

A taxonomic revision of the Palaearctic members of the subgenus *Lasius* s.str. (Hymenoptera, Formicidae)

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Abstract

A revision of the Palaearctic members of the ant subgenus *Lasius* s.str. is presented the fundamentals of which are application of Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT), investigation of type specimens of 58 taxa, critical evaluation of original descriptions of further 22 taxa, and decision-making based on the GAGE species concept. Excluding nomina nuda and unavailable names, 80 taxa are considered which divide into 56 recognized good species (with 16 of these described here as new), 12 junior synonyms, 11 incertae sedis, and one name representing a F1 hybrid. Eighteen phenotypic characters – seven shape, eight seta and two pubescence characters as well as absolute size – were recorded numerically in 4900 worker individuals originating from 1722 nest or spot samples. The subdivision of the subgenera *Lasius* s.str. Ruzsky 1913, *Cautolasius* Wilson 1955, *Dendrolasius* Ruzsky 1913, *Chthonolasius* Ruzsky 1913 and *Austrolasius* Faber 1967 is clearly confirmed by morphological data with each of the 99 recognized Palaearctic species being unambiguously assignable to either subgenus. A key to the 56 Palaearctic species of *Lasius* s.str., subdivided into five geographic regions, is presented. All species are depicted as z-stack photos in two standard positions. The new species *Lasius precursor* sp. nov. is proposed as a model for transition from a largely monogynous-monodomous social type (exemplified by the sister species *Lasius turcicus* Santschi 1921) to a supercolonial type (exemplified by the closely related species *Lasius neglectus* Van Loon et al. 1990).

Keywords: numeric morphology-based alpha-taxonomy | nest centroid clustering | cryptic species |

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1. Introduction

The ant genus *Lasius* Fabricius 1804 has basically a Holarctic distribution. The geographic range of some species touches locally the northern margin of subtropical zones but here these species occur in higher mountain ranges together with faunal elements typical for the temperate zone. The genus is in terms of biomass and flow of matter or energy among the most prominent insect genera of the Holarctic. The yellow meadow ant *Lasius* (*Cautolasius*) *flavus* (Fabricius 1782) achieves in extensively managed pastures of southern England (Waloff & Blackith 1962) and southern Germany (Seifert 2017) the largest biomass known for any ant species worldwide, with estimates of 160 kg fresh weight / ha in the first and of 145 kg in the second study. Seven tons of soil material are here transported to surface per ha and year by a single ant species – the consequences on drainage and aeration of soils are considerable.

Whereas modern taxonomic studies of the Nearctic fauna are missing since the revision of Wilson (1955), the taxonomic situation in the Palaearctic is much better investigated and contains 99 species according to the author's current assessment which includes undescribed species stored in the collection of Senckenberg Museum of Natural History Görlitz. The Palaearctic fauna was

grouped by genetic and morphological criteria in five subgenera (Wilson 1955, Janda et al. 2004, Maruyama et al. 2008). I fully support this subdivision and can confirm the lucky situation that there is not a single Palaearctic species having a doubtful allocation to a particular subgenus based on external morphology. These subgenera are *Lasius* s.str. Ruzsky 1913 (56 Palaearctic species, reported here), *Cautolasius* Wilson 1955 (7 species), *Dendrolasius* Ruzsky 1913 (6 species), *Chthonolasius* Ruzsky 1913 (about 27 species with much problems caused by hybridization) and *Austrolasius* Faber 1967 (2 species). Independent colony foundation is the standard in *Lasius* s.str. and *Cautolasius* – the members of the other subgenera are temporary social parasites and add up to an astonishing figure of 35% of the total species number in the genus.

The subgenus *Lasius* s.str., the topic of this paper, is characterized by large-eyed workers, elongated maxillary palps and more or less intensive above-ground foraging. Most species seem to be monogynous but few species are polygynous-polydomous to supercolonial. The habitats are most variable and range from arid semideserts to wettest quaking *Sphagnum* stands of peat bogs or from paved parking grounds in city centers to damp and dark broad-leafed forest with thick carpets of litter.

Species-level zootaxonomy is generally suffering from two misguided developments caused by arbitrary idiosyncratic approaches: excessive splitting and careless lumping. In *Lasius* s.str. the first extreme is exemplified by the numerous papers of Auguste Forel, Felix Santschi, Horace Donisthorpe, Nikolaj Kusnetzov-Ugamsky or Paul Roeszler. The plethora of names produced mainly by these authors inevitably lead to counter-movements which unfortunately were also based on idiosyncratic views. This development culminated in the revision of Wilson (1955) who, to give an example, synonymized seven taxa with *Lasius alienus* (Foerster 1852): *L. lasioides* Emery 1869, *L. pallitarsus* Provancher 1881, *L. americanus* Emery 1893, *L. grandis* Forel 1909, *L. turcicus* Santschi 1921, *L. obscuratus* Stitz 1930, and *L. illyricus* Zimmerman 1934. These eight taxa do not only represent a minimum of seven clearly distinguishable species – even more: they are members of at least five different species complexes. This remote relatedness is also indicated by the fact that all 270 samples of the six Palaearctic species lumped by Wilson can be separated by exploratory data analyses of phenotypic data with an error of 0% (see this monograph). The historic conflict of the 1950s between William Steel Creighton, a taxonomist standing for a careful but slow mode of working and two other myrmecologists preferring an overly reductionistic and fast approach (“The happy

Harvard team”) was assessed by Buhs (2000). This type of conflict is unfortunately not rare in recent history – it is a constant feature of present taxonomy.

There is only one remedy to cure or mitigate the oversplitting and lumping attitudes: describing character systems by Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT, Seifert 2009). NUMOBAT is the backbone of a working philosophy which has three fundamentals: (a) describe character systems numerically to allow objective hypothesis formation and testing, (b) use a species concept one requirement of which is defining group-specific thresholds for YES/NO decisions and (c) accept as decisive character systems only nuclear DNA and/or their expression products. The architecture of phenotype is such an expression product and is used here as leading indicator of species identities. There are few studies so far combining advanced NUMOBAT and investigation of nuclear DNA. Yet, any of these, considering four ant genera, proved coincident classifications of phenotyping and nuDNA indication (Knaden 2005; Seifert et al. 2010; 2018; Wagner et al. 2017). Following the rationale of testability and decision by thresholds is a movement towards incorruptibility – two of my former taxonomic creations fell victim to it: *Lasius breviscapus* Seifert 1992 and *L. gebaueri* Seifert 1992 were degraded in this monograph to junior synonyms because they clustered with errors > 4%. The points (a) to (c) are elements of an advanced version of the Pragmatic Species Concept of Seifert (2014): the Gene and Gene Expression (GAGE) species concept (Seifert 2020).

