Nyl” and a gyne with the same labels as the previous, but type No. 5029; depository FMNH Helsinki.

Formica exsectopressilabris Forel, 1874

Formica exsecta var. *exsectopressilabris* Forel, 1874 [type investigation]
This taxon has been described from Switzerland. Investigated were three gynes from Samedan, among these the lectotype (des. Agosti 1989) labelled “F. exsecto-pressilabris Samedan” [Forel’s handwriting], “Typus” [red printed label], “F. exsecto-pressilabris Forel”[Forel’s handwriting], “Lectotype” [round printed label], and “ANTWEB CASENT 0911090”; depository MHN Genève. These gynes fully match the characters of the hairy Normal morph of *F. exsecta*. Samedan is not explicitly given by Forel (1874) as finding place of this taxon. A worker labelled “Formica exsecta Nyl. v. exsecto-pressilabris For. Alpes vaudoises” [Forel’s handwriting], “Cotypus” [printed label] and “ANTWEB CASENT 0907600” also belongs to the hairy Normal morph of *F. exsecta* as concluded from inspection of the photos in www.antweb.org.

Formica rubens Forel, 1874

Formica exsecta var. *rubens* Forel 1874 [type investigation]
Forel reported as type locality “Bois de Fermant près d’Apples (Vaud)”. Investigated were 4 syntype workers labelled “v. rubens Forel”[Forel’s handwriting], “Typus” [printed red label], “exsecta (Nl) variér! (Forel) avec esclaves fusca V. Fermaur”; depository MHN Genève. All four specimens belong to the Rubens morph of *Formica exsecta* (see Table 2 in Seifert 2019c).

Formica etrusca Emery, 1909

Formica exsecta var. *etrusca* Emery 1909 [type investigation]
Emery reported as type localities “Im Apennin bei Praccia und in Abetone”. Investigated were 4 type workers from MCSN Genova labelled “exsecta var. etrusca”, “Praccia VII: 905”, “TYPUS”, “ANTWEB CASENT 0905703” and one type worker with the same locality label from NHM Basel. All five specimens belong to the Rubens morph of *Formica exsecta* (see Table 2 in Seifert 2019c).

Formica dalcqi Bondroit, 1918

Formica dalcqi Bondroit, 1918 [type investigation]
This taxon has been described from Mt. Canigou / E Pyrenees. Investigated were 6 syntype workers labelled “Canigou \ Formica dalcqi Type Bondr.” and “Canigou 10-1917 \ F. Dalcqi Type Bondr. “; depository MSNB Bruxelles. The specimens match the characters of the hairy Normal morph of *F. exsecta* (see Table 2 in Seifert 2019c).

Formica sudetica Scholz, 1924

Formica exsecta var. *sudetica* Scholz, 1924 [photo of type, description and zoogeography]
This taxon has been described from Silesia in former Prussia. Scholz reported as collecting data: „im Spätsommer 1923 am Nordrande der hohen Meese“. A specimen from ZIPAS Warszawa labelled “Jauernig 14.9.23”, “Inst. Zool. P.A.N Warszawa 68/60”, “exsecta v sudetica Scholz”, “ANTWEB CASENT 0917233” is in agreement with Scholz’ statements and can be considered as type material. Jauernig (50.39°N, 16.33°E) is now named Jawornica and belongs to Poland. The photos of the type specimen show presence of pubescence hairs surpassing anterior margin of lateral clypeus (ClyPub > 3), very high sqPDO, and a row of semierect setae extending from distal to proximal part of outer flexor margin of hind tibia (nHTfl > 7). Considering the three species potentially occurring in Silesia and the reported type of habitat, this character combination excludes both *Formica foreli* or *F. pressilabris* but clearly indicates *F. exsecta*. The low clypeal setae number, apparent absence of standing setae from 1st gaster tergite and the more developed reddish pigmentation suggest that it might belong to the Rubens morph.

Formica kontuniemii Betrem, 1954

Formica kontuniemii Betrem, 1954 [description and zoogeography]
This taxon has been described from Aksujärvi near Inari in North Finland (69.23°N, 26.89°E). There are only two European species potentially occurring so far north: *Formica exsecta* and *F. suecica*. Betrem reported many semierect hairs in the region of occipital corners, setae on eyes and “5–8 long hairs between spiracle and insertion of hind coxae” which is just the metapleural surface where nMet is counted. This makes clear that *F. kontuniemii* can only belong to more hairy specimens of the Normal morph of *F. exsecta*.

Formica nemoralis Dlussky, 1964

Formica nemoralis Dlussky 1964 [type investigation]
This taxon has been described from the Voronesh Nature reserve (51.809°N, 39.446°E). Investigated were six paratype workers from ZMLU Moskva labelled "Voron.Zap. 29.VIII.1962, Dlussky" [in Cyrillic], "29.8.221" and 3 paratype workers from ZM Petersburg labelled "Voron. Zap. 29.VIII.1962 Dlussky" [in Cyrillic], "Paratypus Formica nemoralis Dlussky". Eight specimens of this nest sample belong to the Rubens morph and one specimen to the Normal morph of *Formica exsecta* (see Table 2 in Seifert 2019c).

All material examined. Numeric phenotypical data were recorded in 255 samples (largely nest samples) with 711 workers and 109 gynes. For details see supplementary information SI1, SI2 and SI3. This material originated from Austria (15 samples), Bulgaria (5), China (9), Denmark (1), Finland (47), France (3), Germany (25), Italy (11), Kazakhstan (5), Mongolia (4), The Netherlands (1), Norway (19), Poland (4), Russia (43), Slovenia (2), Spain (2), Sweden (35), Switzerland (23) and Turkey (1).

Geographic range. Panpalaearctic, submeridional to boreal; from Iberia (7°W) and England/Scotland east to Kamchatka (159°E). An isolated population occurs in NE Tibet. In Europe and Asia Minor going south to 39°N, at this latitude occurring between 1100 and 2600 m. Absent from the driest areas of Pontic and Caspian steppe zones. In Fennoscandia going north to 71°N. The northern and southern distributional borders in Russia correspond to the minus 8°C winter isotherm of soil in 1 m depth and to the southern border of woodland steppe (Berman & al. 1987, Leirich 1989). The vertical distribution in the Austrian Alps is bimodal and corresponds to the frequency of suitable grassland habitats: within a total range of 300 to 2250 m, there is strong decline of abundance within 800 to 1200 m. In NE Tibet at 33.7°N ascending to 3700 m.

Diagnosis: --Worker (Tab. 2, key, Fig. 5; pictures CASENT0173161, CASENT0905703, CASENT0907600, CASENT0911089, CASENT0911091, CASENT0911158, CASENT0913659, CASENT0917233, CASENT10083193 in www.antweb.org): Extremely polymorphic, for detailed data of the Normal, Rubens and Beishan morphs see Tab. 2. Large species; mean and maximum CS over all social types and morphs 1392 and 1631 µm. Head moderately elongated, mean CL/CW over all morphs 1.049. Scape moderately long in the Normal and Rubens morph (SL/CS 1.024) but long in the Beishan morph (SL/CS 1.062). Dorsal excision of petiolar scale rather deep, mean PeINC/CS 5.21 %. Eyes with long, frequently curved or hook-shaped hairs (Fig. 5), mean EyeHL 28.0 µm. Standing setae on clypeus reaching caudad usually to the 3rd or 4th level but in the Rubens morph usually only to the 2nd level with mean ClySet 2.1. Pubescence hairs surpassing anterolateral clypeal margin always present, mean ClyPub 3.2. Region of occipital corners with semierect to subdecumbent pubescence, but in the Rubens morph usually appressed. Single setae in the area of the ocellar triangle almost always present, in the Rubens morph more frequently lacking. Frontal face of forecoxae with variable number of setae, many in the Normal (mean nCox 9.5) but fewer in the Rubens (mean nCox 3.6) and Beishan morph (mean nCox 4.0). Metapleural setae in the Normal morph often present but in the other morphs usually lacking. Setae on posterior margin of gaster tergites usually present on the 1st tergite but in the Rubens morph usually beginning on 2nd tergite. Outer edge of hind tibial flexor side conspicuously hairy, with two size classes of setae, and subdecumbent pubescence; 1st size class of setae with mean nHTfl over all morphs of 8.6. Pubescence distance in ocellar triangle and dorsum of 1st gaster tergite rather high, but on average smaller in the Normal morph. The Rubens morph shows more frequently than the other morphs a reduction of the dark patch on dorsal mesosoma with a more developed reddish color component on whole body.
-- Gyne (Tab. 5, Fig. 7; pictures CASENT0173162, CASENT0911090, CASENT0915632, CASENT1041355 in www.antweb.org): Extremely polymorphic, for detailed data of the Normal, Rubens and Beishan morphs see Tab. 5. Large species, mean and maximum CS over all morphs 1663 and 1791 µm. Head short, shortest in the Normal morph. Scape moderately long but very long in the Beishan morph. Eyes with long, frequently curved or hook-shaped hairs, mean EyeHL over all morphs 43 µm. Standing setae on clypeus reaching caudad usually to the 3rd or 4th level but in the Rubens morph usually only to the 2nd level with mean ClySet 2.1. Pubescence surpassing anterolateral clypeal margin always present, ClyPub 4.8. Single setae in the ocellar area always present in the Normal and Beishan morph but in 38 % of Rubens morph individuals absent. Setae on posterior margin of gaster tergites in the Normal and Beishan morph always present on the 1st tergite but in the Rubens morph usually beginning on 3rd tergite. Frontal face of forecoxae with variable number of setae, many in the Normal (mean nCox 12.7) and fewer in the Rubens (mean nCox 3.8) and Beishan morph (mean nCox 6.3). Setae on outer flexor edge of hind tibia numerous in the Normal (mean nHTfl 12.7) and fewer in the Rubens (mean nHTfl 8.2) and Beishan morph (mean nHTfl 8.3). Pubescence distance in ocellar triangle in the Normal and Beishan morph low (mean sqPDO 4.2) but larger in the Rubens morph (mean sqPDO 5.9).

Taxonomic comments and clustering results. *Formica exsecta* is extremely polymorphic within its Panpalaearctic range. The situation in Europe was reported by Seifert (2019c). In the whole Palaearctic, three morphs can be distinguished (Tab. 2): the Normal morph, the Rubens morph and the Beishan morph that was named after its first discovery in the Beishan National Park in Tibet. The Normal morph is a combination of shorter scape, big distance between lateral ocellae, presence of setae on first gaster tergite and larger seta counts on clypeus, coxae and metapleuron. The Rubens morph combines a shorter scape, big distance between lateral ocellae, absence of setae on first gaster tergite with small seta counts on clypeus, coxae and metapleuron. The Beishan morph is a combination of long scape, small distance between lateral ocellae, presence of setae on first gaster tergite and small seta counts on coxae and metapleuron. Considering 708 workers of the Normal, Rubens and Beishan morph and the characters SL/CS, OceD/CS, ClySet, EyeHL, sqPDO, TERG, nCox and nMet, subjective hypotheses on morph identity were formed and these hypotheses then corrected by a single run of a LDA. These corrected hypotheses, indicating the presence of 345 Normal, 253 Rubens and 110 Beishan morph individuals, were confirmed by a leaf-one-out cross-validation linear discriminant analysis in 98.2 % of 708 individuals (Fig. 27). With a mean sample size of only 3.05 workers per nest sample, as much as 19.5 % of all 231 nest samples were mixtures of different morphs. In detail, 10.0 % of all nest samples were mixtures of the Normal and Rubens morph, 4.8 % mixtures of the Rubens and Beishan morph, 3.0 % of the Normal and Beishan morph and 1.7 % contained all three morphs. There is a clear geographic structure of morph abundance. In NE Tibet, all 35 investigated workers of nine samples belonged to the Beishan morph. In the Palaearctic east of 86°E and excluding NE Tibet, 30.3 % of 132 investigated workers belonged to the Normal, 28.8 % to the Rubens and 40.9 % to the Beishan morph. Within 545 workers from the Palaearctic west of 86°E, 56.7 % were classified as Normal, 39.4 % as Rubens and 3.9 % as Beishan morphs. However, there was a strong bias in the West Palaearctic to investigate preferentially nest samples containing specimens of the Rubens morph. As a matter of fact, *Formica exsecta* samples with reduced setae conditions (suspicious during field sampling or during laboratory sorting to possibly represent *F. bruni*, *F. fennica* or *F. suecica*) were more frequently collected (and analyzed) than the much more frequent hairy samples which do not represent a determination problem. This distorts the estimates of phenotype frequencies in favor of the Rubens morph. An estimate of the real relation between Normal and Rubens morphs for the W Palaearctic should be about 85 : 15. The three morphs are apparently more strongly differentiated in gynes than in workers. A principle component analysis considering the characters CS, CL/CW, SL/CS, ML/CS, ClySet, ClyPub, EyeHL, nOce, OccHD, sqPDO, sqPDG, nCox, MnHL, nHTfl and TERG provides a full separation (Fig. 28).

Biology. See the condensed information in Seifert (2018).

4.4.2 *Formica mesasiatica* Dlussky, 1964

Formica mesasiatica Dlussky, 1964 [type investigation]

This taxon has been described from the Tian Shan. Investigated was a paratype gyne from MCZ Lausanne labelled “Zailijsk. Ala.Tau verkh. rM. Almaatin Y. Kostylev 18.VII.38”, “Formica mesasiatica Dlussky, 1964 paratype”. Furthermore were investigated three nest samples with nine workers from the holotype locality National Park Aksu-Dzabagly. The first sample is labelled “KAZ: 42.407°N, 70.581°E, NP Aksu-Dzabagly, 2000 m, holotype locality, R. Schultz 1998.08.01 - 027” and the other two samples with the same label text but field numbers “...-028” and “...-029”.

All material examined. Numeric phenotypical data were recorded in 51 (largely nest) samples with 109 workers and 19 gynes. For details see supplementary information SI1, SI2 and SI3). This material originated from China (9 samples), Kazakhstan (24) and Kyrghystan (18).

Geographic range. Probably continuously distributed from West Tian Shan (39°N, 68°E), over Central and East Tian Shan, the Dzungarian Alatau (45°N, 80°E), east to Bogda Shan Mountains (43°N, 89°E). In this area occurring between 1500 and 2800 m. The northernmost population occurs in the Tarbagatai Mountains (47°N, 82°E) within an altitudinal range of 1100 m to 2100 m. A very isolated population, 1900 km southeast from the Bogda Shan population, was discovered in the mountains of South Sichuan (29°N, 100°E) where it occurs at altitudes between 3800 and 4200 m.

Diagnosis: --Worker (Tabs. 1, 3, key, Figs 8–9; pictures CASENT0903275 in www.antweb.org): Rather monomorphic throughout its range. Largest species of the subgenus; mean and maximum CS over all social types 1425 and 1631 µm. Head moderately elongated, mean CL/CW 1.046. Scape rather long, mean SL/CS 1.046. Dorsal excision of petiolar scale rather deep, mean PeINC/CS 4.9 %. Eyes with long, frequently curved hairs, mean EyeHL 30.0 µm. Standing setae on clypeus reaching caudad usually to the 3rd or 4th level, mean ClySet 3.9. Pubescence surpassing anterolateral clypeal margin usually present, mean ClyPub 2.6. Single setae in the area of the ocellar triangle present, mean nOce 1.8. Frontal face of forecoxae with fewer setae than in the Normal morph of *F. exsecta*, mean nCox 4.0. Few metapleural setae often present, mean nMet 2.0. Setae on posterior margin of gaster tergites always beginning at the 1st tergite. Outer edge of hind tibial flexor side conspicuously hairy, with two size classes of setae and subdecumbent pubescence, 1st size class of setae with mean nHTfl of 7.6. Pubescence distance in ocellar triangle and dorsum of 1st gaster tergite much lower than in any morph of *F. exsecta*, mean sqPDO 4.24, mean sqPDG 4.75. The isolated population from South

Sichuan differs from the Middle Asian population in having a smaller OceD and nCox (Tab. 4) but cannot be clustered separately considering a wider character set.

-- Gyne (Tab. 5; pictures CASENT0907591 in www.antweb.org): Monomorphic. Largest size within the subgenus, mean and maximum CS 1722 and 1818 µm. Head short, mean CL/CW 0.968. Scape rather long, mean SL/CS 0.958. Eyes with long, frequently curved or hook-shaped hairs, mean EyeHL 48 µm. Standing setae on clypeus usually in four levels present, mean ClySet 4.0. Pubescence surpassing anterolateral clypeal margin always present, mean ClyPub 6.9. Single setae in the ocellar area always present. Setae on posterior margin of gaster tergites always beginning at the 1st tergite. Frontal face of forecoxae and outer flexor edge of hind tibia with a more moderate number of setae, mean nCox 7.7, mean nHTfl 9.0. Pubescence distance in ocellar triangle and on dorsum of 1st gaster tergite significantly lower than in any morph of *Formica exsecta,* mean sqPDO 3.49, mean sqPDG 4.48. Brilliance of dorsal head surface low, microsculptured surfaces dominate, mean GLANZ 1.4. Gynes from the isolated population in high mountains of Sichuan are unknown. Considering the known differences between workers of the Middle Asian and Sichuan populations and adding these to the data of Middle Asian gynes, the unknown Sichuan gynes are predicted to have the following means: CS 1700 µm, CL/CW 0.950, SL/CS 0.958, OceD/CS 0.185, ClySet 3.3, OceSet 1.0, EyeHL 48 µm, TERG 1, nCox 2.5, nHTfl 8.9, sqPDO 3.8, and sqPDG 4.4.

Taxonomic comments and clustering results. *Formica mesasiatica* differs from the Beishan morph of *F. exsecta* by significantly lower pubescence distance on 1st gaster tergite and in ocellar triangle and by a higher distance between lateral ocellae. A linear discriminant analysis considering 109 workers of *F. mesasiatica* and 110 workers of the Beishan morph and the characters CS, CL/CW, SL/CS, OceD /CS, ClySet, ClyPub, nOce, nCox, nMet, TERG, nHTfl, sqPDO and sqPDG classified 99.1 % of individuals correctly. Likewise, *Formica mesasiatica* is well separable from the Rubens morph of *F. exsecta* by having setae on the posterior margin of the 1st gaster tergite and on whole clypeal surface and by much lower pubescence distance on 1st gaster tergite and in ocellar triangle. A linear discriminant analysis considering 253 workers of the Rubens morph, 109 workers of *F. mesasiatica* and the same characters as above classified 97.8 % of individuals correctly. The separation of *F. mesasiatica* from the Normal morph of *F. exsecta* is less clear. Running a LDA considering the same character set, the same *F. mesasiatica* sample and 345 workers of the Normal morph, only 94.7 % of the 454 individuals are classified correctly. In order to check heterospecificity, 43 nest samples of *F. mesasiatica* with 109 workers and 131 nest samples with 357 workers of *F. exsecta* from the whole Palaearctic were run in exploratory data analyses. The selection of the 131 *F. exsecta* samples followed the condition that the intranidal phenotype composition was dominated by Normal morph workers (with Hyp = "exse" and "exse+" in SI2). Considering the characters CL/CW, SL/CS, ClySet, ClyPub, nOce, EyeHL, sqPDO, sqPDG, TERG, nCox, nMet and OceD, the classification error in 174 nest samples was 1.7 % in NC-Ward and NC-part.kmeans, 1.2 % (plus 1.2 % outliers) in NC-part.hclust and 3.4 % in nest means of PCA scores (Fig. 29). This error is small enough to consider *F. mesasiatica* as separate species. The gynes of *F. mesasiatica* and of the Normal morph of *F. exsecta* are fully separable by a principle component analysis considering the characters CL/CW, SL/CS, ML/CS, sqPDO, sqPDG, nCox and nHTfl (Fig. 30). Attention has to be paid to the situation in the northern population of *F. mesasiatica* in the Tarbagatai Mountains which is the only place where it is in direct contact with *F. exsecta*. Here hybridization and introgression appears likely. The observation of flying gynes of *F. mesasiatica* and *F. exsecta* simultaneously assembling at the top of Peak Sarymobe 5 August 2001 indicates that temporal and spatial mating segregation has not been developed in the contact zone.