Writing about the conflict between slower and more careful working philosophies and those resulting in rapid ejection of untested hypotheses, a note on the time spent for stereomicroscopic recording of NUMOBAT data may be of interest for the reader. Considering bilateral double recording and multiple recording for mean-value determination of microstructures, the total number of primary measurements or counts taken in 4900 worker individuals of *Lasius* s.str. was 132 000. This required 2200 working hours alone for stereomicroscopic character recording. The total working time spent by the author between 1979 and 2019 for 940 000 NUMOBAT recordings in 24 ant genera was 15 700 hours. These figures do not include the time for specimen preparation. Those who say they have no time and physical energy to perform such an exercise must answer themselves the question which kind of research they intend to do and which questions they want to answer.

If one party says we develop automatic systems to record NUMOBAT data, which is basically a good idea, they are facing severe problems with the accuracy of data recording and automatic recognition of characters.

Inaccuracy is here caused, for example, by very small size and inappropriate preparation of specimens, reflecting surfaces, diffuse margins of structures, or inaccurate spatial adjustment. Automated recording of geometric landmarks depends upon standardized viewing positions whereas conventional recording is more flexible. If, for instance, the measurement of a structure is impossible in the standard recording position due to an appendage concealing an endpoint of the measurement, a slight rotation of the specimen is an easy game in conventional morphometry to record the accurate value. Furthermore, the automation proponent has to recognize the enormous costs of writing ant-genus-specific software programs. A lot of time-consuming and meticulous work on details has to be done before automatic systems begin to work with the same power as the direct methods of high-resolution stereomicroscopy used in this paper. I generally doubt if science funding will ever spend a similar amount of money for phenotype recording of insects as whole states are spending for automatic face recognition of criminals or space agencies for investigation of exoplanets. Taxonomists in future, inevitably, in the wake of shrinking global economies (Randers 2012), will have to use their inborn human capacities, doing significant parts of their daily work without automated systems and artificial intelligence.

If another party guesses that NUMOBAT is too labor-intensive and intends to concentrate on a taxonomy using adequate markers of nuclear DNA, these protagonists will face the unsolvable dilemma of how to establish the link between delimited gene clusters and name-giving type specimens without damaging the latter (Seifert 2018, p. 77-78). Genetic taxonomy neglecting information from NUMOBAT will have the operational taxonomic units A, B, C and D – without verified zoological names. A Babylonian confusion of taxonomy and allocation of life histories to the corresponding species is the inevitable result. Good genetics can only be done in connection with good phenotyping – for the sake of a verifiable taxonomy.

2. Material

NUMOBAT data were recorded in a total of 1721 samples (largely nest samples) with 4900 worker individuals. 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 supplementary information SI 1. The abbreviations of depositories are as follows

BMNH London – British Museum of Natural History London, England

DBET Wrocław – Department of Evolutionary Taxonomy, University of Wrocław, Poland

MCZ Cambridge – Museum of Comparative Zoology, Cambridge, Massachusetts, USA

MHN Genève – Muséum d'histoire naturelle de Genève, Genève, Switzerland

MNHN Paris – Muséum national d'histoire naturelle Paris

NHM Basel – Naturhistorisches Museum, Basel, Switzerland

NHM Wien – Naturhistorisches Museum, Wien, Austria

SMN Görlitz – Senckenberg Museum für Naturkunde, Görlitz, Germany

ZM Berlin – Zoologische Sammlungen am Museum für Naturkunde, Berlin, Germany

ZMLU Lund – Zoologiska Museet, Lunds Universitet, Sweden

3. Methods

3.1 The applied species concept

As a new synthesis of former concepts published by Seifert (2014) and Seifert (2018, p. 75-77), I repeat here the wording of the Gene and Gene Expression (GAGE) species concept (Seifert 2020). It is applicable to all eukaryotic organisms independent from their evolutionary history and mode of reproduction. The new concept consists of a heading core sentence plus five attached sentences addressing essential conditions for its translation into a sound taxonomic practice:

Species are separable clusters that have passed a threshold of evolutionary divergence and are exclusively defined by nuclear DNA sequences and / or their expression products. Nuclear DNA sequences and their expression products are different character systems but have a highly correlated indicative function. Character systems with the least risk of epigenetic or ontogenetic modification have superior indicative value when conflicts between character systems of integrative studies arise. All character systems have to be described by an adequate numerical system allowing cluster formation and determination of thresholds. Thresholds for each character system should be fixed by consensus among the experts under the principle of avoiding oversplitting or lumping. Clusters must not be the expression of intraspecific polymorphism.

The derivation of the GAGE species concept is explained in detail elsewhere (Seifert 2020). Yet, three comments are necessary in connection with the paper presented here.

(i) This taxonomic revision focuses on one expression product of the nuclear genome – the architecture of phenotype. Phenotype is an indicator system that is highly correlated with the nuclear genome. Several studies integrating NUMOBAT and investigation of nuDNA have shown this for the ant genera *Tetramorium* (Wagner et al. 2017), *Myrmica* (Seifert et al. 2018), *Cataglyphis* (Knaden et al. 2005) or *Formica* (Kulmuni et al. 2010, Seifert et al. 2010).

(ii) An evaluation of expression products of nuDNA should try to describe or approximate their “genetic core” by removing deformations of the signal due to environmental influence. In ants, the architecture of worker phenotypes is strongly influenced by quantity and quality of nutrition during larval development. This results in differences in absolute body size which may be associated with dramatic allometric changes of phenotype. In some ant genera such as *Pheidole* or *Camponotus* small workers have the shape of an “ordinary” ant whereas major workers develop into “walking heads”. Describing and removing allometric variance in a way that small and large workers of the same species show the same shape parameters (Seifert 2008) provides an approximation to the species-specific genetic signal. In *Camponotus* worker ants, removal of allometric variance may reduce overall variance of shape characters from 100% down to 22% which is required to expose genetically determined interspecific differences (Seifert 2019a, 2019c). In the subgenus *Lasius* s.str., allometric effects are less extreme but still significant (see section 3.3).