Biology. The species is found in steppe-like or semidry grasslands and woodland clearings. The highest densities were found in grasslands with shrub. Monodomous isolated nests as well as polydomous colonies were observed. Nuptial flights are delayed with growing elevation and were observed in Middle Asia between 29 June and 8 August.

4.4.3 *Formica fukaii* Wheeler, 1914

Formica exsecta var. *fukaii* Wheeler, 1914 [type investigation]

This taxon has been described from Saitama prefecture in Japan in four workers collected by T. Fukai. Investigated were four syntype workers from MCZ Cambridge labelled "Saitama, Japan, Formica exsecta var. fukai Syntypes, MCZ Cotype 23247".

All material examined. Numeric phenotypical data were recorded in 5 samples with 13 workers from Japan. For details see supplementary information SI1, and SI2.

Geographic range. Restricted to Japan from SW Honshu (35°N, 134°E) to N Hokkaido (45°N, 142°E). Data on altitudinal distribution are sparse. The investigated material was found from sea level up to 1000 m but occurrence at higher elevations is most probable.

Diagnosis: --Worker (Tab. 4; pictures CASENT0906310 in www.antweb.org): Large species; mean and maximum CS 1448 and 1517 µm. Head much elongated, mean

CL/CW 1.064. Scape long, mean SL/CS 1.069. Eyes with rather long hairs, mean EyeHL 28.3 µm. Standing setae on clypeus reaching caudad usually only to 2nd level with mean ClySet 2.1. Few pubescence hairs surpassing anterolateral clypeal margin present. Region of occipital corners with appressed pubescence. Setae in the area of the ocellar triangle reduced, mean nOce 0.9. Frontal face of forecoxae usually without setae, mean nCox 0.1. Metapleural setae always absent. Setae on posterior margin of gaster tergites beginning on 2nd or 3rd tergite, mean TERG 2.7. Outer edge of hind tibial flexor side moderately hairy, mean nHTfl 5.6. Pubescence distance in ocellar triangle and dorsum of 1st gaster tergite extremely low, mean sqPDO 3.74, mean sqPDG 3.95.

-- Gyne (Tab. 5): Description based on a single specimen. Large, CS 1690 µm. Head moderately long, CL/CW 0.979. Scape moderately long, SL/CS 0.958. Eyes with long hairs, EyeHL 46 µm. Region of occipital corners with short decumbent hairs. Setae on promesonotum absent. Setae on posterior margin of gaster tergites beginning on 3rd tergite. Frontal face of forecoxae without setae. Setae on outer flexor edge of hind tibia moderately numerous, nHTfl 7.0. Pubescence distance in ocellar triangle very low (sqPDO 3.11) and on dorsum of 1st gaster tergite extremely low, lower than in any other species (sqPDG 3.23).

Taxonomic comments and clustering results. *Formica fukaii* is an endemic Japanese species and well separable from any species of the subgenus by a combination of large size, extremely dense pubescence on 1st gaster tergite and in ocellar triangle, absence of setae from frontal face of forecoxae and from the first two gaster tergites. The most similar species is *F. mesasiatica* but a full separation is already possible on the individual level by a principal component analysis considering the characters CS, CL/CW, SL/CS, EyeHL, ClySet, nOce, nCox, nMet, TERG, nHTfl, sqPDO and sqPDG.

The 1st principal component is −2.501 ± 0.403 [−2.982, −1.681] in 12 workers of *F. fukaii* and 0.275 ± 0.568 [−1.286, 1.352] in 109 workers of *F. mesasiatica*.

Biology. There is no qualified information available other than that it builds mounds of grass particles and attends aphids and scale insects.

4.4.4 *Formica manchu* Wheeler, 1929

Formica exsecta manchu Wheeler, 1929 [type investigation]

This taxon has been described from Boketu, Manchuria / China. Investigated were three syntype workers on the same pin labeled “Boketu, Manchuria 7. 5. 26”, “M.C.Z. coType 7-10” plus three syntype workers on another pin labeled “Boketu, Manchuria 7. 5. 26”, “M.C.Z. coType 4-6”; depository MCZ Cambridge.

Formica beijingensis Wu, 1990

Formica beijingensis Wu, 1990 [type investigation]
This taxon has been described from Mount Beihua near Beijing / China. Investigated was one paratype worker from the holotype nest with a Chinese locality label “Beihua Shan, Beijing, 1987.X.14 Wang Chang Lu”, „Formica beijingensis Wu“, „PARATYPE“; depository RIFCAF Beijing. Synonym of *F. manchu* (see below).

All material examined. Numeric phenotypical data were recorded in 97 samples (largely nest samples) with 318 workers and 21 gynes. For details see supplementary information SI1, SI2 and SI3. This material originated from China (32 samples), Mongolia (30) and Russia (35).

Geographic range. Continuous range from 92°E in W Mongolia to 131°E in Russian Primorye. The northern range border runs along 53.6°N in the Irkutsk Region and 51.5°N at the middle reaches of Amur River. In China distributed from NE Tibet (Province Qinghai) over Gansu, Manchuria east to the Ussuri River. It ascends to 2300 m at 48.3°N in Mongolia and to 3520 m at 35°N in NE Tibet. The finding on the island of Sakhalin (51.81°N, 143.16°E) represents the easternmost known site.

Diagnosis: --Worker (Tab. 2, Figs 10–11; pictures CASENT0906310 in www.antweb.org): Rather large species; mean and maximum CS over all social types 1358 and 1575 µm. Head distinctly elongated, mean CL/CW 1.075. Scape moderately long, mean SL/CS 1.040. Distance between lateral ocellae smaller than in other species, mean OceD/CS 0.167. Dorsal excision of petiolar scale rather deep, mean PeINC/CS 5.34 %. Eyes with long hairs, mean EyeHL 30.7 µm. Standing setae on clypeus reaching caudad usually only to the 1st or 2nd level, mean ClySet 1.9. Pubescence surpassing anterolateral clypeal margin always present, mean ClyPub 3.1. Region of occipital corners with appressed to decumbent hairs. Setae in the area of the ocellar triangle usually absent or rudimentary, mean nOce 0.42. Frontal face of forecoxae without or with very few setae, mean nCox 1.7. Metapleural setae absent, mean nMet 0.04. Setae on posterior margin of gaster tergites always absent from the 1st and usually absent from the 2nd tergite, mean TERG 2.91. Outer edge of hind tibial flexor side weakly hairy, mean nHTfl 5.2. Pubescence distance in ocellar triangle and dorsum of 1st gaster tergite high, mean sqPDO 6.56, mean sqPDG 7.35.

-- Gyne (Tab. 5): Large species, mean and maximum CS 1635 and 1691 µm. Head rather long, CL/CW 1.002. Scape short, SL/CS 0.911. Distance between lateral ocellae smaller than in other species, mean OceD/CS 0.176. Eyes with very long setae, mean EyeHL 51 µm. Standing setae on clypeus usually only in the two frontal levels present, mean ClySet 1.95. Pubescence surpassing anterolateral clypeal margin always present, ClyPub 5.9. Setae in the ocellar area almost always absent, mean OceSet 0.05. Setae on posterior margin of gaster tergites always absent from the 1st tergite, mean TERG 2.8. Frontal face of forecoxae with few setae, mean nCox 3.2. Setae on outer flexor edge of hind tibia very few, mean nHTfl 3.7. Pubescence distance in ocellar triangle and on dorsum of 1st gaster tergite moderately large, mean sqPDO 4.67, mean sqPDG 6.21.

Taxonomic comments and clustering results. *Formica manchu* may be confused with the Rubens morph of *F. exsecta* and with *F. longiceps* but the separation by exploratory and hypothesis-driven data analyses is very clear. Ninety seven nest samples of *F. manchu* with 315 worker individuals were compared with those 60 nest samples with 227 workers of *F. exsecta* containing a large percentage of Rubens morph individuals (labelled "rube" and "rube+" in supplementary information SI2). Considering the 14 characters CS, CL/CW, SL/CS, ClySet, ClyPub, nOce, OceD/CS, EyeHL, sqPDO, sqPDG, TERG, nCox, nHTfl and nMet, classification errors of exploratory data analyses on the nest sample level were 2.6 % in NC-Ward, 0 % in NC-part.kmeans, 1.3 % (plus 1.3 % outliers) in NC-part.hclust, 0 % in NC-NMDS.kmeans and 0 % in a principle component analysis. This is a mean error of 1.05 % in these five exploratory data analyses. The classification error by a LDA on the individual level was 1.8 % in 542 workers. The posterior probabilities of type samples for allocation to *F. manchu* were 1.0000 in the type series of *F. manchu*, 0.9996 in the type specimen of *F. beijingensis*, 0.0017 in the type series of *F. rubens*, 0.0013 in the type series of *F. etrusca* and 0.0005 in the type series of *F. nemoralis*. Reduction to the 10 characters CL/CW, SL/CS, nOce, OceD/CS, EyeHL, sqPDO, sqPDG, TERG, nCox, and nHTfl reduced the mean error of the five EDAs on the nest sample level to 0.76 % within 157 nest samples (Fig. 31). The separation of the gynes is fully possible by an LDA or PCA considering the characters CL/CW, EyeHL, OceD/CS, sqPDG and nHTfl: the 1st component of the PCA is −1.05 ± 0.40 [−4.09, −1.19] in 21 gynes of *Formica manchu* and 0.79 ± 0.40 [0.52, 4.00] in 28 gynes of the Rubens morph of *F. exsecta*.

A principal component analysis of the 12 characters CS, SL/CS, ClySet, ClyPub, nOce, OceD/CS, EyeHL, TERG, nHTfl, Fu2/CS, Fu3/CS and Fu2/Fu3 allows also a clear separation of 94 nest samples of *Formica manchu* and 15 nest samples of *F. longiceps* workers (Fig. 32). Using the same characters in a LDA, 98.6 % of 365 individual workers were correctly classified and the posterior probabilities for allocation to *F. manchu* were 1.000 in the type series of *F. manchu*, 1.000 in the paratype specimen of *F. beijingensis* and 0.021 in a paratype worker from the holotype series of *F. longiceps*. Only four gynes of *F. longiceps* were available but it seems that they can be clearly distinguished from *F. manchu* gynes alone by absolute size, scape length and relative length of funiculus segments (Tab. 5). Considering CS, CL/CW, SL/CS, Fu2/Fu3, OceD/CS, ML/CS, MnHL, nCox and nHTfl, the 1st principal component was −2.15 ± 0.43 [−2.48, −1.55] in four gynes of *F. longiceps* and 0.41 ± 0.27 [−0.19, 0.87] in 21 gynes of *F. manchu*.

Biology. In Siberia and Tibet it is one of the most abundant *Coptoformica* species with a rather wide habitat spectrum. It is mainly found in grassy open habitats, both natural or grazed, fully open or with shrubs, from xerothermous to rather moist conditions. In Siberia it frequently occupies clearings or margins of the *Larix* Taiga. It forms both monodomous and polydomous colonies. Alates were observed from 26 June to 21 August.

4.4.5 *Formica longiceps* Dlussky, 1964

Formica longiceps Dlussky, 1964 [type investigation]

This taxon has been described from Lake Bouse near Kansk / Russia (appr. 56.20°N, 95.72°E). Investigated was the holotype gyne labelled "Bous'e oz.2 Epshe. gub.VI 02. A. Kozhev" [in Cyrillic], "Holotypus Formica longiceps Dlussky" [red label] and one paratype worker labelled "Bous'e oz.6 Epshe. gub. VI 02 A. Koshev" [in Cyrillic], "Ergatotype F. longiceps Dlussky"; depository ZM St. Petersburg.

Formica dlusskyi Bolton, 1995

This name was proposed as replacement name for *Formica longiceps* Dlussky, 1964 which is a junior primary homonym of *Formica longiceps* Smith, 1863. As *F. longiceps* Smith is in *Camponotus* Mayr, 1861 since 1863 and is in no danger to return to *Formica*, there is according to article 23.9.5. of ICZN no need for a replacement name.

All material examined. Numeric phenotypical data were recorded in 18 samples (largely nest samples) with 55 workers and 4 gynes. For details see supplementary information SI1, SI2 and SI3. This material originated from Mongolia (3 samples) and Russia (15).

Geographic range. Siberian. Known range between 45.9 to 56.2°N and 95.7 to 115.7°E. In Mongolia at 45.9°N ascending to 2000 m.

Diagnosis: --Worker (Tab. 2, Figs 12–13): Rather small; mean and maximum CS 1290 and 1430 µm. Head distinctly elongated, mean CL/CW 1.076. Scape very long, mean SL/CS 1.076. 2nd funiculus segment significantly shorter than 3rd, mean Fu2/Fu3 0.925. Dorsal excision of petiolar scale weak, mean PeINC /CS 3.04 %. Eyes with moderately long hairs, mean EyeHL 23 µm. Standing setae on clypeus reaching caudad usually to the 2nd or 3rd level, ClySet 2.6. Pubescence surpassing anterolateral clypeal margin always present, mean

ClyPub 3.7. Region of occipital corners with appressed to decumbent hairs. Setae in the area of the ocellar triangle often present, mean nOce 1.7. Frontal face of forecoxae often with few setae, mean nCox 2.6. Metapleural setae absent, mean nMet 0.03. Setae on posterior margin of gaster tergites usually beginning with the 1st and 2nd tergite, mean TERG 1.68. Setae on anterior area of 3rd tergite in 98 % of individuals present. Outer edge of hind tibial flexor with rather many setae, mean nHTfl 7.4. Pubescence distance in ocellar triangle and dorsum of 1st gaster tergite high, mean sqPDO 7.06, mean sqPDG 7.35.

-- Gyne (Tab. 5): medium-sized to small, mean and maximum CS 1462 and 1469 µm. Head very long, CL/CW 1.033, Scape long, SL/CS 0.967. 2nd funiculus segment much shorter than 3rd, mean Fu2/Fu3 0.876. Eyes with very long setae, mean EyeHL 48 µm. Standing setae on clypeus reaching caudad usually to the 1st or 2nd level, mean ClySet 1.75. Pubescence surpassing anterolateral clypeal margin always present, ClyPub 5.4. Setae in the ocellar area may be present, mean OceSet 0.5. Region of occipital corners with decumbent to subdecumbent hairs. Setae on posterior margin of gaster tergites beginning with the 2nd or 3rd tergite, mean TERG 2.5. Frontal face of forecoxae without or occasional with setae, mean nCox 0.7. Setae on outer flexor edge of hind tibia few, mean nHTfl 4.8. Pubescence distance in ocellar triangle and on dorsum of 1st gaster tergite moderately large, mean sqPDO 5.04, mean sqPDG 6.62.

Taxonomic comments and clustering results. The clear separation of workers and gynes from *Formica manchu* has been shown in section 4.4.4 but *F. longiceps* can also be confused in the worker caste with *F. fennica*. Considering the 10 characters CS, SL/CS, Fu2/CS, Fu3, Fu2/Fu3, ClyPub, nOce, EyeHL, TERG and T3f, all five exploratory data analyses showed consistent, errorless classifications on the nest sample level and the overall classification error by the LDA was 0.7 % in 146 worker individuals of both species. The posterior probabilities for allocation to *F. longiceps* were 1.000 in the paratype worker from the holotype nest of *F. longiceps* and 0.000 in the paratype workers from the holotype nest of *F. fennica* if run as wild-cards. Excluding the most discriminative and discrete character T3f, which is sometimes difficult to evaluate, did not change the situation. The four available gynes of *F. longiceps* are a unique combination of large CL/CW and SL/CS and very low Fu2/Fu3 and nCox and cannot be confused with any species.

Biology. It is the rarest of the Siberian species. Nearly all nests were found in open steppe habitats and only once in a moister grassland. Alates were observed between 20 July and 2 August.

4.4.6 *Formica fennica* Seifert, 2000

Formica fennica Seifert, 2000 [type investigation]

This taxon has been described from Finland. Investigated were all type specimens mentioned by Seifert (2000). Among this material were the holotype gyne and 6 paratype workers labelled "FIN: 62.07N, 29.48E, road No. 71, Kitee-17W, Puhos-6.5WNW, leg. Seifert 1996.07.13-119" and one paratype gyne plus 11 workers from the same polycalic colony but two remote nests with the codes "1996.07.13-86" and "1996.07.13-105"; depository SMN Görlitz.

All material examined. Numeric phenotypical data were recorded in 25 nest samples with 91 workers and 19 gynes. For details see supplementary information SI1, SI2 and SI3. This material originated from Azerbaijdzan (1 sample), Finland (23 samples) and Georgia (1).

Geographic range. Westpalaearctic with apparently two rather small, disjunct ranges. The Fennoscandian population is confirmed for only four sites in Finland – all are situated in a small south boreal zone between 61 and 64.4°N, 10.6 and 29.8°E, 45 and 130 m altitude. The Caucasian population is known from only two sites in the subalpine zone of Georgia and Azerbaijan between 41.6 and 42.7°N, 45.7 and 47.1°E, 1600 and 1700 m altitude. This distribution suggests a common Pleistocene refuge of both populations in the Ponto-Caspian region.

Diagnosis: --Worker (Tab. 2, Figs 14–15): rather small; mean and maximum CS 1271 and 1468 µm. Head distinctly elongated, mean CL/CW 1.072. Scape moderately long, mean SL/CS 1.022. 2nd funiculus segment only slightly shorter than 3rd, mean Fu2/Fu3 0.988. Dorsal excision of petiolar scale moderately deep, mean PeINC/CS 3.62 %. Eyes with moderately long hairs, mean EyeHL 25 µm. Standing setae on clypeus usually reaching caudad only to the 1st and 2nd level, ClySet 1.8. Pubescence surpassing anterolateral clypeal margin weak, mean ClyPub 2.0. Region of occipital corners with appressed hairs. Setae in the area of the ocellar triangle often absent, mean nOce 0.38. Frontal face of forecoxae only with occasional weak setae, mean nCox 1.05. Metapleural setae absent, mean nMet 0.03. Setae on posterior margin of gaster tergites usually beginning with the 3rd or 4th tergite, mean TERG 3.38. Setae on anterior area of 3rd tergite in 82 % of individuals absent. Outer edge of hind tibial flexor with rather many setae, mean nHTfl 6.8. Pubescence distance in ocellar triangle and dorsum of 1st gaster tergite high, mean sqPDO 6.83, mean sqPDG 7.62.

-- Gyne (Tab. 5, Fig. 16): medium-sized, mean and maximum CS 1538 and 1593 µm. Head rather long, CL/CW 1.019, Scape moderately long, SL/CS 0.932.

2nd funiculus segment as long as 3rd, mean Fu2/Fu3 1.000. Eyes with moderately long setae, mean EyeHL 31 µm. Standing setae on clypeus usually reaching caudad to only the 2nd level, mean ClySet 1.70. Pubescence surpassing anterolateral clypeal margin sparse, ClyPub 3.3. Setae in the ocellar area in 47 % of the individuals present. Region of occipital corners with decumbent hairs. Setae on posterior margin of gaster tergites usually beginning with the 4th tergite, mean TERG 3.65. Frontal face of forecoxae without or with very few setae, mean nCox 2.2. Setae on outer flexor edge of hind tibia rather many, mean nHTfl 7.1. Pubescence distance in ocellar triangle and on dorsum of 1st gaster tergite very high, mean sqPDO 7.12, mean sqPDG 9.00.

Taxonomic comments and clustering results. The clear separation of workers and gynes of *Formica fennica* from *F. longiceps* has been reported in section 4.4.5. The most similar ant occurring within the Westpalaearctic range of *F. fennica* is the Rubens morph of *F. exsecta*. Seifert (2019c) demonstrated a clear separation of the two entities for material from Europe. With material from the whole Palaearctic range that included workers of 25 nest samples of *F. fennica* and 59 nest samples of the Rubens morph, the clustering in a PCA considering the 9 characters CS, CL/CW, OceD/CS, ClyPub, nOce, sqPDG, TERG, nCox and T3f is similarly clear (Fig. 33). The mean classification error of the four variants of NC-clustering was 1.8 % in 84 nest samples. One gyne sample (SaNo 804, FIN:Puhos-6.8WNW,20190519-1) suggests introgression of *exsecta* genes. This case should be re-investigated using indicative nuDNA markers. Workers of *F. fennica* are safely separable from *F. bruni* on the individual level. Using the characters CS, CL/CW, SL/CS, EyeHL, ClySet, nOce, nCox, TERG, nHTfl, sqPDO and sqPDG, all 267 workers of both species are classified by a LDA correctly.

Biology. See the condensed information in Seifert (2018).

4.4.7 *Formica bruni* Kutter, 1967

Formica bruni Kutter, 1967 [type investigation]

This taxon has been described from Switzerland. Investigated were the holotype gyne labelled “Coptoformica bruni n. sp. Typus”, “Zermatt VII-61 leg. Leutert” “Typus”, “172”; three paratype gynes and three paratype workers from the holotype series with a corresponding labeling; one paratype gyne plus three paratype workers labelled “F. (C.) bruni K. det. Kutter”, “Zermatt Trift 6.VIII 19”, “Cotypus”; depository MCZ Lausanne.

All material examined. Numeric phenotypical data were recorded in 64 nest samples with 176 workers and 18 gynes. For details see supplementary information SI1, SI2 and SI3. This material originated from Austria (9 samples), France (5), Germany (4), Kazakhstan (4), Montenegro (1), Serbia (2), Spain (1), Sweden (8), Switzerland (29) and Ukraine (1).

Geographic range. The distribution is poorly known and the abundance is underestimated due to frequent confusion with *F. foreli*, *F. pressilabris* and *F. fennica* before the species delimitation had been clarified by Seifert (2000). Westpalaearctic, submeridional to south temperate, planar to montane. From N Spain (5°W) to SE Kazakhstan (85°E). In Europe north to S Sweden (56°N) and in the Balkans south to 42°N. The altitudinal range in the Alps is bimodal and follows the distribution of grassland biomes: colline-submontane 708 ± 289 [370, 1240] m (n=13) and montane-subalpine 1661 ± 234 [1380, 2150] m (n=21).

Diagnosis: --Worker (Tab. 2; Fig. 6; pictures CASENT-0906305, CASENT0912242 in www.antweb.org): rather small; mean and maximum CS 1275 and 1450 µm. Head relatively short, mean CL/CW 1.047. Scape moderately long, mean SL/CS 1.038. 2nd funiculus segment only slightly shorter than 3rd, mean Fu2/Fu3 0.980. Dorsal excision of petiolar scale rather shallow, mean PeINC/CS 2.98 %. Eyes with rather short hairs, mean EyeHL 16 µm. Standing setae on clypeus usually reaching caudad only to the 1st and 2nd level, ClySet 1.76. Pubescence surpassing anterolateral clypeal margin always present, mean ClyPub 4.1. Region of occipital corners with appressed hairs. Setae in the area of the ocellar triangle often absent, mean nOce 0.63. Frontal face of forecoxae only very occasionally with single weak setae, mean nCox 0.22. Metapleural setae absent, mean nMet 0.01. Setae on posterior margin of gaster tergites usually beginning with the 3rd or 4th tergite, mean TERG 3.22. Setae on anterior area of 3rd tergite in 42 % of individuals present. Outer edge of hind tibial flexor side with rather few setae, mean nHTfl 4.4. Pubescence distance in ocellar triangle very low and dorsum of 1st gaster tergite rather high, mean sqPDO 4.49, mean sqPDG 6.35.

-- Gyne (Tab. 7; pictures CASENT0907579 in www.antweb.org): rather small, mean and maximum CS 1430 and 1503 µm. Head rather short, CL/CW 1.000, Scape rather long, SL/CS 0.948. Eyes with moderately long setae, mean EyeHL 24 µm. Surface of head, mesosoma, gaster and legs covered with a rich subdecumbent pubescence which often shows a rather large basal thickness of hairs making the distinction from setae difficult; surfaces appearing rather matt, mean GLANZ 1.7. Standing setae on clypeus reaching caudad only to the 1st and 2nd level, mean ClySet 1.69. Pubescence surpassing anterolateral clypeal margin always present, ClyPub 5.0. Setae in the ocellar area in 25 % of the individuals present, difficult to distinguish from semierect pubescence. Region of occipital corners with subdecumbent hairs. Setae on posterior margin of gaster tergites usually beginning with the 2nd to 4th tergite, mean TERG 2.8. Frontal face of forecoxae without or with very few setae, mean nCox 1.0.

Setae on outer flexor edge of hind tibia few, mean nHTfl 3.5. Pubescence distance in ocellar triangle and on dorsum of 1st gaster tergite very low, mean sqPDO 3.50, mean sqPDG 4.55.

Taxonomic comments and clustering results. As a combination of dense frontal pubescence, rather short eye hairs and much reduced setae numbers in the ocellar triangle, on frontal face of forecoxae, on gaster tergites and on outer hind tibial flexor margin, the workers of *Formica bruni* cannot be confused with any species. Problems may occasionally arise in the separation from *Formica foreli*. Yet, a save separation from this species is given by a LDA considering the characters CS, EyeHL, ClySet and ClyPub which classifies 98.8 % of 423 worker individuals correctly. Furthermore, based on the same characters, all 133 nest samples of *Formica bruni* and *Formica foreli* were correctly classified by any of the five exploratory data analyses used in this revision. This clear result, however, is only achieved if EyeHL is recorded with high-resolution optics and if ClyPub is recorded with uttermost care. The gynes of *F. brun*i are well separable from any other species in being a combination of rather small size, high ClyPub, low sqPDO, low sqPDG, rough pubescence surface and setae reduction on coxae and gaster tergites.

Seifert (1999) provided evidence for hybridization between *F. bruni* and *F. pressilabris* in samples collected by Malicky in Montana / Switzerland in 1965. This locality, a south-facing subalpine grassland at 1800 m was one of the few geographic spots with known syntopic occurrence of the two species. A re-investigation of the data against the background of a larger comparison sample of Palaearctic *F. pressilabris* and with other forms of analysis basically confirmed the hybridization hypothesis. Investigated were five workers and four gynes of the sample "SWI:Montana-196507-/" (SaNo 201) and six workers of the sample "SWI: Montana-19650726." (SaNo 202) against a background of 118 workers and 18 gynes of *F. bruni* from Europe and 436 workers and 67 gynes of *F. pressilabris* from its whole Westpalaearctic range. Considering workers and the characters CS, CL/CW, SL/CS, EyeHL, ClySet, ClyPub, TERG, nHTfl, sqPDO and sqPDG, a principal component and a linear discriminant analysis were performed – with the workers from the Montana samples run as wild-cards in the LDA (Fig. 34). The data of SaNo 202 (black-margined dots in Fig. 34) suppose a hybrid identity in two workers whereas two workers each should belong to *F. pressilabris* and *F. bruni*. The situation in SaNo 201 is less obvious: both parental species are present while one or two individuals could represent hybrids. However, the gynes of SaNo 201 are clearly exposed as intermediate by a PCA considering the characters CS, CL/CW, SL/CS, EyeHL, OccHD, OceSet, sqPDO, sqPDG, nCox, MnHL, nHTfl, TERG and ML (Fig. 35). As both *F. bruni* and *F. pressilabris* are polygynous, the most likely interpretation is assuming presence of both *F. pressilabris* and *F. bruni* queens in the same nest mound with some of these having been mated by a heterospecific male. Crossmating appears likely as both seasonal and daily times of swarming overlap considerably in both species (Seifert 2018).

Biology. See the condensed information in Seifert (2018).

4.4.8 *Formica forsslundi* Lohmander, 1949

Formica forsslundi Lohmander, 1949 [description, neotype fixation]

Without giving a precise type locality, Lohmander reported as terra typica the region of Värmland, Västra Götland and Närke in Sweden. Types are unknown in the museums of Stockholm and Göteborg. Yet, the morphological description of workers and gynes as well as the reported bog habitat make sufficiently clear that *Formica forsslundi* does not belong to one of the other six species occurring in Fennoscandia. The gyne was described to be very small, to have a brilliantly shining cuticular surface, a dilute but long pubescence, a blackish brown to black overall coloration with only anterior pronotum, caudal propodeum and basal scale showing a light yellowish component. As difference to *F. pressilabris* Lohmander reported the upper margin of scale to be more deeply and more narrowly excised, the margin of scale to carry hairs (in fact elongated pubescence hairs) and the pubescence to be longer. Lohmander also noted that *F. suecica*, which has similarly small gynes, has a higher pubescence density. As the *Formica forsslundi* species complex contains three cryptic species in the Palaearctic, a neotype was fixed by present designation in a worker labelled "SWE: 57.114°N, 13.785°E, Torskinge-1.4 km W, 150 m, Torfmoos, Eriophorum, B. Seifert 1996.08.02-100"; depository SMN Görlitz.

Formica strawinskii Petal, 1963

Formica forsslundi ssp. *strawinskii* Petal, 1963 [type investigation]

This taxon has been described from the peat bog Rakowskie Bagno near Frampol / Poland. Investigated were 4 paratype workers and 1 paratype gyne on different pins labelled "Polonia. Rakowskie Bagno. K. Frampola distr. Lublin 24 VII 58 leg. J. Petal", "Formica forsslundi Lohm ssp. strawinskii Petal allotyp", Inst. Zool. P.A.N. Warszawa 77/63"; depository ZIPAS Warszawa.

All material examined. Numeric phenotypical data were recorded in 43 samples with 112 workers and 22 gynes. For details see supplementary information SI1, SI2 and SI3. This material originated from China (5 samples), Denmark (1), Finland (11), Germany (10), Kazakhstan (4), Poland (2), Sweden (7) and Switzerland (3).

Geographic range. West and Central Palaearctic, from 8.5°E to 100°E. The main range in Europe is north temperate to boreal from N Germany (54°N) across Denmark, SE Norway, Sweden and Finland north to 66°N. The Finnish population stretches south to E Poland. Six isolated populations are known from 4 bogs in SW Germany and 2 bogs in N Switzerland – all between 47.1 and 47.7°N and 695 to 880 m. A predicted population on mineral soils of the Alps between 1300 and 2200 m altitude is not confirmed so far by reliably identified voucher specimens. In Asia found in Kazakhstan (Tarbagatai and Saur Mountains), and NE Tibet (Province Xinghai, here at 35°N and 100°E ascending to 3500 m). Only in NE Tibet sympatric with *F. brunneonitida*.

Diagnosis: --Worker (Tab. 3; Figs 4, 17–18; pictures CASENT0906306 in www.antweb.org): small size; mean and maximum CS 1250 and 1378 µm. Head relatively short, mean CL/CW 1.045. Scape rather short, mean SL/CS 1.008. 2nd funiculus segment much shorter than 3rd, mean Fu2/Fu3 0.922. Dorsal excision of petiolar scale moderately deep, mean PeINC/CS 3.35 %. Eyes with minute hairs, mean EyeHL 7 µm. Standing setae on clypeus usually reaching caudad only to the 2nd level, ClySet 2.00. Pubescence surpassing anterolateral clypeal margin often present, mean ClyPub 1.9. Region of occipital corners with appressed hairs. Setae in the area of the ocellar triangle usually present, mean nOce 1.48. Frontal face of forecoxae often with few setae, mean nCox 1.82. Metapleural setae almost always completely absent, mean nMet 0.02. Setae on posterior margin of gaster tergites usually beginning with the 1st tergite, mean TERG 1.14. Setae on anterior area of 3rd tergite always present. Outer edge of hind tibial flexor side with rather many setae, mean nHTfl 6.4. Pubescence distance in ocellar triangle and dorsum of 1st gaster tergite very high, mean sqPDO 7.29, mean sqPDG 7.06.

-- Gyne (Tab. 6): very small size, mean and maximum CS 1237 and 1296 µm. Head short, CL/CW 0.988, Scape short, SL/CS 0.853. Eyes only with minute setae, mean EyeHL 7.5 µm. Surface of head, mesosoma, gaster brilliantly shining, on gaster tergites sometimes with very weak transverse microripples, mean GLANZ 2.95. Standing setae on clypeus often reaching caudad only to the 2nd level, mean ClySet 1.83. Single pubescence hairs surpassing anterolateral clypeal margin often present, mean ClyPub 1.6. Setae in the ocellar area in 73 % of the individuals present. Region of occipital corners with decumbent or appressed hairs, mean OccHD 6 µm. Setae on posterior margin of gaster tergites usually beginning with the 1st tergite, mean TERG 1.2. Frontal face of forecoxae often with very few setae, mean nCox 1.9. Setae on outer flexor edge of hind tibia rather few, mean nHTfl 4.0. Pubescence distance in ocellar triangle and on dorsum of 1st gaster tergite high, mean sqPDO 5.91, mean sqPDG 6.72. Color of head, mesosoma and gaster dark to blackish brown, red color components absent, yellowish ones may be present.

Taxonomic comments and clustering results. Based on investigation of a much larger sample than available for Seifert (2000), we decided to recognize *Formica brunneonitida* Dlussky 1964 as a taxon separate from *F. forsslundi*. A principal component analysis considering the characters CS, CL/CW, SL/CS, EyeHL, ClySet, ClyPub, nOce, nCox, TERG, nHTfl, sqPDO and sqPDG offered an apparently full separation of 80 nest samples of both species (Fig. 36). The classification errors of other exploratory data analyses relative to the controlling LDA were 0 % in NC-Ward, 2.5 % in NC-NMDS.kmeans, 2.5 % in NC-part.kmeans and 0 % error plus 7.5 % outliers in NC-part.hclust. This gives a mean error of 1.0 % in five exploratory data analyses. The classification error in the LDA on the individual level was 7.1 % in 255 workers. If run as wild-cards in a LDA, the type samples are allocated to the *F. brunneonitida* cluster with the following posterior probabilities: p=0.0149 in *F. forsslundi*, p=0.0004 in *F. strawinskii* and p=0.7805 in *F. brunneonitida*. Problematic is the weak signal in the type series of *F. brunneonitida*. This placement in the periphery of the cluster is repeated in the PCA (Fig. 36). Three methods of NC clustering allocated this type series to the *F. brunneonitida* cluster but NC-part.hclust placed it as an outlier. The small sample size available in gynes does not allow a credible multivariate analysis but the average differences shown in Tab. 6 provide additional support for separating *F. brunneonitida* from *F. forsslundi*. Most problematic are two gynes of SaNo 882 from Khairkhan Dulaan / Mongolia which show the setae conditions of *F. forsslundi* in the ocellar triangle and gaster tergites but correspond in other characters to *F. brunneonitida*. The workers of SaNo 882 are allocated by a LDA to the *F. brunneonitida* cluster with p=0.919. This sample and the type sample of *F. brunneonitida* may suggest introgression and incomplete species separation. The separation of *F. forsslundi* from *F. caucasicola* spec. nov. is shown in section 4.4.10.

Biology. See the condensed information in Seifert (2018).

4.4.9 *Formica brunneonitida* Dlussky, 1964

Formica brunneonitida Dlussky, 1964 [type investigation]

This taxon has been described from Mongolia. Investigated were six paratype workers from the holotype nest labelled “Mongolia, Cherulen Buudal, 120 km E Ulan Bator, 7.VI.1962 leg. Pisarski & R. Bielawski”; depository ZIPAS Warszawa.

All material examined. Numeric phenotypical data were recorded in 41 nest samples with 143 workers and 13 gynes. For details see supplementary information SI1, SI2 and SI3.

This material originated from Mongolia (13 nest samples), Russia (15) and Tibet (13).

Geographic range. In Siberia it is distributed from W Mongolia (47.6°N, 96.9°E) eastwards to the Ussuri region (45.4°N, 135.3°E) and Ochotsk (59.40°N, 143.19°E). The population on the Tibetan Plateau is probably isolated from the Siberian population. Outstanding are two samples collected during the German Tibet Expedition 1938/39 from approximately 28°N, 88.3°E and an elevation of 4750 m. This locality is 1400 km SW from the nearest site in NE Tibet (Lake Koko Nur) and should represent the highest site known for any *Coptoformica* species.

Diagnosis: --Worker (Tab. 3; pictures CASENT0907594 and CASENT0913662 in www.antweb.org): small; mean and maximum CS 1255 and 1412 µm. Head relatively short, mean CL/CW 1.054. Scape rather short, mean SL/CS 1.024. 2nd funiculus segment distinctly shorter than 3rd, mean Fu2/Fu3 0.955. Dorsal excision of petiolar scale rather shallow, mean PeINC/CS 3.05 %. Eyes with minute hairs, mean EyeHL 7 µm. Standing setae on clypeus in 67 % of specimens only present on the 1st level, mean ClySet 1.33. Pubescence surpassing anterolateral clypeal margin almost always absent, mean ClyPub 0.1. Region of occipital corners with appressed hairs. Setae in the area of the ocellar triangle usually absent, mean nOce 0.28. Frontal face of forecoxae almost always without setae, mean nCox 0.10. Metapleural setae always completely absent, mean nMet 0.0. Setae on posterior margin of gaster tergites usually beginning with the 1st and more frequently with 2nd tergite, mean TERG 1.78. Setae on anterior area of 3rd tergite in 97 % of specimens present. Outer edge of hind tibial flexor side with rather few setae, mean nHTfl 5.0. Pubescence distance in ocellar triangle and dorsum of 1st gaster tergite very high, mean sqPDO 7.65, mean sqPDG 6.77.

-- Gyne (Tab. 6): small, mean and maximum CS 1267 and 1313 µm. Head rather short, CL/CW 0.996, Scape longer than in *F. forsslundi*, mean SL/CS 0.871. Eyes only with minute setae, mean EyeHL 7.7 µm. Surface of head, mesosoma and gaster brilliantly shining, on gaster tergites sometimes with very weak transverse microripples, mean GLANZ 3.0. Standing setae on clypeus only present on anterior margin, mean ClySet 1.0. Single pubescence hairs surpassing anterolateral clypeal margin always absent, mean ClyPub 0.0. Minute setae in the ocellar area in only 23 % of the individuals present. Region of occipital corners with appressed hairs, mean OccHD 1 µm. Setae on posterior margin of gaster tergites usually beginning with the 3rd tergite, mean TERG 2.92. Frontal face of forecoxae always without setae, mean nCox 0.0. Setae on outer flexor edge of hind tibia few, mean nHTfl 3.0. Pubescence distance in ocellar triangle and on dorsum of 1st gaster tergite very high, mean sqPDO 6.57, mean sqPDG 7.91. Color of head, mesosoma and gaster dark to blackish brown, red color components absent.

Taxonomic comments and clustering results. The separation from *F. forsslundi* has already been discussed in section 4.4.8. There is apparently no geographic overlap between *F. brunneonitida* and the Westpalaearctic *F. pressilabris* because the latter is not known from east of 65°E. However, since there is a similarity of the two species (Tab. 3) and because it cannot be excluded that *F. pressilabris* goes east the Baikal region, we have to consider species separation. This is apparently no problem. Considering the twelve characters CS, CL/CW, SL/CS, OceD/CS, ClySet, nCox, EyeHL, TERG, T3f, nHTfl, sqPDO, sqPDG and 72 nest samples of both species, the classification error is 0 % in the PCA and 1.4 % in NC-part.kmeans, NC-part.hclust, NC-NMDS.kmean and NC-Ward. The classification error on the individual level by a LDA is only 3.2 % in 252 workers. The separation of gynes by an LDA considering the characters SL/CS, EyeHL, TERG and nHTfl is incomplete: 15 % of 13 *F. brunneonitida* gynes are misclassified whereas all 67 *F. pressilabris* gynes are classified correctly.