(iii) Threshold determination for the methods of NUMOBAT applied here was derived from 14 studies dealing with the discrimination of some 100 pairs of cryptic species of eight ant genera (Seifert 2013; Seifert et al. 2013, 2014a, 2014b 2014c; Seifert and Csösz 2015; Seifert 2016; Seifert and Galkowski 2016; Seifert et al. 2017a, 2017b, 2018; Seifert 2019a, 2019b, 2019c). These studies allowed to collect extensive experience on the behavior of several algorithms of Nest Centroid Clustering (Seifert et al. 2013, see section 3.4). The obtained morphological clusters of these data sets were related to several sources of independent corollary information. This included rather little information on genetics, moderately strong information on behavior and biology and thorough information on spatial distribution. Integrating all these data, I found that heterospecificity should be accepted when the classification error of exploratory data analyses relative to controlling discriminant analyses was <4%. These 4% appeared to be a narrow tipping point – accepting < 5% as threshold, the number of proposed cryptic species would be inflated whereas a lot of undoubtedly good species would fall under synonymy when accepting < 3%.

3.2 Recording of NUMOBAT 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. The mean relative measuring error over all magnifications was 0.2–0.5%. 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 morphometric characters (seven shape, eight seta and two pubescence characters as well as absolute size (indicated by CS) are defined below – figures assisting the definition of these characters are given in Seifert (2018). All bilateral characters were recorded as arithmetic mean of both sides. MaDe and PLF are frequently not recordable or difficult to evaluate – the former because of complete mandibular adduction and the latter because of conglutination of pubescence hairs. As a consequence, MaDe and PLF are usually excluded from multiple NUMOBAT analyses and only the 16 remaining characters are called “standard characters”.

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

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

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

dCIAn – torulo-clypeal distance: the shortest distance from posterior clypeal suture (PCS) to inner margin of antennal torulus (socket). The right spatial adjustment is given when upper and lower portions of this inner margin superimpose. If no surface structure indicates the position of PCS, the center of the dark line is taken as the anterior measuring point.

EYE – eye-size: the arithmetic mean of the large (EL) and small diameter (EW) of the elliptic compound eye under consideration of all structurally visible ommatidia - i.e., including also unpigmented ones.

GuHL – maximum length of setae on underside of head ("gula").

MaDe – number of mandibular dents; suggested denticles may score in the count as 0.5.

MP6 – length of the sixth (terminal) segment of maxillary palps.

nGen – with head in full face view, number of setae on head sides frontal of anterior eye margin ("gena"). The bilateral sum is halved.

nGu – number of setae on underside of head ("gula") as seen in full profile. The bilateral sum is halved.

nHT – setae number on extensor profile of hind tibia under exclusion of the very apical setae. The bilateral sum is halved.

nOcc – setae number projecting from hind margin of vertex frontad to caudal end of eye. Counting is done with head in full face view and by rotating the head within visual plane to avoid a parallax error in estimating the 20 μm projecting distance. Keep care to avoid the parallax error when determining the anterior end of the counting line that is at level of posterior eye margin. The bilateral sum is halved.

nSc – setae number on dorsal plane of scape under exclusion of the most apical setae, counted with view on the small scape diameter. The bilateral sum is halved.

nSt – setae number on lateral and caudolateral surface of metapleuron. The upper margin of the counting area is an imagined line parallel to the lower straight margin of metapleuron and crossing the lower margin of the cuticular ring of propodeal spiracle. Protective setae fringing the orifice of the metapleural gland are excluded. The bilateral sum is halved.

PLF – mean length of pubescence hairs on head between the frontal carinae. At least seven measurements in each individual are averaged. In case of extremely dense pubescence making length measurement impossible, a partial ablation of pubescence may be performed.

PnHL – length of the longest hair on pronotum.

PoOc – postocular distance. Use a cross-scaled ocular micrometer and adjust the head to the measuring position of CL. Caudal measuring point: median occipital margin; frontal measuring point: median head at the level of the posterior eye margin. Note that many heads are asymmetric and average the left and right postocular distance.

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

sqPDCL – square root of pubescence distance PDCL on clypeus. The number of pubescence hairs crossing or

just touching a census line from caudomedian clypeus to lateral clypeal depression is counted. Hairs crossing / touching the census line are counted as 1 / 0.5. Erroneous zero counts in surface areas with torn-off pubescence can be avoided when the basal points of the missing hairs can be visualized by adequate illumination and high-resolution optics and when average pubescence hair length is considered. Square root data transformation is applied to normalize positively skewed distributions.

3.3 Removal of allometric variance

There is a strong intraspecific variance of body size in *Lasius* ants which is determined by age and social structure of the colonies and by nutrition. In order to create comparative tables in which shape variables differ between the species independent of body size, a removal of allometric variance (RAV) was performed following the basic procedure described by Seifert (2008). Evaluation of scatter plots suggested a use of linear monophasic allometry functions. RAV was calculated assuming all individuals to have a cephalic size of $CS=900 \mu\text{m}$. RAV functions were calculated as the arithmetic mean of the species-specific functions of 47 Palaearctic *Lasius* s.str. species with sufficient sample size. The RAV functions of six shape, eight seta, two pubescence and one dentition character are given in the following.

$$CL/CW_{900} = CL/CW / (-0.2290 \cdot CS + 1.2804) \cdot 1.0743$$

$$SL/CS_{900} = SL/CS / (-0.2095 \cdot CS + 1.1771) \cdot 0.9886$$

$$nSC_{900} = nSc / (+13.04 \cdot CS - 2.50) \cdot 9.23$$

$$nGen_{900} = nGen / (+7.11 \cdot CS - 1.89) \cdot 4.50$$

$$nOcc_{900} = nOcc / (+9.00 \cdot CS + 3.27) \cdot 11.37$$

$$nGu_{900} = nGu / (+8.38 \cdot CS - 1.54) \cdot 6.00$$

$$nHT_{900} = nHT / (+19.02 \cdot CS - 6.73) \cdot 10.39$$

$$nSt_{900} = nSt / (+7.14 \cdot CS - 2.73) \cdot 3.70$$

$$sqPDCL_{900} = sqPDCL / (-0.992 \cdot CS + 5.619) \cdot 4.726$$

$$PoOc/CL_{900} = PoOc/CL / (-0.0194 \cdot CS + 0.2517) \cdot 0.2342$$

$$EYE/CS_{900} = EYE/CS / (-0.0704 \cdot CS + 0.3017) \cdot 0.2383$$

$$dCIAn/CS_{900} = 100 \cdot dCIAn/CS / (+0.287 \cdot CS + 4.249) \cdot 4.507 \text{ [given in \%]}$$