Biology. The species was found in open, semidry to freshdry grassland and with a similar frequency also within grassy and sunny spots of broad-leafed, mixed and coniferous forest. It constructs small mounds of finely cut grass pieces. Occurrence in harsh environments at 4750 m altitude in SW Tibet and near Okhotsk in E Siberia indicates a high frost resistance. It is unknown if the species forms polygynous-polydomous colonies. Alates occur 11 July ± 18 days [26 June – 10 August] n= 6 which is just the same period as in *F. forsslundi* (Seifert 2018). Host species for socially parasitic colony foundation is most probably *Formica picea candida* Smith, 1878 which was present in any locality where *F. brunneonitida* was found.

4.4.10 *Formica caucasicola* spec. nov.

urn:lsid:zoobank.org:act: EFC74CC6-8FDA-4335-B902-E17C87AC8BB3

Etymology. Meaning “Caucasus dweller”, referring to the region where the species is endemic.

Type material. Holotype worker plus 4 paratype workers on three pins labelled “GEO: 42.665°N, 44.620°E, Kazbeg, 2224 m, Weide, am Wegrand, Hügel aus kleinen Grashalmstückchen, J. Trettin 2004.06.10”; depository SMN Görlitz.

All material examined. Numeric phenotypical data were recorded in 7 nest samples with 35 workers and 2 gynes. For details see supplementary information SI1, SI2 and SI3. This material originated from Georgia (6 nest samples) and Azerbaijdshan (1).

Geographic range. Great Caucasus at altitudes between 1744 and 2500 m.

Diagnosis: --Worker (Tab. 3, Figs 19–20): slightly larger than *F. forsslundi*, mean and maximum CS 1306 and 1380 µm. Head relatively short, mean CL/CW 1.056. Scape much shorter than in *F. forsslundi*, mean SL/CS 0.972. 2nd funiculus segment distinctly shorter than 3rd, mean Fu2/Fu3 0.948. Dorsal excision of petiolar scale rather shallow, mean PeINC/CS 3.48 %. Eyes with minute hairs, mean EyeHL 6.5 µm. Standing setae on clypeus in 54 % of specimens only present on the 1st level, mean ClySet 1.46. Pubescence surpassing anterolateral clypeal margin almost always absent, mean ClyPub 0.1. Region of occipital corners with appressed hairs. Setae in the area of the ocellar triangle usually absent, mean nOce 0.20. Frontal face of forecoxae almost always without setae, mean nCox 0.06. Metapleural setae always completely absent, mean nMet 0.0. Setae on posterior margin of gaster tergites usually beginning with the 1st tergite, mean TERG 1.17. Setae on anterior area of 3rd tergite always present. Outer edge of hind tibial flexor side with rather few setae, mean nHTfl 5.7. Pubescence distance in ocellar triangle and dorsum of 1st gaster tergite very high, mean sqPDO 7.15, mean sqPDG 6.65.

-- Gyne (Tab. 6): only two gynes available; very small size, mean CS 1216 µm. Head moderately long, CL/CW 1.007, Scape much shorter than in any other species, mean SL/CS 0.799. Eyes only with minute setae, mean EyeHL 5.0 µm. Surface of head, mesosoma and gaster brilliantly shining, on gaster tergites sometimes with very weak transverse microripples, mean GLANZ 3.0. Standing setae on clypeus present in one gyne only on anterior margin, in the other gyne an accessory 2nd level seta present, mean ClySet 1.5. Single pubescence hairs surpassing anterolateral clypeal margin absent, mean ClyPub 0.0. Setae in the ocellar area absent. Region of occipital corners with appressed hairs, mean OccHD 0 µm. Setae on posterior margin of gaster tergites beginning with the 1st tergite, mean TERG 1.0. Frontal face of forecoxae without setae, mean nCox 0.0. Setae on outer flexor edge of hind tibia rather few, mean nHTfl 4.5. Pubescence distance in ocellar triangle and on dorsum of 1st gaster tergite very high, mean sqPDO 6.46, mean sqPDG 7.82. Color of head, mesosoma and gaster dark to blackish brown, red color components absent.

Taxonomic comments and clustering results. *F. caucasicola* spec. nov. is an endemic sister species of *F. forsslundi*. A principal component analysis considering the characters CS, CL/CW, SL/CS, OceD/CS, ClySet, ClyPub, nOce, nCox, nHTfl, sqPDO and sqPDG offers a perfect separation of workers of the two species on the nest sample level (Fig. 37). Using the same characters, a LDA classifies 94.0 % of 133 individuals of both species correctly. The posterior probabilities for allocation to the *F. caucasicola* cluster were 0.0036 in the neotype nest of *F. forsslundi* and 0.9827 in the holotype nest of *F. caucasicola* if run as wild-cards in the LDA.

Biology. It was found in moderately grazed, highly montane to alpine grasslands and constructs mounds of finely cut grass pieces. It seems to be largely monodomous but in one locality the arrangement of nests suggested a polydomous colony structure. In each of the six localities *Formica picea* Nylander 1846 was present and socially parasitic colony foundation in this species is evidenced by the finding of a mixed nest. Three findings of alates in the nests were between 27 July and 1 August.

4.4.11 *Formica pressilabris* Nylander, 1846

Formica pressilabris Nylander, 1846 [type investigation]

This taxon has been described from Finland. Investigated were the lectotype worker plus 2 paratype workers on the same pin labelled "Lectotype (top specimen) Formica pressilabris Nyl." "H:fors W. Nyland." "Spec. typ. No. 5033" and two paratype workers labelled "H:fors W. Nyland." "Spec. typ. No. 5032", 1 paratype worker "H:fors W. Nyland." "Spec. typ. No. 5031"; depository FMNH Helsinki. The type series is allocated to the *F. pressilabris* cluster with p= 0.9998 if run as wild-card in a LDA differentiating against *F. foreli*.

Formica rufomaculata Ruzsky, 1895

Formica exsecta var. *rufomaculata* Ruzsky, 1895 [type investigation]

This taxon has been described from Simbirsk (today named Ulyanovsk) at the middle reaches of Volga river. Investigated were four type workers apparently sent by Ruzsky both to Auguste Forel (stored in MHN Genève) and Gustav Mayr (stored in NHM Wien). The former specimens are labelled "F. pressilabris Nyl. var. rufomaculata Ruzsky Ssimbirsk (Ruzsky)" and the latter ones "Simbirsk Coll. G. Mayr" and "f exs. v. rufo-maculata" – the latter label seems to be an original label of Ruzsky. The type series is allocated to the *F. pressilabris* cluster with p= 0.9990 if run as wild-card in a LDA differentiating against *F. foreli*.

All material examined. Numeric phenotypical data were recorded in 123 samples with 477 workers and 67 gynes. For details see supplementary information SI1, SI2 and SI3. This material originated from Austria (1 sample), Denmark (5), Estonia (1), Finland (15), France (5), Germany (21), Netherlands (1), Poland (12), Russia (6), Slovakia (3), Sweden (12) and Switzerland (41).

Geographic range. Euro-Siberian, temperate to south boreal, planar to subalpine, continental. Total range from the Netherlands (6°E) and the W Alps east to W Siberia (61°E). Isolated and probably small populations exists in the E Pyrenees (at 1–2°E) and the Caucasus. The boreal European range goes north to 62.5°N in Sweden and

65.5°N in Finland and stretches SW to the Netherlands. The current continental range fuses with the boreal one in the eastern Baltic states and extends from there west to E Brandenburg (Germany) and W Slovakia. The alpine population is found in the W Alps between 6°E and 10°E; the vertical distribution of 41 sites ranges here 1802 ± 200 [1460, 2250] meters. This translates into 4.5°C lower mean air temperatures from May to August compared to sympatric sites of *F. foreli*. The main alpine population concentrates to elevations of 1750–2250 m. Absent from the E Alps.

Diagnosis: --Worker (Tab. 3, Figs 21–22; pictures CASENT0173872, CASENT0280393, and CASENT0915634 in www.antweb.org): small; mean and maximum CS 1254 and 1386 µm. Head relatively short, mean CL/CW 1.046. Scape short, mean SL/CS 0.997. Dorsal excision of petiolar scale very shallow, mean PeINC/CS 2.2 %. Eyes with minute hairs, mean EyeHL 5 µm. Standing setae on clypeus usually only present in the 1st level, mean ClySet 1.03. Pubescence surpassing anterolateral clypeal margin nearly always absent, mean ClyPub 0.02. Region of occipital corners with appressed hairs. Setae in the area of the ocellar triangle always absent. Frontal face of forecoxae almost always without setae, mean nCox 0.01. Metapleural setae always completely absent. Setae on posterior margin of gaster tergites usually beginning with the 3rd tergite, mean TERG 3.2. Setae on anterior area of 3rd tergite in 30 % of specimens present. Outer edge of hind tibial flexor side with few setae, mean nHTfl 2.9. Pubescence distance in ocellar triangle and dorsum of 1st gaster tergite high, mean sqPDO 6.47, mean sqPDG 6.69.
-- Gyne (Tab. 6): small size, mean and maximum CS 1286 and 1341 µm. Head short, CL/CW 0.991, Scape short, mean SL/CS 0.845. Eyes without or only with minute setae, mean EyeHL 4.6 µm. Surface of head, mesosoma and gaster shining, mean GLANZ 2.56. Standing setae on clypeus only present on anterior margin, mean ClySet 1.0. Pubescence hairs surpassing anterolateral clypeal margin and setae in the ocellar area always absent. Region of occipital corners only with appressed hairs. Setae on posterior margin of gaster tergites usually beginning with the 4th tergite, mean TERG 3.8. Frontal face of forecoxae always without setae. Setae on outer flexor edge of hind tibia very few, mean nHTfl 1.3. Pubescence distance in ocellar triangle and on dorsum of 1st gaster tergite high, mean sqPDO 6.04, mean sqPDG 7.32. Color of head, mesosoma and gaster dark to blackish brown, red color components absent.

Taxonomic comments and clustering results. The clear separation of *Formica pressilabris* from *F. brunneonitida* and *F. foreli* is shown in sections 4.4.9 and 4.4.12 respectively. Hybridization with *F. bruni* is reported in section 4.4.7.

Biology. See the condensed information in Seifert (2018).

4.4.12 *Formica foreli* Bondroit, 1918

Formica foreli Bondroit, 1918 [type investigation]

This taxon has been described under the infrasubspecific name *Formica exsecta pressilabris* var. *foreli* Emery 1909 based on material collected by Auguste Forel near his country estate at Morges / Switzerland. Investigated was the type worker from MCSN Genova, labelled “Meorgete Vaux Forel ...”, “exsecta foreli Emery = pressilabris For.”, “Typus”, “ANTWEB CASENT 0905704”. The specimen is allocated to the *Formica foreli* cluster with p=0.9991 if run as wild-card in a LDA. Investigated was also a series of six gynes from the type locality with any of these being allocated to the *F. foreli* cluster with p> 0.999.

Formica naefi Kutter, 1957

Formica naefi Kutter, 1957 [type investigation]

This taxon has been described from the lower Engadin valley in Switzerland. The original description does not mention collecting data except for “Schuls” (=Scuol) and “Pradella” and gives no information on types. Investigated were three samples with 11 workers, all labelled as “Cotypus” and “Bain Jonnair Schuls 10.7.54 Kutter”, “Bain Jonnair Schuls 19.7.55 Kutter”, “Bain Jonnair Schuls 1956 Kutter”; depository MCZ Lausanne. The material is homogenous and comes apparently from the three nests mentioned by Kutter in the original description. Each sample was classified as *F. foreli* with p> 0.999 if run as wild-card in a LDA differentiating against *F. pressilabris*.

Formica tamarae Dlussky, 1964

Formica tamarae Dlussky, 1964 [type investigation]
This taxon was described from Omalo in Georgia / Great Caucasus. Investigated were two paratype workers labelled “671. Omalo, v pochve 9.VIII.60.”[in Cyrillic] plus three workers labelled “Omalo, V. Svanetia 10.9.59 T. Shishilasvili”. The 1st series is explicitly mentioned in the original description and is allocated to the *F. foreli* cluster with p= 0.9948 if run as wild-card in a LDA differentiating against *F. pressilabris*.

Formica goesswaldi Kutter, 1967

Formica goesswaldi Kutter, 1967 [type investigation]
This taxon was described from near Soglio in Valle Bregaglia in Switzerland. The original description does not mention collecting data except for “Soglio... 1150 m... near to a cattle stable” and Kutter determined two (!) holotypes – one in a worker and one in gyne. Investigated were four samples with 20 workers and 3 gynes

from Soglio, collected in the years 1956, 1961 and 1964, all labelled either as "Typus" or "Cotypus" and deposited in MCZ Lausanne. The unclear type designation does not represent a taxonomic problem because all material was homogenous (apparently collected from the same supercolony) and because any nest series was allocated to the *F. foreli* cluster with p> 0.998 if run as wild-card in a LDA differentiating against *F. pressilabris*.

All material examined. Numeric phenotypical data were recorded in 147 samples with 499 workers and 70 gynes. For details see supplementary information SI1, SI2 and SI3. This material originated from Austria (2 samples), Czechia (3), Georgia (6), Germany (77), Iran (1), Italy (2), Kazakhstan (4), Norway (1), Slovakia (2), Spain (2), Sweden (10), Switzerland (30), Turkey (6) and Ukraine (1).

Geographic range. Westpalaearctic, submeridional to south temperate, planar to submontane, from N Iberia to SE Kazakhstan (85°E). The southernmost populations are in Asia Minor and the Iranian Elburs Mountains (here at 36.2°N ascending to 3160 m). In Europe from 41.7°N (Apennine) to 59.1°N (Norway) and 57°N (Sweden). Absent from the British Isles, Belgium and the Netherlands. The northernmost populations, but not only these, became isolated after the broad introduction of intensive grassland management in Europe. In the Alps it is largely restricted to valleys with xerothermous local climate. The vertical distribution of 12 sites ranges here 1121 ± 349 [552, 1780] meters (Seifert 2018). This translates into 4.5°C higher mean air temperatures from May to August compared to sympatric sites of *F. pressilabris*. In Germany planar to colline.

Diagnosis: --Worker (Tab. 3; pictures CASENT0173871, CASENT09057047, CASENT0912244, and CASENT0912245 in www.antweb.org): small; mean and maximum CS 1246 and 1456 µm. Head relatively short, mean CL/CW 1.052. Scape rather long, mean SL/CS 1.034. Dorsal excision of petiolar scale very shallow, mean PeINC/CS 2.4 %. Eyes with minute hairs, mean EyeHL 6 µm. Standing setae on clypeus usually only present in the 1st level, mean ClySet 1.07. Pubescence surpassing anterolateral clypeal margin nearly always absent, mean ClyPub 0.07. Region of occipital corners with appressed hairs. Setae in the area of the ocellar triangle always absent. Frontal face of forecoxae always without setae. Metapleural setae always completely absent. Setae on posterior margin of gaster tergites usually beginning with the 4th tergite, mean TERG 3.9. Setae on anterior area of 3rd tergite in only 10 % of specimens present. Outer edge of hind tibial flexor side with few setae, mean nHTfl 2.7. Pubescence distance in ocellar triangle very low and on dorsum of 1st gaster tergite low, mean sqPDO 4.69, mean sqPDG 6.11.

-- Gyne (Tabs. 6, 7; pictures CASENT0907580 in www.antweb.org): rather small, mean and maximum CS 1352 and 1472 µm. Head short, CL/CW 0.984, Scape rather long, mean SL/CS 0.845. Eyes without or only with minute setae, mean EyeHL 6.1 µm. Surface of head, mesosoma on average less shining than in *F. pressilabris*, mean GLANZ 1.87. Standing setae on clypeus only present on anterior margin, mean ClySet 1.0. Pubescence hairs surpassing anterolateral clypeal margin always absent. Setae in the ocellar area always absent. Region of occipital corners only with appressed hairs. Setae on posterior margin of gaster tergites usually beginning with the 4th or 5th tergite, mean TERG 4.64. Frontal face of forecoxae always without setae. Setae on outer flexor edge of hind tibia very few, mean nHTfl 1.3. Pubescence distance in ocellar triangle very low and on dorsum of 1st gaster tergite low, mean sqPDO 4.02, mean sqPDG 5.41. Color of head, dorsal mesosoma and gaster usually dark to blackish brown; pro-, meso- and metapleurae usually reddish; dorsal head in some populations with much reddish pigment.

Taxonomic comments and clustering results. The clear separation of *Formica foreli* from *F. pressilabris* in both workers and gynes has already been demonstrated in detail by Seifert (2000). Evaluation of the material gathered since then did not produce new insights. We report here briefly the current status of knowledge. Considering 892 workers of both species and the characters CS, CL/CW, SL/CS, EyeHL, sqPDO, sqPDG, TERG and nHTfl, the mean error rate of five exploratory data analyses relative to the controlling LDA was only 0.76 % in 234 nest samples. Misclassification was 0.42 % in NC-Ward, 0.85 % in both NC-part.kmeans and NC-NMDS.kmeans, 1.28 % in NC-part.hclust and 0.42 % in a PCA (Fig. 38). The very clear allocation of any type series to either the *Formica foreli* or *F. pressilabris* cluster is reported in the synonymy account above. A problem appears with the sample of three workers from the Iranian Elburs Mountains from 5 km W of Nesen (SaNo 761). Though being allocated by any of the five exploratory data analyses to the *F. foreli* cluster, a wild-card run in the LDA supports this classification only weakly with a posterior probability of 0.5111. Support for the *F. foreli* hypothesis is given by zoogeography – the Elburs population might be considered as a continuation of the *F. foreli* population in Turkish Asia Minor and SE Georgia where *F. pressilabris* is unknown so far. The separation of 137 gynes of both species considering the characters CS, CL/CW, SL/CS, ML/CS, sqPDO, sqPDG and nHTfl appears also very clear. A principal component analysis offers a perfect separation (Fig. 39) and a LOOCV-LDA changed only 0.7 % of this classification.

Strong indications for hybridization between *F. foreli* and *F. pressilabris* are missing so far. Due to the high similarity of the species, this is hardly demonstrable by morphology – at least with the character system used here. There are very few samples from the contact zones of both species which appear phenotypically ambiguous. We need an indicative system of nuDNA markers to investigate hybridization or introgression.

Biology. See the condensed information in Seifert (2018).

4.4.13 *Formica suecica* Adlerz, 1902

Formica suecica Adlerz, 1902 [type investigation]

This taxon has been described from the island of Alnö near Sundsvall in the Swedish province Medelpad. Investigated were five type gynes from the collection of Auguste Forel labelled "Formica suecica Madelpad (Suede) (Adlerz)"; depository MHN Genéve.

All material examined. Numeric phenotypical data were recorded in 30 samples with 73 workers and 28 gynes. For details see supplementary information SI1, SI2 and SI3. This material originated from Austria (12 samples), Finland (1), Norway (1), and Sweden (16).

Geographic range. European, boreo-alpine species. The known range of the boreal population includes Fennoscandia between 56°N and 68°N, Estonia, and the region of Arkhangelsk. The alpine relict population is restricted to two sites (Obergurgl and Vent) in the upper Ötztal / Austria at elevations of 1940–2200 m. Agosti (1989) reported a finding at Tevris (57.51°N, 72.40°E) in W Siberia, leg. Reznikova 16 August 1974, with the sample probably being deposited in Donat Agosti's private collection to which there was no access. As Reznikova (2003) did only report findings of *Formica exsecta* from the environs of Tevris, we consider a Siberian distribution of *F. suecica* as doubtful.