$$GuHL/CS_{900} = GuHL/CS / (-0.0108 \cdot CS + 0.1179) \cdot 0.1082$$

$$PnHL/CS_{900} = PnHL/CS / (+0.0001 \cdot CS + 0.1425) \cdot 0.1425$$

$$MP6/CS_{900} = MP6/CS / (-0.0806 \cdot CS + 0.2512) \cdot 0.1886$$

$$PLF_{900} = PLF / (+21.99 \cdot CS + 9.49) \cdot 29.19$$

$$MaDe_{900} = MaDe / (+0.55 \cdot CS + 7.62) \cdot 8.11$$

3.4 Explorative and supervised data analyses, classification and statistical testing

Analyzing the NUMOBAT data, four different forms of exploratory data analyses (EDA) were run using nest centroids as input data (NC clustering). These were firstly hierarchical NC-Ward clustering, secondly and thirdly the hierarchical method NC-part.hclust and the iterative vector-quantization method NC-part.kmeans – both implemented in partitioning algorithms based on recursive thresholding (for details see Csösz & Fisher 2015). Accessorily, as fourth method, nonmetric multidimensional scaling combined with iterative vector-quantization NC-NMDS.kmeans (Seifert et al. 2013). The first three methods were run as the standard working routine.

Checking samples with controversial classifications was done by an interaction of NC clustering and a controlling linear discriminant analysis (LDA) in which these samples were run as wild-cards, following the rationale described in Seifert et 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. The decision to recognize a cluster as a valid species was based on the criterion of the GAGE species concept (section 3.1) which requires that the mean classification error of the applied EDAs determined by the controlling LDA must be <4%.

If more than two clusters are indicated by NC-part.hclust, NC-part.kmeans and NC-Ward in a data set and if disagreements between the methods occur, clustering was carried out in a stepwise exclusion procedure, which becomes more important the more difficult species delimitation is and when character selection becomes imperative on a later stage of analysis. In the first step, EDA-LDA data analyses with all samples of all species involved are run with the three standard methods and the most clearly separable cluster is determined. The samples of this cluster are then excluded from the 2nd EDA-LDA run in which the next most clearly separable cluster is identified and excluded from the 3rd run. In theory, the analysis has to be terminated when no cluster previously separated can be further subdivided with an error rate < 4%.

One may suggest that this stepwise exclusion procedure is basically that which is implemented in the partitioning algorithms of Csösz & Fisher (2015). Yet, there are two differences to the fully automated approach of these authors: there is (a) the option of supervision by the taxonomist after each step, relating the morphological results to other sources of information

(e.g., zoogeography) and there is (b) the option to run the subsequent analyses with the most adequate character selection. Character selection may be indicated by the interaction of exploratory and supervised data analyses and I repeat that it may be essential to avoid an overfitting of the controlling LDA when the relation between the remaining number of elements in a class and the number of characters becomes increasingly low towards the end of an analysis.

NC-NMDS.kmeans clustering and a principal component analysis (PCA) were used when a species was present in the data pool with only a single or two sample/s, making the application of NC-part.hclust, NC-part.kmeans and NC-Ward problematic or impossible. NC-NMDS.kmeans and PCA were then used to check the position of the single-sample data set in the vectorial space relative to the next similar species.

LDA, two-step cluster analysis (TSCA), ANOVA and χ^2 tests were run with the SPSS 15.0 software package.

3.5 Figure legends

All photos with given specimen identifiers “CASENT” have been downloaded from www.antweb.org. All photos without the name of the photographer given are by Roland Schultz.

4. Results

4.1 Opinion on current taxonomic use and diagnosis of the subgenus *Lasius* s. str.

The morphological separation of the five Palaearctic subgenera of the genus *Lasius* was already outlined by Wilson (1955). The situation is comfortable as each of the 99 species I know from the area can be clearly allocated to one of these entities. And even more: we have full congruence of morphology and life histories given by the fact that all species of *Dendrolasius*, *Austrolasius* and *Chthonolasius* are temporary social parasites whereas all species of *Cautolasius* and *Lasius* s.str. can found their colonies independently. To complete the story, genetic studies of Janda et al. (2004) and Maruyama et al. (2008) confirmed this subgeneric subdivision. This clear situation justifies raising each of these subgenera to genus level. No taxonomic confusion would result from this use as the word “*lasius*” is contained in each generic name. Any researcher will immediately know which species is behind the names *Cautolasius flavus* or *Chthonolasius umbratus*.

Furthermore, an environmental impact assessment over the whole research field of myrmecology is expected to reveal more positive than negative aspects. However, I refrain here from changing the current use without having launched an opinion poll among all myrmecologists. This poll has to encompass both academic tree constructors in ivory towers and those who work on solid ground studying the life histories of ants.

As for a diagnosis of the subgenus *Lasius* s. str., the morphological separation from the three socially parasitic subgenera needs no comments here. However, one may ask if there are occasional difficulties to distinguish members of the non-parasitic subgenera *Lasius* s.str. and *Cautolasius*. The answer is no. The much larger eye size and longer terminal segment of maxillary palps in *Lasius* s. str. offers a safe discrimination. As palp segments are often difficult to measure in dry preparations of *Cautolasius*, I tested a simple method with easily measurable characters. Collecting 3226 workers of the 56 Palaearctic *Lasius* s. str. species and their hybrids and 445 workers of 7 Palaearctic *Cautolasius* species, a linear discriminant analysis of two simple measurements offered a perfect separation. With all measurements in mm the discriminant

$$D(2) = 49.11 \cdot CL + 236.88 \cdot EYE - 43.736$$

was -3.488 ± 1.597 [$-9.59, -0.54$] in *Cautolasius* and 5.342 ± 0.887 [$0.54, 8.97$] in *Lasius* s. str.

4.2 Comments on the taxonomic significance of characters and delimitation of species groups

There are allometries in characters that have frequently been used in verbal species descriptions. One of these is mesosomal shape where relative depth of the metanotal groove, height of the propodeum and convexity of mesonotal profile generally show a strongly positive allometry. In *Lasius uzbeki*, for instance, propodeal dome profile changes from rather flat and rounded in smaller or medium-sized specimens to elevated-conically in larger specimens. These allometries make species delimitation by mesosomal shape difficult – with the exception of very few species.