Diagnosis: --Worker (Tab. 4, Figs 23–24; pictures CASENT0906303, CASENT0911094, CASENT0912246 in www.antweb.org): rather large and monomorphic; mean and maximum CS 1337 and 1428 µm. Head very short, mean CL/CW 1.020. Scape rather long, mean SL/CS 1.040. Dorsal excision of petiolar scale moderately deep, mean PeINC/CS 3.5 %. Eyes with minute hairs, mean EyeHL 6 µm. Standing setae on clypeus usually distributed caudad to 4th level, mean ClySet 3.99. Few pubescence hairs surpassing anterolateral clypeal margin occasionally present, mean ClyPub 0.64. Region of occipital corners with appressed hairs. Setae in the area of the ocellar triangle always present, mean nOce 1.96. Frontal face of forecoxae always with setae, mean nCox 4.6. Metapleural setae sometimes present, mean nMet 1.1. Setae on posterior margin of gaster tergites nearly always beginning with the 1st tergite, mean TERG 1.01. Setae on anterior area of 3rd tergite in 86 % of specimens present. Outer edge of hind tibial flexor side with rather many setae, mean nHTfl 6.5. Pubescence distance in ocellar triangle and on dorsum of 1st gaster tergite low, mean sqPDO 4.76, mean sqPDG 5.24. Dorsal head never with the contrasting reddish and blackish pigmentation pattern as frequently seen in the other *Coptoformica* species; head normally homogenously reddish, more rarely dark reddish brown.

-- Gyne (Tab. 6): smaller than the workers, mean and maximum CS 1266 and 1300 µm. Head short, CL/CW 0.979. Scape longer than in other species with small-sized gynes, mean SL/CS 0.932. Eyes without or only with minute setae, mean EyeHL 7 µm. Surface of head and mesosoma shining, mean GLANZ 2.38. Standing clypeal setae sparsely distributed over whole clypeus, mean ClySet 3.97. Single pubescence hairs surpassing anterolateral clypeal margin occasionally present, mean ClyPub 0.46. Setae in the ocellar area always present. Region of occipital corners only with appressed hairs. Dorsal mesosoma always with standing setae, mean MnHL 98 µm. Setae on posterior margin of gaster tergites beginning with the 1st tergite, mean TERG 1.0. Frontal face of forecoxae always with setae, mean nCox 8.0. Outer flexor edge of hind tibia with rather many setae, mean nHTfl 6.2. Pubescence distance in ocellar triangle and on dorsum of 1st gaster tergite very low, mean sqPDO 3.97, mean sqPDG 4.75. The dark brown body color has often a yellowish tinge.

Taxonomic comments and clustering results. Workers of other species having reddish and short heads have been misclassified in the past as *Formica suecica* (e.g., by Gunhold 1949 or Haeseler 1977) but this species is in fact unmistakable when structural characters are considered. In the worker, there is no other species combining presence of setae on 1st gaster tergite and coxae and minute or absent eye setae with high pubescence density in occellar triangle and on gaster tergites. The gyne combines small size with high pubescence density and presence of rather many setae on coxae and clypeus. *Formica suecica* is very monomorphic and there are no differences detectable between the boreal Fennoscandian and the disjunct endemic population in the Alps (Glaser & Seifert 1999).

Biology. See the condensed information in Seifert (2018).

4.4.14 *Formica pisarskii* Dlussky, 1964

Formica pisarskii Dlussky, 1964 [type investigation]

This taxon has been described from Songino, 24 km SW of Ulan Bator /Mongolia. Investigated were three paratype workers from the holotype nest labelled "Mongolia, Songino, 24 km SW Ulan Bator, 22.V.1962, leg. B. Pisarski et R. Bielawski, 3297" and "Paratypes F. pisarskii Dlussky"; depository ZMLU Moskva. From the collection of ZIPAS Warszawa were investigated three paratype workers labelled "Mongolia, Songino, 24 km SW Ulan Bator, 22.V.1962, leg.

B. Pisarski et R. Bielawski, 3298" and "Formica pisarskii Dlussky, 1964 paratype" and two paratype workers labelled "Mongolia, Songino, 24 km SW Ulan Bator, 22.V.1962, leg. B. Pisarski et R. Bielawski, 3299" and "Formica pisarskii Dlussky, 1964 paratype". Paratype fixations in material from the site Gorchi, 50 km NE Ulan Bator are not valid as this site is not mentioned in the original description.

Formica fossilabris Dlussky, 1965

Formica fossilabris Dlussky, 1965 [type investigation]
This taxon has been described from material collected by the Kozlov expedition at Lake Koko Nur in NE Tibet in August 1901. Investigated were the holotype worker plus three paratype workers from ZMLU Moskva with collecting data: southern shore of Lake Koko Nur, mid August 1901, 10500 feet.

All material examined. Numeric phenotypical data were recorded in 35 samples with 92 workers and 5 gynes. For details see supplementary information SI1, SI2 and SI3. This material originated from China (8 samples), Mongolia (20), and Russia (7).

Geographic range. Central Siberia and NE Tibet between 91 and 115°E. In N Mongolia and the Baikal and Transbaikal region of adjacent Russia found between 45.9 and 53.2°N at elevations from 470 to 2327 m. In NE Tibet occurring between 33 and 39°N at elevations between 3100 and 3920 m.

Diagnosis: --Worker (Tab. 4, Figs 25–26; pictures CASENT0907593, CASENT0911159, CASENT0913660, CASENT0922318 and CASENT0922319 in www.antweb.org): small-sized, mean and maximum CS 1246 and 1359 µm. Head and scape rather long, mean CL/CW 1.069, mean SL/CS 1.044. Dorsal excision of petiolar scale rather shallow, mean PeINC/CS 3.1 %. Eyes with minute hairs, mean EyeHL 7 µm. Standing setae on clypeus usually distributed caudad to 4th level, mean ClySet 3.92. Single pubescence hairs surpassing anterolateral clypeal margin may be present, mean ClyPub 1.07. Region of occipital corners with appressed hairs. Setae in the area of the ocellar triangle always present, mean nOce 2.34. Frontal face of forecoxae almost always with setae, mean nCox 3.0. Standing setae on pronotum in the Siberian population in contrast to other species usually present. Metapleural setae absent. Setae on posterior margin of gaster tergites always beginning with the 1st tergite. Setae on anterior area of 3rd tergite in 99 % of specimens present. Outer edge of hind tibial flexor side with rather many setae, mean nHTfl 7.4. Pubescence distance in ocellar triangle and on dorsum of 1st gaster tergite very high, mean sqPDO 7.38, mean sqPDG 7.31.
-- Gyne (Tab. 6): small, mean and maximum CS 1221 and 1263 µm. Head elongated, CL/CW 1.025. Scape rather long, mean SL/CS 0.899. Eyes without or only with minute setae, mean EyeHL 6 µm. Surface of head and mesosoma always strongly shining, mean GLANZ 3.0. Standing clypeal setae sparsely distributed over whole clypeus, the most caudal ones usually at 4th level, mean ClySet 3.5. Pubescence hairs surpassing anterolateral clypeal margin usually absent, mean ClyPub 0.10. Setae in the ocellar area always present. Region of occipital corners only with appressed hairs. Dorsal mesosoma always with standing setae, mean MnHL 99 µm. Setae on posterior margin of gaster tergites beginning with the 1st tergite, mean TERG 1.0. Frontal face of forecoxae with single setae, mean nCox 2.2. Outer flexor edge of hind tibia with rather many setae, mean nHTfl 5.8. Pubescence distance in ocellar triangle and on dorsum of 1st gaster tergite very high, mean sqPDO 7.10, mean sqPDG 8.29. The dark brown body color has often a yellowish tinge.

Taxonomic comments and clustering results. Sparsely haired workers of *Formica pisarskii* can be confused with more hairy specimens of *F. forsslundi*. A LDA considering the characters CS, CL/CW, SL/CS, EyeHL, ClySet, ClyPub, nOce, nCox, TERG, nHTfl, sqPDO and sqPDG classifies 95.6 % of 204 worker individuals and 100 % of 74 nest samples of both species correctly. If run as wild-cards in the LDA, the posterior probabilities for allocation to the *F. pisarskii* cluster were 0.0004 in the neotype nest of *F. forsslundi*, 0.0130 in the paratype sample *F. strawinskii*, 0.9967 in the holotype sample of *F. fossilabris* and 0.9997 in the holotype sample of *F. pisarskii*. Considering the characters CS, CL/CW, SL/CS, ClySet, ClyPub and sqPDG, all five exploratory data analyses (PCA, NC-Ward, NC-part.hclust, NC-part.kmeans, NC-NMDS.kmeans) classified any of the 74 samples in agreement with the LDA indication (Fig. 40). The small number of *F. pisarskii* gynes does not allow a reliable analysis. Yet, the very strong separation of five *F. pisarskii* and 21 *F. forsslundi* gynes provided by a PCA considering the characters CS, ClySet, sqPDO and sqPDG provides hope that this may hold after investigation of more material.

Biology. Main habitat is open and rather dry steppe, but it may also occur in fresh meadows and light woodland. *F. pisarskii* constructs the typical mounds of finely-cut grass particles but in the stony mountain steppe of Mongolia it was predominately nesting under stones – as a rule without adherent piles of grass particles. A most probable host species for socially parasitic colony foundation is *Formica picea candida* which was observed in any site where *F. pisarskii* was found. Alates were seen in the nests 1 August 2001 in NE Tibet and 8 August 2003 in Mongolia.

4.5 Comments on Incertae Sedis

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, most probably, could 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 separately under Incertae Sedis. We prefer the latter solution and recommend future revisers not to synonymize these names as long as no reliably identified type specimens have been discovered. Below, we present the Incertae Sedis and unavailable names in alphabetic order.

Formica exsectorubens Ruzsky, 1905

This name was given by Ruzsky (1905, p. 359) to light-colored specimens from the Volga river region which had a reddish patch on frontal face of 1st gaster tergite and which he considered as transitionary form between what he called *Formica exsecta* and *F. exsecta* var. *rubens*. Ruzsky did not made further descriptive statements nor did he report collecting data or an explicit type locality.

Formica exsecta var. *wheeleri* Stitz, 1939

First available use of *Formica exsecta exsecta wheeleri* Krausse, 1926; unresolved junior primary homonym of *Formica wheeleri* Creighton, 1935. It was described from near Eberswalde / Germany. The description does not allow even a guess to which of the three species occurring near Eberswalde this taxon might belong.

Formica liophtalma Chang & He, 2002

This taxon has been described from Wuwei, 3400 m, Gansu Province / China. The description clearly indicates a *Coptoformica* species but does not allow a species identification. The material investigated during this revision indicated four species to occur in Gansu: the Beishan morph of *Formica exsecta*, *Formica pisarskii*, *Formica manchu* and *Formica brunneonitida*. The very rough, unskilled description of Chang & He, mentioning "hairs very sparse" and a weakly notched petiolar crest, could possibly indicate a synonymy with *F. brunneonitida* but this remains a speculation.

4.7 Acknowledgements

Among some 50 persons who provided ant samples over 41 years of Bernhard Seifert's professional activity as ant researcher in Görlitz we wish to thank in particular Alina Kupyanskaya / Khabarovsk, Igor Antonov / Irkutsk, Frode Odegaard / Oslo, Pekka Puntilla / Helsinki, Michael Saaristo / Turku (deceased), Uwe Sörensen / Süderlügum, Günther Stöckel / Neustrelitz and Bernd Wesenigk-Sturm / Potsdam.

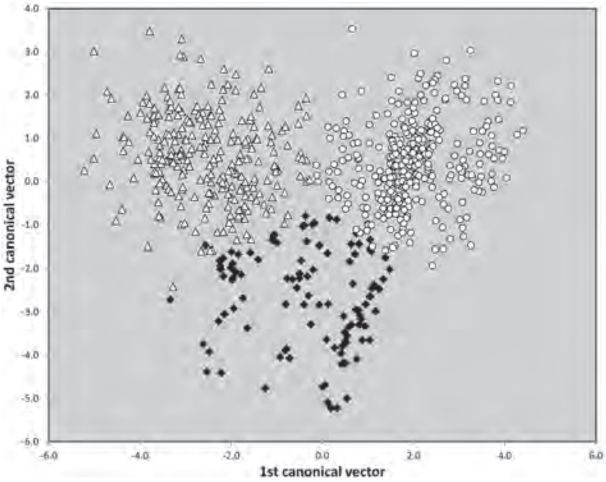

Fig. 27: Linear discriminant analysis separating 345 workers of the Normal morph (white circles), 253 workers of the Rubens morph (white triangles) and 110 workers of the Beishan morph (black rhombs) of *Formica exsecta*. Eight morphological characters were considered. The structuring within the clusters of the Normal and Beishan morphs is an artefact caused by the discrete 1-2-3-4-5 data format of ClySet.

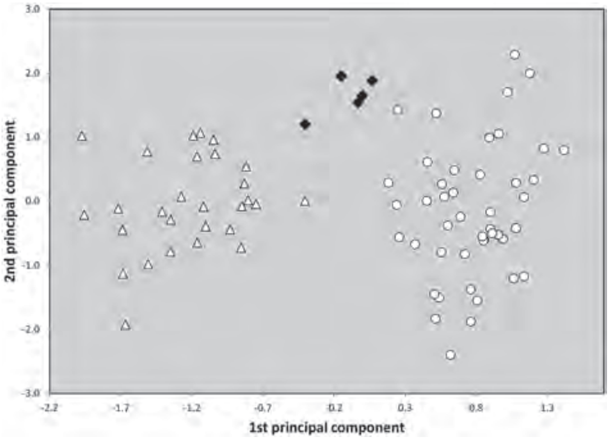

Fig. 28: Principal component analysis separating 45 gynes of the Normal morph (white circles), 28 gynes of the Rubens morph (white triangles) and 5 gynes of the Beishan morph (black rhombs) of *Formica exsecta*. Fifteen morphological characters were considered.

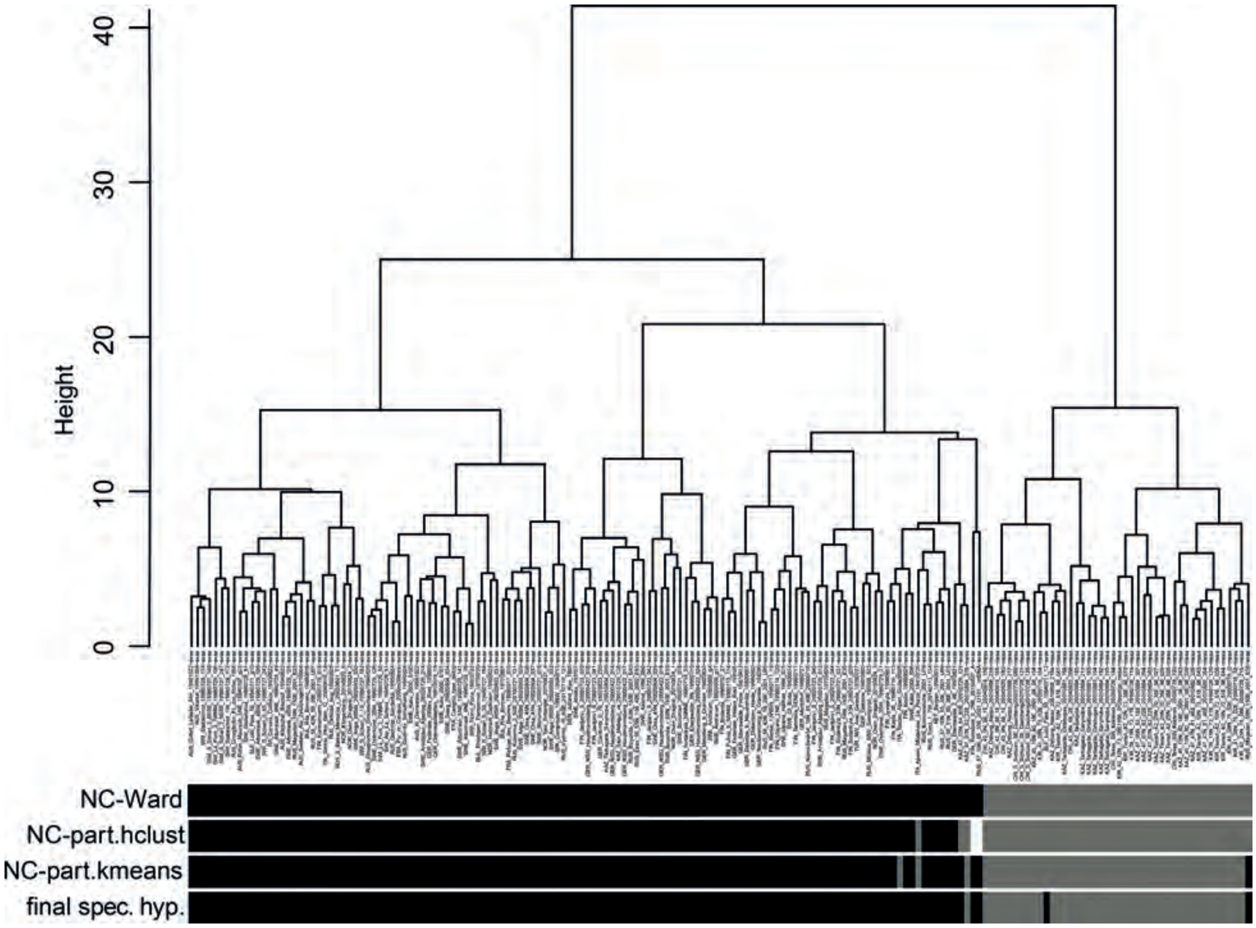

Fig. 29: Classification by three variants of NC-clustering of 131 worker nest samples of *Formica exsecta* containing a large percentage of Normal morph workers (black bars) and of 43 worker nest samples of *F. mesasiatica* (grey bars). White bars indicate outliers in NC-part.clust. The mean error of three analyses is 1.5 %. Twelve phenotypic characters were considered.

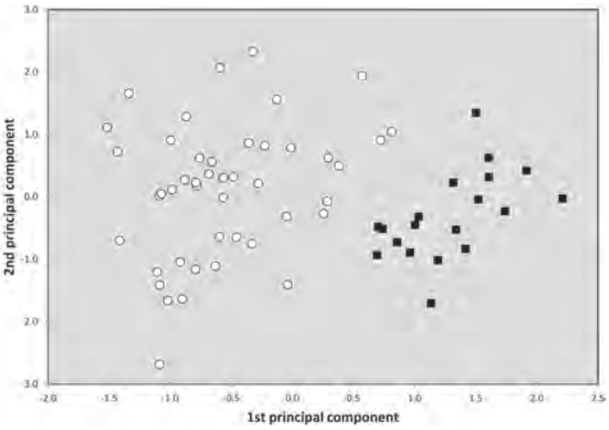

Fig. 30: Principal component analysis of gynes of *Formica exsecta* (white dots) and of *F. mesasiatica* (black squares). Seven morphological characters were considered.