Coloration is also imperfect for species delimitation because there is both allometric variance and color dimorphism. In species with light yellowish or reddish coloration of mesosoma in particular, such as for example *Lasius brunneus* or *L. emarginatus*, small workers often do not develop the corresponding pigments and show a more homogeneously dark brown coloration. In contrast, in species such as *L. psammophilus*, where other pigments are involved, the largest workers become dark homogeneously brown whereas medium-sized and smaller workers are

lighter and suggestedly bicolored with paler yellowish brown mesosomas. Color dimorphism is also rather frequent. In *Lasius emarginatus*, *L. grandis*, *L. uzbeki*, *L. flavescens* and *L. japonicus*, there are homogeneously dark morphs with little or no size-dependent variation and light bicolored morphs with usually the mesosoma being lighter than head and gaster. These morphs often show regional abundance differences and are certainly genetically determined.

Only a small part of the Palaearctic *Lasius* s.str. species can be placed in species complexes on the basis of external morphology. The following four species complexes appear to be sufficiently justified.

Lasius brunneus species complex

Mean number of mandibular dents low (MaDe₉₀₀ 7.0–7.3). Dorsum and slope of propodeum in lateral view linear and forming a distinct, obtuse angle. Petiole scale in lateral view thin and forming an acute tip; its dorsal crest in anterior view straight, slightly concave or slightly emarginate. Pubescence on scape and tibiae and many other body parts very smooth, appressed. Mean length of pubescence hairs on frons very low (PLF₉₀₀ 23.2–25.1 μm). Setae numbers on all body parts low (nOcc₉₀₀ + nGu₉₀₀ + nSt₉₀₀ <10). All species show affinities to habitats with trees. Five species: *Lasius brunneus* (Latreille 1798), *Lasius lasioides* (Emery 1869), *Lasius himalayanus* Bingham 1903, *Lasius silvaticus* sp. nov., and *Lasius excavatus* sp. nov.

Lasius turcicus species complex

Mean number of mandibular dents low (MaDe₉₀₀ 7.3–7.7). Petiole scale in lateral view thin and forming an acute tip; its dorsal crest in anterior view straight or slightly emarginate. Clypeal pubescence dilute (sqPDCL₉₀₀ 5.1–5.5). Mean length of pubescence hairs on frons larger (PLF₉₀₀ 30–38 μm). Dorsum of scape without or with only very few setae. Setae numbers on head and mesosoma larger than in the *L. brunneus* complex (nOcc₉₀₀ + nGu₉₀₀ + nSt₉₀₀ 11.8–29). Six species: *Lasius turcicus* Santschi 1921, *Lasius neglectus* Van Loon et al. 1990, *Lasius austriacus* Schlick-Steiner 2003, *Lasius tapinomoides* Salata & Borowiec 2018, *Lasius precursor* sp. nov. and *Lasius israelicus* sp. nov.

Lasius obscuratus species complex

Mean number of mandibular dents not reduced (MaDe₉₀₀ 8.1–8.4). Scape and head not elongated (SL/CS₉₀₀ 0.926–0.962, CL/CW₉₀₀ 1.059–1.087). Dorsum of scape without or with few semierect setae (nSc₉₀₀ 0.4–0.8). Hind margin of head always with rather many setae (nOcc₉₀₀ 8.2–11.0). Four species: *Lasius obscuratus* Stitz 1930, *Lasius piliferus* Seifert 1992, *Lasius psammophilus* Seifert 1992 and *Lasius creticus* sp. nov.

***Lasius paralienus* species complex**

Mean number of mandibular dents not reduced (MaDe₉₀₀ 8.0–8.5). Pubescence very dense and rather long (sqPDCL₉₀₀ 3.39–3.51, PLF₉₀₀ 31.8–38.9). Scape and head moderately elongated (SL/CS₉₀₀ 0.968–1.007, CL/CW₉₀₀ 1.066–1.076). Dorsum of scape without or with very few semierect setae (nSc₉₀₀ 0.2–1.3). Number of setae on extensor profile of hind tibia low (nHT₉₀₀ 1.8–8.6). Hind margin of head always with rather many setae (nOcc₉₀₀ 8.2–12.4). Four species: *Lasius paralienus* Seifert 1992, *Lasius casevitzi* Seifert & Galkowski 2016, *Lasius bombycina* Seifert & Galkowski 2016 and *Lasius kritikos* sp. nov.

4.3 Key to the workers of *Lasius* s.str.

Truly cryptic species constitute more than 50% of the 56 species and some members of one species group may share some characters typical for other species groups.

This makes the writing of a dichotomous key a frustrating business. Regrettably, the only way to classify all species recognized here is using adequate microscopic equipment, recording the full set of NUMOBAT characters under meticulous consideration of character definitions and running discriminant functions using the morphometric data provided in supplementary information SI2. Candidate species for LDA runs can be selected beforehand by combined consideration of morphometric tables, pictures and geographic distribution. Here I present a dichotomous key which should work for a good number of species with acceptable error rates but in the end using this key is probably more time consuming than running discriminant functions on the basis of SI2. All absolute measurements used in the key as input in discriminant functions are given in mm. All setae counts are arithmetic means of the data from the left and right body half. Note that the morphometric tables Tabs. 1–11 show RAV-corrected values in order to show interspecific differences more clearly. The key, in contrast, always uses primary data.