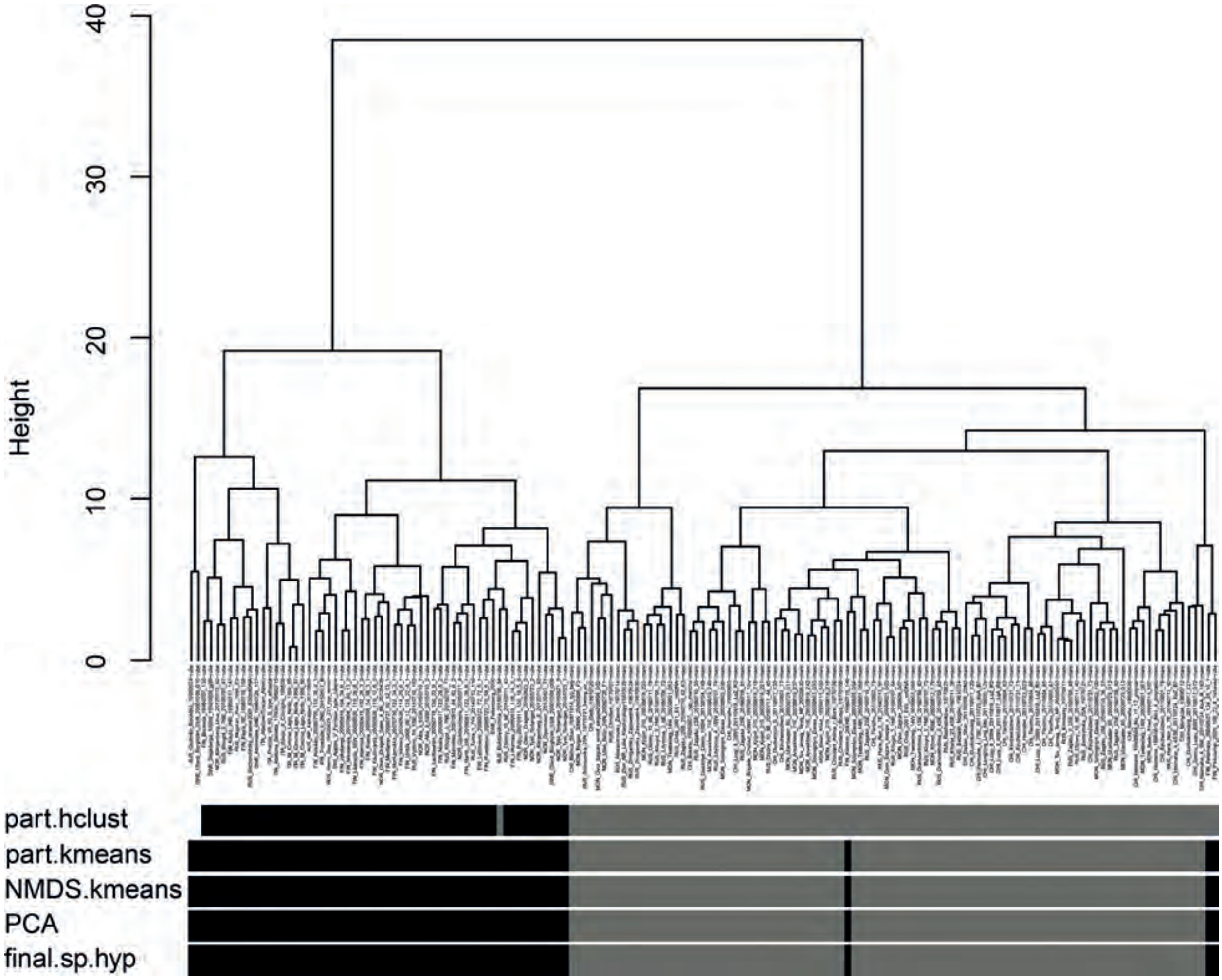

Fig. 31: Classification by four variants of NC-clustering and a principal component analysis of 97 nest samples of *F. manchu* (grey bars) and 60 nest samples of *F. exsecta* containing a large percentage of Rubens morph individuals (black bars). The white gaps indicate outliers in NC-part.clust. The mean error of five exploratory data analyses is 0.8 %. Ten phenotypic characters were considered.

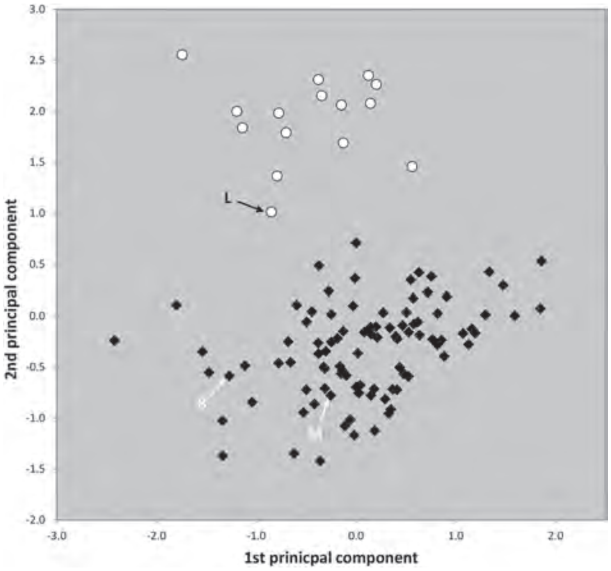

Fig. 32: Nest sample means of the 1st and 2nd principal components of 94 nest samples of *Formica manchu* (black rhombs) and 15 nest samples of *F. longiceps* workers (white discs). Twelve phenotypic characters were considered. Arrows point to the type series of *F. longiceps* (L), *F. manchu* (M) and *F. beijingensis* (B).

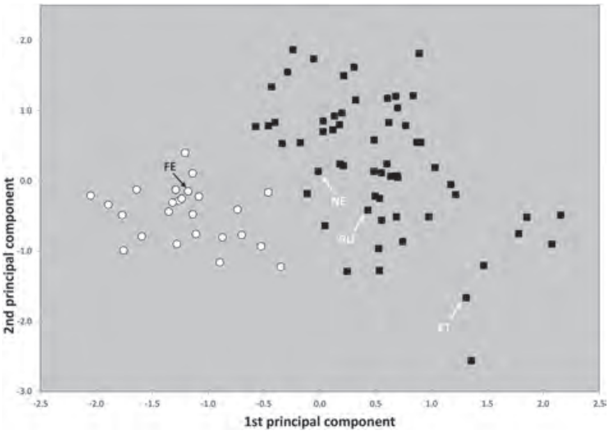

Fig. 33: Nest sample means of the 1st and 2nd principal components of 25 nest samples of *Formica fennica* (white discs) and 59 nest samples of *F. exsecta* containing a large percentage of Rubens morph workers (black squares). Nine phenotypic characters were considered. Arrows point to the type series of *F. fennica* (FE), *F. rubens* (RU), *F. etrusca* (ET) and *F. nemoralis* (NE).

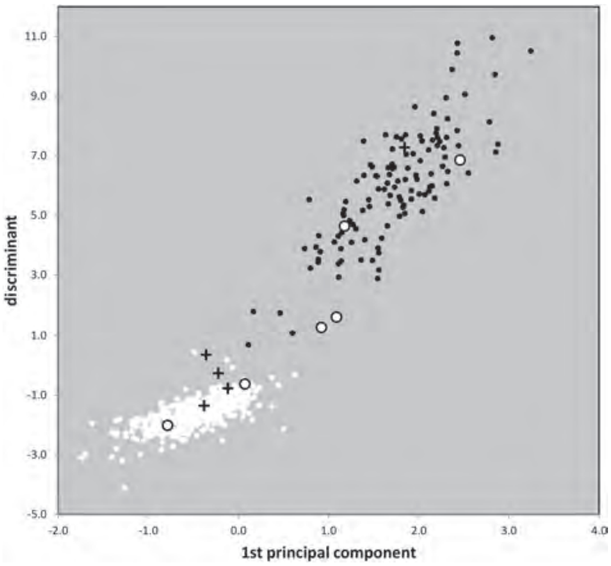

Fig. 34: Linear discriminant scores plotted against the first principal component considering ten morphological characters of workers of *Formica bruni* (small black dots, n=118), *F. pressilabris* (small white dots, n=436) and of two mixed nest samples from Montana / Switzerland containing hybrids as well as supposedly pure-bred specimens (black crosses mixed sample SaNo 201, black-margined white dots mixed sample SaNo 202). All specimens from the mixed samples were run as wild-cards in the discriminant analysis.

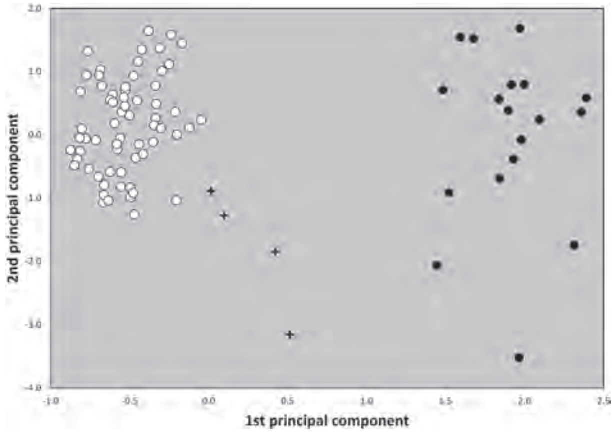

Fig. 35: Principal component analysis considering 13 morphological characters of gynes of *Formica bruni* (small black dots, n=18), *F. pressilabris* (small white dots, n=67) and of the mixed sample SaNo 201 (black crosses) in which at least three gynes should be hybrids *F. bruni* x *pressilabris*.

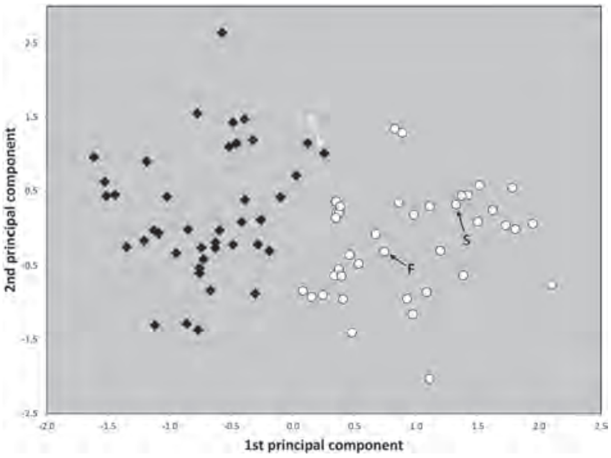

Fig. 36: Principal component analysis of workers of *Formica forsslundi* (white dots) and of *F. brunneonitida* (black rhombs). Arrows mark the type series of *F. brunneonitida* (B), *F. forsslundi* (F) and *F. strawinskii* (S).

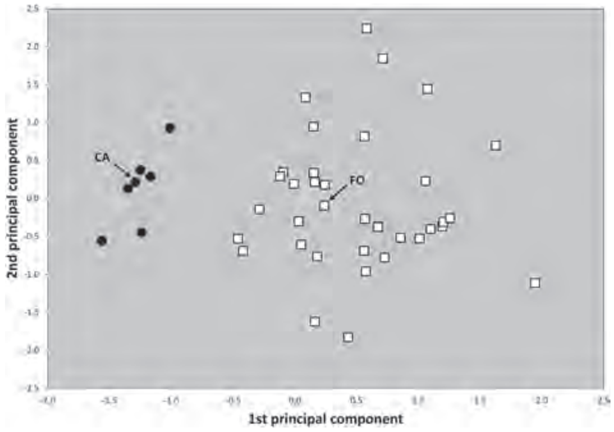

Fig. 37: Nest sample means of the 1st and 2nd principal components considering eleven morphological characters of workers of *Formica caucasicola* spec. nov. (black dots, n=7) and *F. forsslundi* (white squares, n=35). Arrows point to the type series of *F. caucasicola* spec. nov. (CA) and *F. forsslundi* (FO).

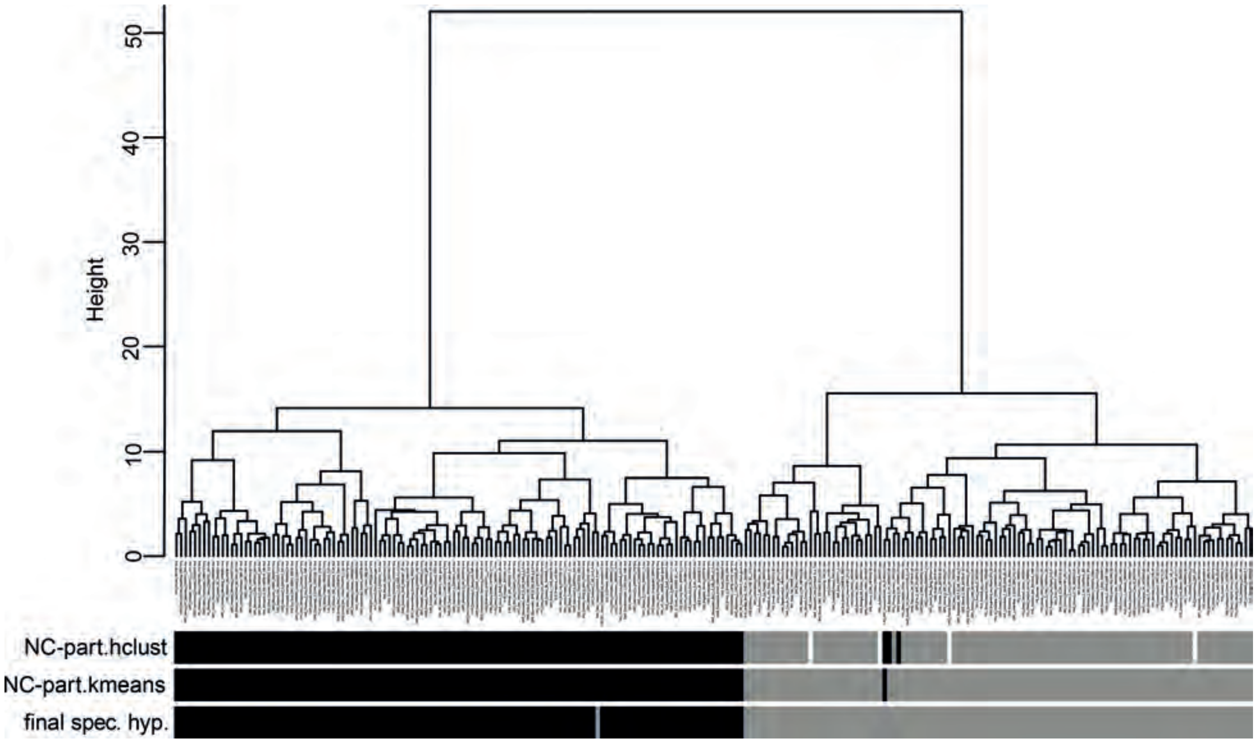

Fig. 38: Classification by NC-Ward clustering (dendrogram shown), NC-part.hclust clustering and NC-part.kmeans clustering of 234 worker nest samples of *Formica foreli* (black bars) and *F. pressilabris* (grey bars) considering eight morphological characters. White bars indicate outliers in NC-part.hclust. The mean error of the three exploratory analyses relative to the controlling LDA is 0.85 %.

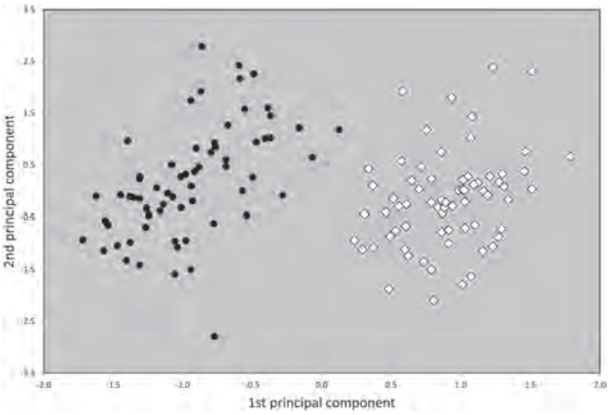

Fig. 39: Principal component analysis of 137 gynes of *Formica foreli* (white rhombs) and *F. pressilabris* (black dots) considering seven morphological characters.

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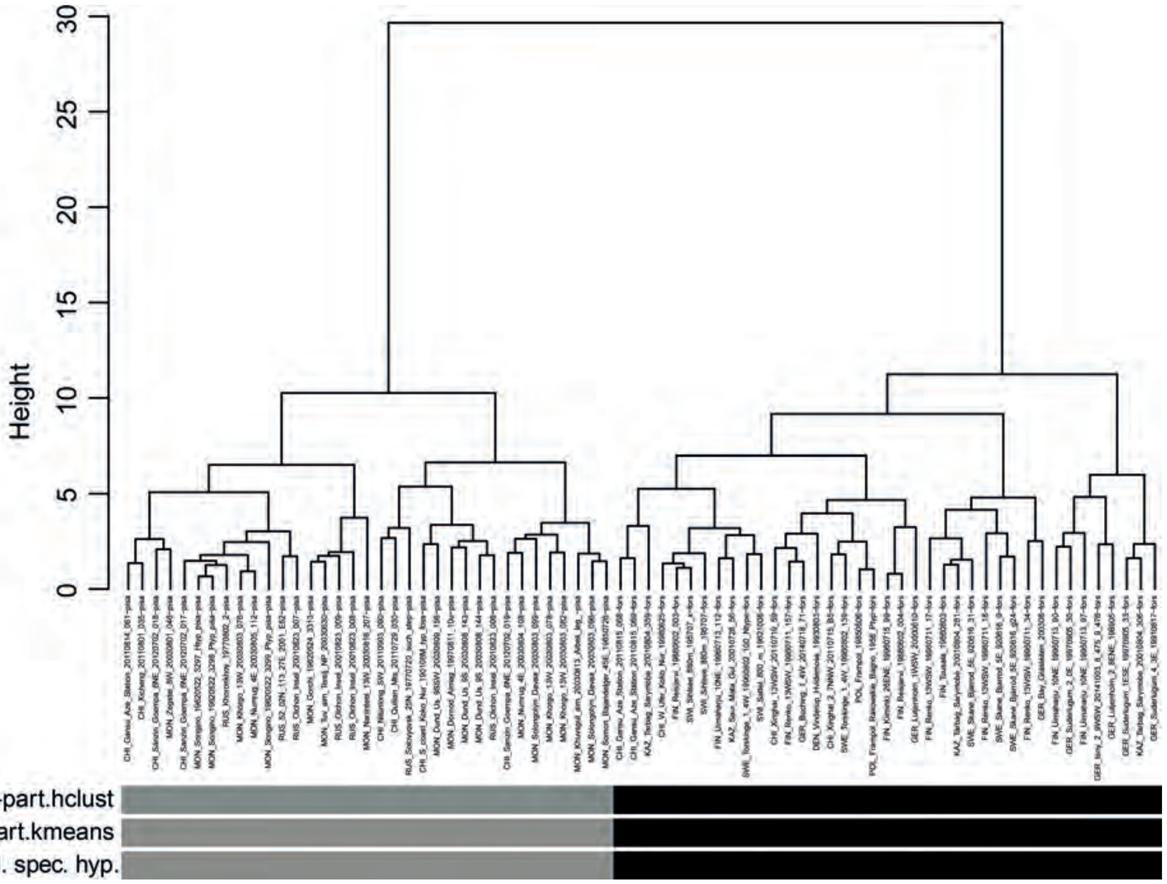

Fig. 40: Classification by NC-Ward clustering (dendrogram shown), NC-part.hclust clustering and NC-part.kmeans clustering of 74 worker nest samples of *Formica forsslundi* (black bars) and *F. pisarskii* (grey bars) considering six morphological characters. The mean error of the three exploratory analyses relative to the controlling LDA is 0 %.

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Tab. 1: Slope of allometry a_1 of scape length index (function SL /CW = a_1*CS + b_1) and of allometry a_2 of head length index (function CL/CW = a_2*CS + b_2) in different subgenera of *Formica*. Only data sets with more than 37 workers available per species or morph were considered. Data are given as arithmetic mean ± standard deviation [minimum, maximum]; n = number of species / morphs evaluated.