- 1 Europe, Mediterranean islands, Caucasus and Asia Minor.....6
 2 Canaries, North Africa, Middle East, Iran.....26
 3 Afghanistan, Tadjikistan, Uzbekistan, Kyrgyzstan, Kazakhstan, Russian Siberia, Mongolia.....39
 4 Himalaya, Meghalaya and Tibet.....47
 5 China, Korea, Russian Far East, Japan.....54
 6a Eyes and torulo-clypeal distance very small, scape shorter; nest means: EYE/CS 0.209 ± 0.010 , dClAn/CS 0.0257 ± 0.0034 , SL/CS 0.928 ± 0.023 . Discriminant $110.85 * \text{EYE} - 18.91 * \text{SL} + 45.21 * \text{dClAn} - 5.91 < 0$ [error 0% in 40 individuals]. Subterranean species. S Moravia and E Austria, Asia Minor (Figs. 11–12, Tab. 2).*austriacus*
 6b Eyes and torulo-clypeal distance larger, scape with exception of *L. brunneus* longer. Discriminant > 0 [error 0% in 2445 individuals]7
 7a Nest sample means. Scape short, SL/CS 0.865 ± 0.016 . Pronotal setae short, PnHL/CS 0.097 ± 0.007 . Medium-sized and larger workers bicolored: head dark yellowish brown, mesosoma lighter yellowish brown, gaster dark brown. Setae numbers on whole body strongly reduced, nOcc 2.1 ± 0.8 . Dorsal and posterior profile of propodeum linear and forming a distinct, obtuse angle. Frontal line long and well marked. Pubescence on whole body and appendages very smooth, appressed and short. Mean number of mandibular dents only 7.06. Nest means of discriminant $19.4 * \text{SL} - 26.63 * \text{CW} + 0.001 * \text{nOcc} + 0.33 * \text{nSt} + 42.13 * \text{PnHL} - 15.09 * \text{GuHL} + 3.929 < 0$ [error 0% in 32 nest samples]. Arbicolous. (Figs. 1–2, Tab. 1).....*brunneus*
 7b Nest sample means given. Scape longer, SL/CS > 0.904 . PnHL/CS in most species > 0.110 ; if similarly short, then SL/CS and /or nOcc much higher. Nest means of discriminant > 0 [error 0% in 1161 nest samples].....8
 8a Mesosoma, petiole, gaster and appendages yellow; head and gaster sometimes a littler darker with a brownish tinge. Scape and maxillary palp long (nest sample means SL/CS 1.020 ± 0.021 , MP6/CS 0.206 ± 0.009). Pubescence on clypeus and sides of head extremely dilute, nest sample mean sqPDCL 6.49 ± 0.73 . Setae on hind margin of head long and numerous but absent from scape; nOcc 14.4 ± 3.2 , nSc 0.2 ± 0.3 . Asia Minor only (Figs. 45–46, Tab. 5).....*schulzi*
 8b Character combination in at least two characters strongly deviating.....9
 9a Nest means given. Standing setae on area below propodeal spiracle usually absent (nSt 0.34 ± 0.45). Pronotal setae rather long PnHL/CS 0.152 ± 0.007 . Clypeal pubescence moderately dense (sqPDCL 4.16 ± 0.26). Scape rather short SL/CS 0.962 ± 0.036 . Discriminant $9.098 * \text{SL} / \text{CS} - 32.38 * \text{PnHL} / \text{CS} + 0.453 * \text{sqPDCL} + 0.678 * \text{nSt} - 6.643 < 0$ [error 4.2% in 48 nest samples]. (Figs. 41–42, Tab. 5).....*alienus*

- 9b** Nest means given. At least few standing setae on area below propodeal spiracle present; if absent, then scape longer (*lasioides*), pronotal setae shorter (*lasioides*) or clypeal pubescence denser (*paralienus* and Cretan *kritikos* sp. nov.) Discriminant > 0 [error 1.0% in 794 nest samples].....**10**
- 10a** All workers in a nest very small, CL 0.66–0.75 mm. Metanotal groove very shallow; as result dorsal profile of mesosoma more or less approaching linearity. Pubescence on head sides ventral of the eye extremely reduced. Pronotal setae rather long, PnHL/CS 0.154 ± 0.007. Number of standing setae on surface below propodeal spiracle comparatively large, nSt 3.3 ± 0.3. Cretan endemic living in moist, closed canopy forests (Figs. 19–20, Tab. 2)*tapinomoides*
- 10b** Larger, dorsal mesosomal profile not approaching linearity, whole character combination different.....**11**
- 11a** Due to appressed pubescence all body surfaces completely smooth. Dorsal plane of scape, tibiae and genae without standing setae. Nest means of nOcc+nGu+nHT < 5.5. Dorsal and posterior profile of propodeum linear and forming a distinct, obtuse angle. Nest means of SL/CS 0.992 ± 0.030, number of mandibular dents only 6–8. Holo-mediterranean, Middle East, Iran (Figs. 9–10, Tab. 1).....*lasioides*
- 11b** Pubescence on all body surfaces not completely smooth. Nest mean of nOcc+nGu+nHT > 5.5. Dorsal and posterior profile lines of propodeum not distinctly linear**12**
- 12a** Mean number of mandibular dents <8. Pubescence distance on clypeus very large, sqPDCL 5.4 ± 0.4. Setae on scape and hind tibiae usually absent, nSc+nHT 0.4 ± 0.5. Pronotal setae short, barely longer than gular setae, PnHL/CS 0.127 ± 0.007, GuHL/CS 0.124 ± 0.012. Petiole scale in lateral view thin, with sharp dorsal crest.....**13**
- 12b** Character combination in at least one character strongly deviating.....**15**
- 13a** Discriminant of nest sample means: 17.41*SL/CS+0.584*nOcc–0.50*nGu–45.1*GuHL/CS +88.9*dCIAn/CS +67.884*EYE/CS –34.60 >0 [error 0% in 67 nest sample means]. Supercolonial invasive species, widely distributed but not reaching subboreal and boreal regions (Figs. 13–14, Tab. 2).....*neglectus*
- 13b** Discriminant of nest sample means <0 [error 0% in 128 nest sample means].....**14**
- 14a** Nest sample means given. On average smaller, CS 0.768 ± 0.038 mm. Postocular distance larger, PoOc/CL 0.241 ± 0.006. Eye larger, EYE/CS 0.245 ± 0.004, torulo-clypeal distance smaller dCIAn/CS 3.75 ± 0.22 %. Discriminant 17.32*CS +20.79*CL/CW + 32.86*SL/CS +0.625*nGen +0.599*sqPDCL +126.0*dCIAn/CS –50.71*PoOc/CL –93.03*EYE/CS –43.41 <0 [error 0% in 51 nest samples]. Western Anatolia and its coastal Islands. Often polydomous. (Figs. 15–16, Tab. 2)*precursor* sp. nov.
- 14b** Nest sample means given. On average larger, CS 0.858 ± 0.047 mm. Postocular distance smaller, PoOc/CL 0.229 ± 0.006. Eye smaller, EYE/CS 0.237 ± 0.006, torulo-clypeal distance larger dCIAn/CS 4.00 ± 0.35 %. Discriminant > 0 [error 1.3% in 77 nest samples]. Western Aegean, Asia Minor, N Syria, N Iran. Often monodomous (Figs. 17–18, Tab. 2)*turcicus*
- 15a** Nest sample means. Medium-sized, CS 0.912 mm. Head broad CL/CW 1.034. Scape long, SL/CS 1.022. Pronotal hairs short, only slightly longer than gular setae, PnHL/CS 0.108, GuHL/CS 0.094. Torulo-clypeal distance small, dCIAn/CS 4.25%. Terminal segment of maxillary palp short, MP6/CS 0.177. Genae almost without standing setae, nGen 0.4. Only one sample known from Pindos Mountains / Greece (Figs. 43–44, Tab. 5).....*karpinisi*
- 15b** Character combination in at least one character strongly deviating. Rather similar to *L. karpinisi* is *L. illyricus* but nest sample means here PnHL/CS 0.124–0.152, GuHL/CS 0.104–0.140, dCIAn/CS 4.54–6.34%, MP6/CS 0.196–0.244, nGen 3.0–9.2**16**
- 16a** Head and gaster yellowish brown, remaining body parts yellowish. Nest sample means: Scape long, SL/CS 0.994–1.021; eye small, EYE/CS 0.228–0.233; clypeal pubescence distance very large, sqPDCL 5.43–5.66 but frontal pubescence in contrast rather dense and long. All surfaces of head and mesosoma with numerous standing setae of medium to large length (PnHL/CS 0.158–0.161, GuHL/CS 0.125–0.132, nGu 8.5–11.8, nOcc 18.3–19.2, nGen 9.5–10.0). Only known from Asia Minor (Figs. 63–64, Tab. 5).*flavoniger*
- 16b** Character combination strongly deviating.....**17**
- 17a** Scape without or only single standing setae, nSc 0.6 ± 0.8; pubescence distance on clypeus very low, sqPDCL 3.49 ± 0.16; torulo-clypeal distance rather small, dCIAn/CS 4.21 ± 0.38%. (Figs. 33–40, Tab. 4).*paralienus*, *bombycina*, *casevitzi*, *kritikos* sp. nov.
- 17b** Scape without or only single standing setae, nSc 0.6 ± 1.3; pubescence distance on clypeus larger, sqPDCL 4.61 ± 0.41; torulo-clypeal distance rather small, dCIAn/CS 4.00 ± 0.39%. (Figs. 23–30, Tab. 3)*obscuratus*, *psammophilus*, *piliferus*, *creticus* sp. nov.
- 17c** Scape usually with more standing setae; if not (*illyricus*), then torulo-clypeal distance and clypeal pubescence distance large: dCIAn/CS 5.5 ± 0.4%, sqPDCL 5.38 ± 0.58**18**
- 18a** Clypeal pubescence distance low (sqPDCL 3.58 ± 0.29), scape rather short (SL/CS 0.979 ± 0.018), prono-

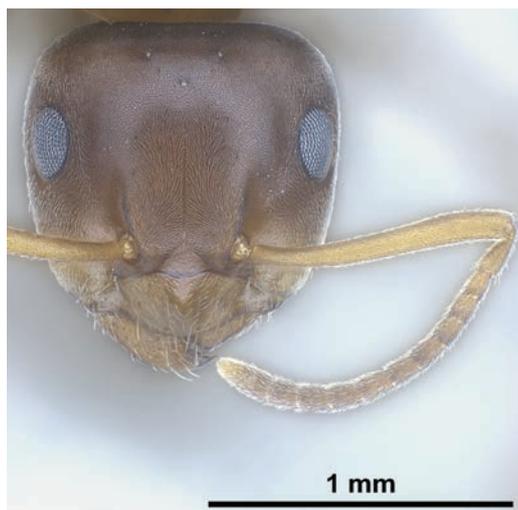
- tal and gular setae rather short (PnHL/CS 0.124 ± 0.008 , GuHL/CS 0.092 ± 0.009). Discriminant $21.967*SL/CS + 51.739*GuHL/CS + 52.02*PnHL/CS + 0.731*sqPDCL - 37.01 < 0$ [error 0% in 68 nest samples]. Widely distributed from $10^{\circ}W$ to $108^{\circ}E$ (Figs. 49–50, Tab. 6) **niger**
- 18b** Clypeal pubescence distance higher; scape, pronotal and gular setae often longer. Discriminant > 0 [error 0.4% in 230 nest samples] **19**
- 19a** Postocular distance large (PoOc/CL 0.247 ± 0.006), head and scape short (CL/CW 1.037 ± 0.020 , SL/CS 0.965 ± 0.018), pronotal setae long (PnHL/CS 0.164 ± 0.008). Discriminant $10.953*CS + 48.26*CL/CW + 15.306*SL/CS - 115.44*PoOc/CL - 29.18*PnHL/CS - 45.905 < 0$ [error 0% in 52 nest samples] **20**
- 19b** Postocular distance smaller, head and scape longer, pronotal setae shorter. Discriminant > 0 [error 0% in 178 nest samples] **21**
- 20a** Widely distributed from $10^{\circ}W$ to $105^{\circ}E$. Discriminant $1.034*sqPDCL - 0.175*nSc + 0.511*nSt + 0.127*nHT - 9.351 < 0$ [error 0% in 111 worker individuals] (Figs. 57–58, Tab. 6) **platythorax**
- 20b** Endemic of Cyprus. Differing from the former by more dilute pubescence on petiole scale and clypeus (sqPDCL 5.91), smaller postocular distance (0.234), shorter and fewer scape setae (nSc 12.1) combined with extremely long setae on posterior margin of vertex, and the yellowish component of body color. Discriminant > 0 [error 0% in 5 worker individuals] (Figs. 59–60, Tab. 6) **cyperus sp. nov.**
- 21a** Top summits of Mallorca island between 800 and 1400 m. Small (CS 0.69–0.93 mm), number of standing setae on basically all body parts very high (nOcc 21.8, nGen 7.8, nGu 6.4, nSc 29.4, nHT 11.3, nSt 6.2). Terminal segment of maxillary palp rather short and postocular distance rather large (MP6/CS 0.186, PoOc/CL 0.234) (Figs. 71–72, Tab. 7) **balearicus**
- 21b** Character combination deviating **22**
- 22a** Maltese Islands. Terminal segment of maxillary palp very long (MP6/CS 0.236 ± 0.012), head longer and postocular distance large (CL/CW 1.095 ± 0.023 , PoOc/CL 0.227 ± 0.009), all body parts with very numerous standing setae (nGen 13.9 ± 2.3). Discriminant $45.42*PoOc/CL - 0.183*CL/CW + 55.63*MP6/CL + 0.312*nGen - 25.59 > 0$ [error 0% in 4 nest samples] (Figs. 79–80, Tab. 8) **maltaeus sp. nov.**
- 22b** Character combination differing. Discriminant < 0 [error 0% in 112 nest samples] **23**
- 23a** Cuticular surface of dorsal head and mesosoma completely matt, caused by fine punctures within the meshes of the microreticulum or in interspaces of microrugae. Discriminant $12.08*CS + 38.08*MP6/CS + 15.289*SL/CS - 0.21*nGu + 33.36*GuHL/CS + 0.530*nSt - 38.48 < 0$ [error 0% in 20 nest samples]. Iberia and S France (Figs. 69–70, Tab. 7) ...
..... **cinereus**
- 23b** Cuticular surface of dorsal head and mesosoma not completely matt. Discriminant > 0 [error 4.4% in 91 nest samples] **24**
- 24a** Eye and clypeal pubescence distance smaller (EYE/CS 0.234 ± 0.006 , sqPDCL 4.37 ± 0.39), terminal segment of maxillary palps shorter (MP6/CS 0.208 ± 0.009), scape setae usually more numerous and more erect (nSc 19.5 ± 5.7). Discriminant $23.02*CS + 26.17*SL/CS + 175.34*EYE/CS + 0.88*sqPDCL - 0.121*nSc - 0.225*nGu + 0.332*nGen - 94.23 < 0$ [error 0% in 47 nest samples]. Iberia, S France, Corsica, Sardinia (Figs. 65–66, Tab. 7) **grandis**
- 24b** Eye and clypeal pubescence distance usually larger, terminal segment of maxillary palps longer, scape setae usually less numerous and less erect. Discriminant > 0 [error 0% in 44 nest samples] **25**
- 25a** Dorsum of scape, tibiae and metapleuron with rather many setae (nSc 11.5 ± 7.0 , nHT 20.3 ± 6.0 , nSt 4.2 ± 1.1). Discriminant $0.072*nSc - 0.173*nHT + 0.386*nSt - 32.94*PoOc - 11.20*CS + 14.05 > 0$ [error 2.0% in 152 specimens]. Temperate and submediterranean zone of Europe. Sympatric with *L. illyricus* in Balkans and Ukraine (Figs. 75–76, Tab. 8) **emarginatus**
- 25a** Setae numbers on scape, tibiae and metapleuron lower (nSc 2.5 ± 3.4 , nHT 8.7 ± 3.3 , nSt 2.7 ± 1.1). Discriminant < 0 [error 1.0% in 94 specimens]. Submediterranean and mediterranean zone of the Balkans, Ukraine, southern Caucasus, Asia Minor, north Iran (Figs. 77–78, Tab. 8) **illyricus**
- 26a** Nest sample means. Scape short, SL/CS 0.899 ± 0.013 . Torulo-clypeal distance very small, dClAn/CS $3.37 \pm 0.33\%$. Medium-sized and larger workers bicolored: head dark yellowish brown, mesosoma lighter yellowish brown, gaster dark brown. Setae numbers on whole body strongly reduced, setae numbers on gula as large or larger than on postocular head margin (nOcc 3.3 ± 0.8 , nGu 3.8 ± 0.8). Dorsal and posterior profile of propodeum linear and forming a distinct, obtuse angle. Pubescence on whole body and appendages very smooth, appressed and short. Mean number of mandibular dents only 7.3. Nest means of discriminant $33.83*CW - 30.38*SL - 129.0*dClAn - 0.073*nOcc + 0.138*nHT + 0.103 > 0$ [error 0% in 9 nest sample means]. Arboricolous. N Iran. (Figs. 3–4, Tab. 1) **silvaticus sp. nov.**
- 26b** Character combination deviating. Discriminant < 0 [error 0% in 479 nest sample means] **27**
- 27a** Pubescence on scapes and tibiae (and on whole body) appressed and surfaces as a consequence ideally smooth. Dorsal