Subgenus	slope a_1 of index SL/CW	slope a_2 of index CL/CW	n
Coptoformica	0.0123 ± 0.0245 [−0.0388, 0.0480]	0.0316 ± 0.0581 [−0.0451, 0.1293]	14
Serviformica	−0.1874 ± 0.0447 [−0.3067,−0.0985]	−0.1183 ± 0.0296 [−0.1768,−0.0578]	35
Formica s.str.	−0.1151 ± 0.0154 [−0.1462,−0.0887]	−0.1022 ± 0.0123 [−0.1170,−0.0770]	14
Raptiformica	−0.0745	−0.0836	1

Tab. 2: Morphometric data of worker individuals of *Formica* (*Coptoformica*) species with mean EyeHL > 17 µm. Given are arithmetic mean ± standard deviation [lower extreme, upper extreme] number of individuals.

	mesasiatica	*exsecta* Normal morph	*exsecta* Rubens morph	*exsecta* Beishan morph	*manchu*	*longiceps*	*fennica*
CS	1425 ± 78 [1223,1597] 109	1392 ± 85 [1143,1631] 349	1396 ± 82 [1145,1608] 253	1387 ± 68 [1198,1575] 110	1358 ± 80 [1130,1586] 318	1290 ± 58 [1149,1430] 55	1271 ± 84 [1050,1468] 91
CL/CW	1.044 ± 0.019 [0.990,1.083] 109	1.047 ± 0.023 [0.983,1.119] 349	1.049 ± 0.018 [1.008,1.105] 253	1.053 ± 0.016 [1.007,1.090] 110	1.075 ± 0.019 [1.018,1.131] 318	1.076 ± 0.017 [1.030,1.117] 55	1.072 ± 0.020 [1.019,1.123] 91
SL/CS	1.046 ± 0.023 [0.977,1.094] 109	1.028 ± 0.022 [0.966,1.085] 349	1.020 ± 0.022 [0.956,1.078] 253	1.062 ± 0.021 [1.003,1.120] 110	1.040 ± 0.021 [0.963,1.110] 318	1.089 ± 0.020 [1.045,1.135] 55	1.022 ± 0.025 [0.960,1.084] 91
Fu3/CS %	13.86 ± 0.50 [12.65,14.85] 33	13.77 ± 0.51 [12.19,14.63] 60	13.70 ± 0.53 [12.43,15.07] 194	14.08 ± 0.53 [12.66,15.56] 99	13.66 ± 0.54 [12.13,14.91] 310	14.19 ± 0.47 [13.13,15.18] 55	13.43 ± 0.62 [11.73,15.25] 91
Fu2 /Fu3	1.001 ± 0.039 [0.937,1.085] 33	0.985 ± 0.039 [0.896,1.077] 60	0.974 ± 0.035 [0.885,1.085] 194	0.976 ± 0.030 [0.912,1.058] 99	0.967 ± 0.037 [0.824,1.068] 310	0.925 ± 0.025 [0.877,0.977] 55	0.988 ± 0.038 [0.868,1.094] 91
OCED /CS	0.186 ± 0.011 [0.160,0.209] 109	0.188 ± 0.010 [0.155,0.215] 345	0.187 ± 0.011 [0.158,0.217] 253	0.173 ± 0.011 [0.146,0.206] 110	0.167 ± 0.010 [0.134,0.198] 316	0.180 ± 0.008 [0.158,0.195] 55	0.179 ± 0.009 [0.156,0.198] 91
PeINC /CS [%]	4.88 ± 1.30 [2.06,7.68] 48	4.89 ± 1.60 [0.00,9.11] 128	5.16 ± 1.64 [1.54,11.40] 170	5.74 ± 1.58 [1.93,10.26] 98	5.34 ± 1.99 [0.65,10.45] 108	3.04 ± 1.00 [0.61,5.51] 55	3.62 ± 1.00 [2.10,6.50] 50
EyeHL	29.7 ± 4.9 [13.9,45.0] 109	27.8 ± 6.7 [0.0,60.3] 349	27.6 ± 7.6 [0.0,44.8] 253	29.3 ± 5.4 [11.8,40.0] 110	30.7 ± 8.3 [0.23,50.0] 318	22.7 ± 8.3 [15.0,33.1] 55	24.9 ± 4.5 [16.2,38.1] 91
ClySet	3.94 ± 0.71 [2.0,5.0] 109	4.10 ± 0.52 [3.0,5.0] 349	2.08 ± 0.48 [1.0,3.0] 253	3.24 ± 0.82 [1.0,4.5] 110	1.89 ± 0.52 [1.0,4.0] 318	2.65 ± 0.92 [1.0,5.0] 55	1.77 ± 0.54 [1.0,3.0] 91
ClyPub	2.59 ± 1.13 [0.0,7.0] 109	3.20 ± 1.02 [0.8,6.5] 349	3.41 ± 1.30 [0.0,6.5] 253	3.02 ± 1.18 [0.7,5.5] 110	3.07 ± 1.34 [0.3,7.5] 318	3.68 ± 1.44 [0.0,7.0] 55	1.97 ± 0.90 [0.0,4.3] 91
nOce	1.78 ± 0.39 [0.7,3.0] 109	2.14 ± 0.56 [0.7,6.0] 349	1.43 ± 0.74 [0.0,4.0] 253	1.81 ± 0.43 [0.0,3.0] 110	0.42 ± 0.58 [0.0,2.0] 315	1.71 ± 0.61 [0.0,3.0] 55	0.38 ± 0.64 [0.0,2.5] 91
nCox	4.01 ± 1.84 [0.8, 8.5] 109	9.47 ± 2.99 [2.5,18.5] 349	3.62 ± 2.09 [0.2,13.1] 253	4.02 ± 1.94 [0.0,9.5] 110	1.73 ± 1.00 [0.0,4.5] 318	2.57 ± 1.25 [0.2,5.0] 55	1.05 ± 0.97 [0.0,3.7] 91
nMet	1.97 ± 1.71 [0.0,6.5] 109	2.46 ± 2.22 [0.0,10.5] 349	0.35 ± 0.77 [0.0,7.0] 253	0.12 ± 0.32 [0.0,1.5] 110	0.04 ± 0.12 [0.0,0.73] 318	0.03 ± 0.10 [0.0,0.5] 55	0.03 ± 0.11 [0.0,0.5] 91
TERG	1.00 ± 0.00 [1.00,1.00] 109	1.02 ± 0.16 [1.0,3.0] 349	2.23 ± 0.96 [1.0,4.0] 253	1.05 ± 0.22 [1.0,2.0] 110	2.91 ± 0.33 [2.0,4.0] 317	1.68 ± 0.68 [1.0,3.5] 55	3.38 ± 0.70 [2.0,6.0] 91
GHL/ CS [%]	6.28 ± 2.82 [0.0,10.21] 38	4.92 ± 3.44 [0.00,12.68] 129	0.28 ± 1.25 [0.00, 7.83] 175	4.58 ± 4.15 [0.00,11.94] 98	0.00 ± 0.00 [0.00,0.00] 318	1.65 ± 3.27 [0.00,10.70] 55	0.00 ± 0.00 [0.00,0.00] 91
T3f	1.00 ± 0.00 [1.00,1.00] 33	0.96 ± 0.17 [0.0,1.0] 182	0.70 ± 0.44 [0.0,1.0] 231	1.00 ± 0.03 [0.7,1.0] 109	0.91 ± 0.28 [0.0,1.0] 313	0.98 ± 0.15 [0.0,1.0] 55	0.18 ± 0.37 [0.0,1.0] 91
nHTfl	7.63 ± 1.32 [5.2,10.6] 109	9.25 ± 1.95 [5.0,15.5] 349	7.67 ± 1.45 [3.8,13.1] 253	8.35 ± 1.33 [4.5,11.5] 110	5.16 ± 1.07 [2.75, 7.4] 318	7.36 ± 1.08 [5.5,10.0] 55	6.77 ± 1.78 [3.5,13.9] 91
sqPDO	4.24 ± 0.59 [2.90,6.20] 109	5.39 ± 1.00 [3.21,8.91] 349	6.60 ± 1.55 [3.74,15.22] 253	6.50 ± 1.19 [4.11,10.34] 110	6.56 ± 1.36 [4.46,14.77] 318	7.06 ± 0.91 [5.44,11.14] 55	6.83 ± 1.11 [4.52,12.74] 91
sqPDG	4.75 ± 0.64 [3.61,6.63] 109	6.90 ± 1.18 [3.93,9.84] 349	7.52 ± 1.19 [4.33,10.30] 253	7.29 ± 1.07 [4.37,10.73] 110	7.35 ± 1.14 [4.39,10.42] 318	7.35 ± 0.55 [6.24,9.01] 55	7.62 ± 0.55 [6.53,8.94] 91

Tab. 3: Morphometric data of worker individuals of *Formica* (*Coptoformica*) species with mean EyeHL < 18 µm. Given are arithmetic mean ± standard deviation [lower extreme, upper extreme] number of individuals.

	bruni	*caucasicola* **sp. nov.**	*forsslundi*	*brunneonitida*	*pressilabris*	*foreli*
CS	1275 ± 70 [1062,1450] 176	1306 ± 37 [1233,1380] 35	1250 ± 66 [1018,1378] 112	1255 ± 68 [1082,1412] 143	1255 ± 69 [1032,1386] 477	1246 ± 73 [997,1456] 499
CL/CW	1.047 ± 0.018 [1.001,1.100] 176	1.056 ± 0.017 [1.029,1.106] 35	1.045 ± 0.018 [1.000,1.084] 112	1.054 ± 0.021 [1.004,1.107] 143	1.046 ± 0.022 [0.969,1.149] 477	1.052 ± 0.020 [0.975,1.118] 499
SL/CS	1.038 ± 0.025 [0.969,1.095] 176	0.972 ± 0.017 [0.938,1.011] 35	1.008 ± 0.018 [0.965,1.057] 112	1.024 ± 0.023 [0.961,1.073] 143	0.997 ± 0.024 [0.919,1.078] 477	1.034 ± 0.023 [0.951,1.107] 499
Fu3/CS [%]	13.86 ± 0.51 [13.21,15.04] 19	12.61 ± 0.35 [12.00,13.37] 35	12.94 ± 0.43 [11.85,13.72] 49	13.14 ± 0.53 [12.05,14.47] 34	13.51 ± 0.42 [12.82,14.27] 27	13.50 ± 0.35 [12.86,14.24] 25
Fu2 /Fu3	0.980 ± 0.030 [0.936,1.051] 19	0.948 ± 0.028 [0.904,1.008] 35	0.922 ± 0.033 [0.821,0.998] 47	0.952 ± 0.039 [0.856,1.011] 34	0.923 ± 0.031 [0.869,0.978] 20	0.948 ± 0.033 [0.887,1.022] 25
OCED/ CS	0.190 ± 0.010 [0.168,0.216] 24	0.182 ± 0.007 [0.166,0.198] 35	0.181 ± 0.010 [0.156,0.212] 98	0.186 ± 0.010 [0.166,0.217] 131	0.184 ± 0.010 [0.158,0.229] 121	0.185 ± 0.010 [0.164,0.210] 117
PeINC /CS [%]	2.98 ± 0.75 [1.90,4.52] 16	3.48 ± 0.89 [1.94,5.70] 35	3.35 ± 1.00 [1.42,5.43] 96	3.05 ± 0.88 [0.93,4.76] 77	2.17 ± 0.75 [0.84,3.87] 41	2.39 ± 0.87 [1.10,4.67] 40
EyeHL	16.0 ± 5.4 [4.0,30.0] 176	6.5 ± 2.1 [4.0,13.0] 35	6.7 ± 2.2 [0.0,15.0] 112	6.8 ± 3.1 [0.0,25.0] 143	4.8 ± 2.0 [0.0,10.0] 477	5.6 ± 2.3 [0.0,15.5] 465
ClySet	1.76 ± 0.52 [1.0,3.0] 176	1.46 ± 0.51 [1.0,2.0] 35	2.00 ± 0.59 [1.0,4.0] 112	1.33 ± 0.50 [1.0,3.0] 143	1.03 ± 0.16 [1.0,2.0] 359	1.07 ± 0.25 [1.0,2.0] 343
ClyPub	4.14 ± 1.36 [1.0,8.1] 118	0.10 ± 0.22 [0.0,0.7] 35	1.87 ± 1.36 [0.0,6.2] 112	0.08 ± 0.39 [0.0,3.5] 143	0.02 ± 0.14 [0,2.1] 451	0.07 ± 0.31 [0.0,2.9] 343
nOce	0.63 ± 0.81 [0.0,3.1] 176	0.20 ± 0.36 [0.0,1.3] 35	1.48 ± 1.04 [0.0,3.9] 112	0.28 ± 0.54 [0.0,2.0] 143	0.00 ± 0.00 [0.0,0.0] 472	0.00 ± 0.00 [0.0,0.0] 499
nCox	0.22 ± 0.57 [0.0,3.3] 172	0.06 ± 0.16 [0.0,0.5] 35	1.82 ± 1.39 [0.0,5.5] 112	0.10 ± 0.36 [0.0,3.0] 143	0.01 ± 0.07 [0.0,1.0] 475	0.00 ± 0.00 [0.0,0.0] 493
nMet	0.01 ± 0.08 [0.0,1.0] 176	0.00 ± 0.00 [0,0.0] 35	0.02 ± 0.15 [0,1.2] 112	0.00 ± 0.00 [0,0.0] 143	0.0 ± 0.0 [0,0.0] 475	0.00 ± 0.00 [0,0.0] 499
TERG	3.22 ± 0.69 [2.0,5.0] 176	1.17 ± 0.45 [1.0,3.0] 35	1.14 ± 0.38 [1.0,3.0] 112	1.78 ± 0.75 [1.0,3.0] 143	3.22 ± 0.48 [2.0,5.0] 477	3.86 ± 0.41 [3.0,5.0] 499
GHL/ CS [%]	0.00 ± 0.00 [0.00, 0.00] 176	1.12 ± 2.28 [0.00,8.24] 35	5.55 ± 2.96 [0.00,9.84] 24	0.85 ± 1.94 [0.00,7.60] 63	0.00 ± 0.00 [0.00, 0.00] 36	0.00 ± 0.00 [0.00, 0.00] 31
T3f	0.42 ± 0.50 [0.0,1.0] 26	1.00 ± 0.00 [1.0,1.0] 35	1.00 ± 0.00 [1.0,1.0] 27	0.97 ± 0.16 [0.0,1.0] 132	0.30 ± 0.44 [0.0,1.0] 120	0.10 ± 0.30 [0.0,1.0] 31
nHTfl	4.36 ± 1.50 [1.2,10.9] 176	5.69 ± 1.10 [3.2,8.5] 35	6.40 ± 1.39 [3.6,12.0] 112	4.96 ± 1.59 [1.2,9.8] 143	2.88 ± 1.15 [0.0,7.1] 458	2.72 ± 1.22 [0.0,7.5] 468
sqPDO	4.49 ± 0.50 [3.11,6.08] 176	7.15 ± 0.93 [5.69,9.44] 35	7.29 ± 0.92 [5.99,11.30] 112	7.65 ± 1.63 [5.15,17.75] 143	6.47 ± 0.75 [4.38,11.63] 475	4.69 ± 0.63 [3.39,8.24] 499
sqPDG	6.35 ± 0.48 [5.14,7.73] 176	6.65 ± 0.49 [5.90,8.74] 35	7.06 ± 0.53 [5.62,9.17] 112	6.77 ± 0.65 [4.02,8.24] 143	6.69 ± 0.42 [5.62,8.63] 475	6.11 ± 0.46 [4.45,7.41] 499

Tab. 4: Morphometric data of worker individuals of *Formica* (*Coptoformica*) species of different relatedness. Given are arithmetic mean ± standard deviation [lower extreme, upper extreme] number of individuals. F and p values of an univariate ANOVA compare the data of the Middle Asian and Sichuan populations of *Formica mesasiatica*. F values of most significant differences given in heavy type.

	suecica	*pisarskii*	*mesasiatica* Middle Asia	ANOVA $F_{1,107}$, p	*mesasiatica* Sichuan	*fukaii*
CS	1337 ± 50 [1198,1428] 73	1246 ± 66 [1096,1359] 92	1428 ± 78 [1223,1597] 99	1.26 n.s.	1399 ± 77 [1314,1540] 10	1448 ± 42 [1380,1517] 13
CL/CW	1.020 ± 0.017 [0.965,1.056] 73	1.069 ± 0.018 [1.035,1.112] 92	1.046 ± 0.019 [0.990,1.083] 99	7.03 0.009	1.029 ± 0.016 [1.004,1.062] 10	1.064 ± 0.012 [1.034,1.076] 13
SL/CS	1.040 ± 0.019 [0.991,1.084] 73	1.044 ± 0.020 [0.998,1.085] 92	1.046 ± 0.023 [0.977,1.094] 99	0 n.s.	1.046 ± 0.021 [1.005,1.076] 10	1.069 ± 0.014 [1.043,1.090] 12
Fu3/CS [%]	14.06 ± 0.56 [12.99,14.99] 24	13.50 ± 0.49 [12.03,14.31] 35	13.78 ± 0.58 [12.65,14.85] 23		14.04 ± 0.17 [13.80,14.23] 10	no data
Fu2/Fu3	0.961 ± 0.028 [0.901,1.028] 24	0.950 ± 0.026 [0.903,1.004] 35	1.004 ± 0.039 [0.937,1.085] 23		0.995 ± 0.039 [0.944,1.052] 10	no data
OceD /CS	0.170 ± 0.009 [0.152,0.185] 24	0.183 ± 0.009 [0.165,0.208] 61	0.187 ± 0.011 [0.163,0.209] 99	**18.58** 0.000	0.172 ± 0.009 [0.160,0.186] 10	0.173 1
PeINC /CS [%]	3.52 ± 0.80 [2.30,5.25] 24	3.12 ± 1.70 [0.74,8.21] 29	4.72 ± 1.29 [2.06,7.68] 38		5.48 ± 1.18 [3.95,7.12] 10	no data
EyeHL	6.4 ± 1.9 [0.0,13.0] 73	7.2 ± 3.6 [0.0,21.5] 92	29.4 ± 5.0 [13.9,45.0] 99	3.34 n.s.	32.4 ± 2.4 [29.6,35.5] 10	25.3 ± 2.1 [22.0,29.0] 12
ClySet	3.99 ± 0.12 [3.0,4.0] 73	3.92 ± 0.67 [2.0,5.0] 92	4.00 ± 0.70 [2.0,5.0] 99	**9.50** 0.003	3.30 ± 0.48 [3.0,4.0] 10	1.69 ± 0.48 [1.0,2.0] 13
ClyPub	0.64 ± 0.51 [0.0,2.2] 73	1.07 ± 1.05 [0.0,5.5] 92	2.69 ± 1.06 [0.5,7.0] 99	**9.36** 0.003	1.59 ± 1.35 [0.0,3.5] 10	no data
nOce	1.96 ± 0.32 [1.0,2.8] 73	2.34 ± 0.56 [0.0,4.6] 92	1.76 ± 0.40 [0.7,3.0] 99	3.60 n.s.	2.00 ± 0.00 [2.0,2.0] 10	0.90 ± 0.50 [0.0,2.0] 12
nCox	4.57 ± 1.41 [1.0,8.0] 69	2.96 ± 1.19 [0.0,5.8] 92	4.26 ± 1.74 [0.8, 8.5] 99	**24.45** 0.000	1.52 ± 0.55 [1.0, 2.5] 10	0.07 ± 0.23 [0.0,0.8] 12
nMet	1.06 ± 0.71 [0.0,3.4] 73	0.02 ± 0.10 [0,0.5] 91	2.17 ± 1.67 [0.0,6.5] 99	**16.73** 0.000	0.00 ± 0.00 [0.0,0.0] 10	0.00 ± 0.00 [0,0] 12
TERG	1.01 ± 0.12 [1.0,2.0] 73	1.00 ± 0.00 [1.0,1.0] 92	1.00 ± 0.00 [1.00,1.00] 99	0 n.s.	1.00 ± 0.00 [1.00,1.00] 10	0.00 ± 0.00 [0.0,0.0] 13
GHL/CS [%]	5.34 ± 1.29 [3.2,7.7] 24	8.31 ± 2.09 [0.0,11.11] 32	6.28 ± 2.82 [0.0,10.2] 38		no data	0.00 ± 0.00 [0.0,0.0] 13
T3f	0.86 ± 0.35 [0.0,1.0] 29	0.99 ± 0.06 [0.7,1.0] 46	1.00 ± 0.00 [1.0,1.0] 23		1.00 ± 0.00 [1.0,1.0] 10	1.0 1
nHTfl	6.47 ± 0.92 [4.5,8.3] 73	7.36 ± 1.18 [5.0,10.3] 92	7.69 ± 1.34 [5.2,10.6] 99	2.17 n.s.	7.05 ± 0.92 [6.0,8.5] 10	5.58 ± 1.89 [0.7,8.6] 12
sqPDO	4.76 ± 0.71 [3.96,6.50] 25	7.38 ± 0.68 [6.01,8.97] 92	4.15 ± 0.54 [2.90,6.20] 99	**26.3** 0.000	5.06 ± 0.42 [4.42,5.86] 10	3.74 ± 0.33 [3.24,4.47] 13
sqPDG	5.24 ± 0.40 [4.63,6.20] 25	7.31 ± 0.54 [5.98,8.84] 92	4.76 ± 0.65 [3.61,6.63] 99	0.02 n.s.	4.73 ± 0.58 [4.00,5.64] 10	3.95 ± 0.13 [3.70,4.18] 12

Tab. 5: Morphometric data of gyne individuals of rather large *Formica* (*Coptoformica*) species with mean EyeHL > 25 µm. Given are arithmetic mean ± standard deviation [lower extreme, upper extreme] number of evaluated specimens.

	fukaii	*mesasiatica*	*exsecta*	*exsecta*	*exsecta*	*manchu*	*longiceps*	*fennica*
CS	1690	1722 ± 51 [1648,1818] 19	1682 ± 41 [1584,1791]76	1597 ± 28 [1567,1641] 5	1625 ± 27 [1567,1677] 28	1635 ± 26 [1566,1691] 21	1462 ± 9 [1452,1469] 4	1538 ± 34 [1475,1593] 19
CL/CW	0.979	0.968 ± 0.023 [0.926,1.001]19	0.950 ± 0.022 [0.900,1.008]76	0.992 ± 0.015 [0.975,1.005] 5	0.980 ± 0.021 [0.938,1.016] 28	1.002 ± 0.015 [0.969,1.032] 21	1.033 ± 0.024 [1.002,1.059] 4	1.019 ± 0.015 [0.997,1.054]19
SL/CS	0.956	0.958 ± 0.021 [0.918,0.986]19	0.932 ± 0.024 [0.851,0.988]76	0.982 ± 0.024 [0.953,1.004] 5	0.911 ± 0.015 [0.879,0.943] 28	0.911 ± 0.017 [0.879,0.941] 21	0.967 ± 0.024 [0.944,0.993] 4	0.932 ± 0.021 [0.893,0.978]19
Fu2/CS	no data	13.64 ± 0.45 [12.86,14.45]10	12.79 ± 0.75 [11.49,13.99]15	13.47 ± 0.33 [13.13,13.86] 5	12.61 ± 0.52 [11.69,13.62] 28	12.30± 0.42 [11.51,13.25] 21	12.54± 0.11 [12.45,12.69] 4	12.97± 0.62 [11.72,14.20]19
Fu2/Fu3	no data	1.004 ± 0.025 [0.963,1.035]10	0.979 ± 0.039 [0.916,1.052]15	0.980 ± 0.013 [0.965,0.996] 5	0.973 ± 0.036 [0.924,1.058] 28	0.968 ± 0.044 [0.906,1.077] 21	0.876 ± 0.029 [0.839,0.905] 4	1.000 ± 0.043 [0.944,1.141]19
OceD/CS	no data	0.202 ± 0.007 [0.190,0.215]18	0.202 ± 0.013 [0.181,0.224]17	0.187 ± 0.009 [0.177,0.199] 5	0.194 ± 0.009 [0.180,0.209] 28	0.176 ± 0.009 [0.158,0.189] 21	0.190 ± 0.008 [0.183,0.199] 4	0.188 ± 0.008 [0.172,0.202]19
ML/CS	1.745	1.746 ± 0.033 [1.661,1.801]19	1.715 ± 0.051 [1.613,1.812]76	1.741 ± 0.022 [1.707,1.767] 5	1.696 ± 0.030 [1.639,1.748] 28	1.680 ± 0.033 [1.620,1.727] 21	1.618 ± 0.013 [1.608,1.637] 4	1.700 ± 0.032 [1.637,1.762]19
ClySet	no data	4.03 ± 0.42 [3.0,5.0] 19	4.00 ± 0.48 [2.0,5.0] 45	3.50 ± 0.70 [2.5,4.0] 5	2.09 ± 0.61 [1.0,3.0] 28	1.95 ± 0.38 [1.0,2.5] 21	1.75 ± 0.50 [1.0,2.0] 4	1.71 ± 0.56 [1.0,3.0] 19
ClyPub	no data	6.94 ± 2.13 [3.0,10.5] 19	4.89 ± 1.78 [2.5,10.0] 45	6.74 ± 0.86 [6.0, 8.0] 5	4.16 ± 1.25 [1.5, 7.0] 28	5.86 ± 2.51 [2.0,10.0] 21	5.38 ± 0.25 [5.0, 5.5] 4	3.34 ± 1.52 [1.5,7.5] 19
OceSet	no data	1.00 ± 0.00 [1.0,1.0] 19	1.00 ± 0.00 [1.0,1.0] 76	1.00 ± 0.00 [1.0,1.0] 6	0.62 ± 0.44 [0.0,1.0] 28	0.05 ± 0.21 [0.0,1.0] 21	0.50 ± 0.58 [0.0,1.0] 4	0.47 ± 0.51 [0.0,1.0] 19
EyeHL	46	47.5 ± 5.9 [40,57] 19	45.5 ± 7.4 [31,69] 76	45.4 ± 4.4 [39,51] 5	36.2 ± 7.4 [25,56] 28	51.1 ± 6.2 [34,61] 21	48.5 ± 4.0 [45,54] 4	30.7 ± 8.3 [17,50] 19
GLANZ	2.0	1.39 ± 0.31 [1.0,2.0] 19	1.70 ± 0.38 [1.0,2.5] 76	2.08 ± 0.37 [1.5,2.5] 5	1.44 ± 0.38 [1.0,2.5] 28	1.17 ± 0.22 [1.0,1.5] 21	1.18 ± 0.12 [1.0,1.3] 4	1.37 ± 0.27 [1.0,2.0] 19
OccHd	15	41.5 ± 14.1 [20, 73] 19	46.2 ± 22.0 [7,107] 70	24.4 ± 3.5 [19,28] 5	31.4 ± 18.0 [6,62] 28	33.2 ± 9.8 [16, 52] 21	45.0 ± 5.4 [39,50] 4	21.6 ± 10.5 [6,38] 19
MnHL	0.0	192.9 ± 29.5 [114,233] 19	178.0 ± 45.0 [0,256] 76	115.4 ± 77.3 [0,217] 5	66.8 ± 63.8 [0,172] 28	80.9 ± 60.6 [0,164] 21	150.5 ± 113.1 [88,320] 4	56.5 ± 41.2 [0,99] 19
TERG	3	1.00 ± 0.00 [1.0,1.0] 19	1.00 ± 0.00 [1.0,1.0] 76	1.00 ± 0.00 [1.0,1.0] 5	2.95 ± 0.80 [1.0,4.0] 28	2.76 ± 0.54 [1.5,4.0] 21	2.50 ± 0.58 [2.0,3.0] 4	3.65 ± 0.72 [2.0,5.0] 19
nCox	0.0	7.74 ± 3.36 [1.5,14.0] 19	12.70 ± 4.12 [3.5,23.0] 76	6.30 ± 1.46 [4.0, 8.0] 5	3.84 ± 1.72 [0.5, 7.0] 28	3.21 ± 1.11 [0.5, 5.5] 21	0.70 ± 0.48 [0.0,1.0] 4	2.24 ± 1.96 [0.0,6.5] 19
nHTfl	7.0	8.98 ± 2.07 [6.0,15.0] 19	12.69 ± 3.14 [8.0,22.0] 76	8.34 ± 1.88 [5.0, 9.5] 5	8.16 ± 1.36 [5.5,11.0] 28	3.69 ± 1.23 [1.5, 6.5] 21	4.75 ± 0.87 [3.5, 5.5] 4	7.05 ± 1.70 [4.5,11.5] 19
sqPDO	3.11	3.49 ± 0.27 [2.87,3.85] 19	4.26 ± 0.48 [3.34,5.75] 76	4.23 ± 0.23 [3.93,4.42] 5	5.93 ± 0.76 [4.71,7.78] 28	4.67 ± 1.01 [3.43,7.56] 21	5.04 ± 0.22 [4.82,5.31] 4	7.12 ± 2.40 [4.50,14.10] 19
sqPDG	3.23	4.48 ± 0.51 [3.67,5.77] 19	6.19 ± 1.15 [3.83,9.25] 76	7.57 ± 0.86 [6.24,8.44] 5	8.53 ± 1.07 [5.89,11.10] 28	6.21 ± 1.41 [4.02,7.93] 21	6.62 ± 0.27 [6.41,6.97] 4	9.00 ± 0.88 [7.47,11.00] 19

Tab. 6: Morphometric data of gyne individuals of rather small *Formica* (*Coptoformica*) species with mean EyeHL < 20 µm. Given are arithmetic mean ± standard deviation [lower extreme, upper extreme] number of evaluated specimens.

	suecica	*pisarskii*	*caucasicola*	*forsslundi*	*brunneonitida*	*pressilabris*	*foreli*
CS	1266 ± 22 [1226,1300] 28	1221 ± 28 [1192,1263] 5	1216 ± 6 [1212,1220] 2	1237 ± 28 [1204,1296] 22	1267 ± 50 [1156,1313] 13	1286 ± 34 [1202,1341] 67	1352 ± 35 [1286,1472] 70
CL/CW	0.979 ± 0.010 [0.951,0.994] 28	1.025 ± 0.029 [0.996,1.069] 5	1.007 ± 0.006 [1.003,1.011] 2	0.988 ± 0.020 [0.938,1.022] 22	0.996 ± 0.014 [0.974,1.020] 13	0.991 ± 0.020 [0.950,1.031] 67	0.984 ± 0.022 [0.934,1.042] 70
SL/CS	0.932 ± 0.013 [0.898,0.952] 28	0.899 ± 0.003 [0.897,0.903] 5	0.799 ± 0.003 [0.797,0.801] 2	0.853 ± 0.023 [0.812,0.891] 22	0.871 ± 0.018 [0.853,0.907] 13	0.845 ± 0.020 [0.787,0.893] 67	0.903 ± 0.022 [0.862,0.957] 70
Fu2/CS	12.67 ± 0.35 [11.94,13.24] 19	11.13 ± 0.57 [10.32,11.63] 4	9.93 ± 0.10 [9.86,10.00] 2	10.58 ± 0.53 [9.69,11.53] 16	10.73 ± 0.65 [9.34,11.60] 13	10.86 ± 0.40 [10.06,11.80] 25	11.71 ± 0.36 [11.00,12.36] 20
Fu2/Fu3	0.993 ± 0.020 [0.953,1.025] 19	0.942 ± 0.028 [0.904,0.970] 4	0.958 ± 0.011 [0.950,0.965] 2	0.971 ± 0.039 [0.907,1.040] 16	0.935 ± 0.049 [0.846,1.028] 13	0.969 ± 0.034 [0.906,1.042] 25	0.965 ± 0.028 [0.905,1.025] 20
OceD/CS	0.199 ± 0.009 [0.179,0.215] 20	0.189 ± 0.001 [0.188,0.190] 4	0.194 ± 0.006 [0.192,0.197] 2	0.194 ± 0.006 [0.178,0.201] 16	0.196 ± 0.010 [0.187,0.214] 13	0.195 ± 0.009 [0.179,0.221] 25	0.199 ± 0.009 [0.179,0.215] 20
ML/CS	1.630 ± 0.044 [1.534,1.695] 28	1.532 ± 0.010 [1.521,1.544] 4	1.520 ± 0.011 [1.512,1.527] 2	1.512 ± 0.042 [1.425,1.597] 22	1.590 ± 0.057 [1.492,1.668] 13	1.582 ± 0.030 [1.499,1.650] 67	1.648 ± 0.026 [1.598,1.703] 70
ClySet	3.97 ± 0.26 [3.0,4.5] 19	3.50 ± 1.12 [1.5,4.0] 5	1.50 ± 0.71 [1,2] 2	1.83 ± 0.58 [1,3] 21	1.00 ± 0.00 [1.0,1.0] 13	1.01 ± 0.12 [1.0,2.0] 67	1.01 ± 0.12 [1.0,2.0] 70
ClyPub	0.46 ± 0.50 [0,1.5] 19	0.10 ± 0.22 [0,0.5] 5	0.00 ± 0.00 [0,0] 2	1.59 ± 1.22 [0,4.0] 21	0.00 ± 0.00 [0,0.0] 13	0.00 ± 0.00 [0,0.0] 67	0.00 ± 0.00 [0,0.0] 70
OceSet	1.00 ± 0.00 [1,1] 19	1.0 ± 0.0 [1,1] 5	0.0 ± 0.0 [0,0] 2	0.73 ± 0.46 [0,1] 22	0.23 ± 0.44 [0,1] 13	0.00 ± 0.00 [0,0.0] 67	0.00 ± 0.00 [0,0.0] 70
EyeHL	7.0 ± 2.6 [0,14] 28	6.4 ± 2.1 [3,8] 5	5.0 ± 2.8 [3,7] 2	7.5 ± 3.7 [0,20] 22	7.7 ± 2.0 [4,10] 13	4.6 ± 1.8 [0,8] 67	6.1 ± 3.7 [0,21] 70
GLANZ	2.38 ± 0.35 [2.0,3.0] 28	3.00 ± 0.00 [3.0,3.0] 5	3.00 ± 0.00 [3.0,3.0] 2	2.95 ± 0.15 [2.5,3.0] 22	3.00 ± 0.00 [3.0,3.0] 13	2.56 ± 0.41 [1.5,3.0] 67	1.87 ± 0.35 [1.0,2.5] 70
OccHD	0.6 ± 3.0 [0,16] 28	0.0 ± 0.0 [0,0] 5	0.0 ± 0.0 [0,0] 2	6.5 ± 7.7 [0,20] 22	0.7 ± 2.5 [0,9] 13	0.0 ± 0.0 [0,0] 67	0.0 ± 0.0 [0,0] 70
MnHL	97.5 ± 10.7 [80,123] 28	99.2 ± 19.3 [69,120] 5	0.0 ± 0.0 [0,0] 2	82.6 ± 52.2 [0,166] 22	3.5 ± 12.5 [0,45] 13	0.0 ± 0.0 [0,0] 67	0.0 ± 0.0 [0,0] 70
nCox	8.00 ± 1.33 [5.0,10.0] 22	**2.20** ± 0.91 [1.0,3.0] 5	0.0 ± 0.0 [0,0.0] 2	1.88 ± 1.26 [0,5.0] 21	0.00 ± 0.0 [0,0.0] 13	0.0 ± 0.0 [0,0] 67	0.0 ± 0.0 [0,0] 70
TERG	1.00 ± 0.00 [1,1] 28	1.00 ± 0.0 [1,1] 5	1.00 ± 0.0 [1,1] 2	1.23 ± 0.42 [1,2] 22	2.92 ± 0.95 [1,4] 13	3.82 ± 0.57 [3,5] 67	4.64 ± 0.57 [2,5] 70
nHTfl	6.15 ± 0.90 [4.5,8.0] 27	5.80 ± 2.80 [2.5,9.0] 5	4.50 ± 0.70 [4.0,5.0] 2	4.01 ± 1.90 [1.5,8.5] 22	2.97 ± 1.41 [0.5,5.0] 13	1.31 ± 0.67 [0,3.5] 67	1.27 ± 0.70 [0,4.0] 70
sqPDO	3.97 ± 0.29 [3.58,5.03] 28	7.10 ± 0.56 [6.43,7.84] 5	6.46 ± 0.70 [5.97,6.96] 2	5.91 ± 0.40 [4.80,6.71] 22	6.57 ± 0.54 [5.97,7.89] 13	6.04 ± 0.77 [4.49,7.85] 67	4.02 ± 0.33 [3.36,4.77] 70
sqPDG	4.75 ± 0.41 [4.24,5.67] 28	8.29 ± 0.80 [7.43,9.41] 5	7.82 ± 0.20 [7.68,7.96] 2	6.72 ± 0.66 [5.06,8.07] 22	7.91 ± 0.58 [7.06,9.25] 13	7.34 ± 0.66 [5.48,8.60] 67	5.41 ± 0.54 [4.54,6.68] 70

Tab. 7: Morphometric data of gyne individuals of *Formica* (*Coptoformica*) *foreli* and *F.* (*C.*) *bruni* as arithmetic mean ± standard deviation [lower extreme, upper extreme] number of evaluated specimens.

	foreli		***bruni***	
CS	1352 ± 35 [1286,1472]	70	1430 ± 35 [1347,1503]	18
CL/CW	0.984 ± 0.022 [0.934,1.042]	70	1.000 ± 0.024 [0.935,1.030]	18
SL/CS	0.903 ± 0.022 [0.862,0.957]	70	0.948 ± 0.023 [0.896,0.982]	18
Fu2/CS	11.71 ± 0.36 [11.00,12.36]	20	12.43 ± 0.50 [11.56,13.32]	9
Fu2/Fu3	0.965 ± 0.028 [0.905,1.025]	20	0.970 ± 0.025 [0.936,1.006]	9
OceD/CS	0.199 ± 0.009 [0.179,0.215]	20	0.191 ± 0.014 [0.165,0.208]	9
ML/CS	1.648 ± 0.026 [1.598,1.703]	70	1.650 ± 0.038 [1.577,1.709]	18
ClySet	1.01 ± 0.12 [1.0,2.0]	70	1.69 ± 0.46 [1,2]	8
ClyPub	0.00 ± 0.00 [0,0.0]	70	5.00 ± 1.16 [3.5,6.5]	8
OceSet	0.00 ± 0.00 [0,0.0]	70	0.25 ± 0.39 [0,1]	18
EyeHL	6.1 ± 3.7 [0,21]	70	24.1 ± 4.7 [16,34]	18
GLANZ	1.87 ± 0.35 [1.0,2.5]	70	1.72 ± 0.28 [1.0,2.0]	18
OccHD	0.0 ± 0.0 [0,0]	70	22.9 ± 6.0 [11,30]	18
MnHL	0.0 ± 0.0 [0,0]	70	74.1 ± 10.9 [48,91]	18
nCox	0.0 ± 0.0 [0,0]	70	1.00 ± 0.99 [0.0,3.0]	18
TERG	4.64 ± 0.57 [2,5]	70	2.83 ± 1.04 [1.0,4.0]	18
nHTfl	1.27 ± 0.70 [0,4.0]	70	3.47 ± 1.36 [2.0, 7.0]	18
sqPDO	4.02 ± 0.33 [3.36,4.77]	70	3.50 ± 0.34 [3.05,4.24]	18
sqPDG	5.41 ± 0.54 [4.54,6.68]	70	4.55 ± 0.46 [3.76,5.28]	18