- and posterior profile of propodeum linear and forming a distinct, obtuse angle. Petiole scale in lateral view thin with a sharp dorsal crest. Seta numbers on scape, hind tibia, head and mesosoma very low (nOcc 3.0 ± 1.0 , nGen 0.2 ± 0.5 , nGu 0.5 ± 0.7 , nSc 0.0 ± 0.1 , nHT 0.0 ± 0.1 , nSt 1.8 ± 1.1). Frontal pubescence short (PLF $23.6 \pm 3.0 \mu\text{m}$)**28**
- 27b** Character combination deviating**29**
- 28a** Less xerothermous sites with some trees in the highland desert of Iran. Head short (CL/CW 1.028 ± 0.017). Posterior margin of head at least suggested excavated and postocular distance small (PoOc/CL 0.222 ± 0.003). Medium-sized (CS $900 \pm 31 \mu\text{m}$). Scape of medium length (SL/CS 0.974 ± 0.015). Mesosoma usually lighter than head and gaster. (Figs. 7–8, Tab. 1)**excavatus sp. nov.**
- 28b** In the reference area widely distributed. Head longer (CL/CW 1.073 ± 0.023). Posterior margin of head not suggested excavated and postocular distance larger (PoOc/CL 0.240 ± 0.009). Often smaller (CS $813 \pm 67 \mu\text{m}$). Scape often longer (SL/CS 0.991 ± 0.032). Head, mesosoma and gaster usually concolorous. (Figs. 9–10, Tab. 1)**lasioides**
- 29a** Setae number on head and hind tibia low (nOcc 6.8 ± 3.0 , nGen 1.2 ± 1.1 , nHT 1.2 ± 1.6). Scape and terminal segment of maxillary palp shorter (SL/CS 0.969 ± 0.028 , MP6/CS 0.187 ± 0.016). Discriminant $14.67*SL - 17.85*CL + 26.36*MP6 + 0.292*nHT - 0.051*nOcc + 0.062*nGen - 3.273 < 0$ [error 0% in 594 worker individuals]**30**
- 29b** Setae number on head and hind tibia large (nOcc 17.3 ± 6.1 , nGen 9.4 ± 3.9 , nHT 21.9 ± 6.6). Scape and terminal segment of maxillary palp longer (SL/CS 1.022 ± 0.025 , MP6/CS 0.207 ± 0.016). Discriminant < 0 [error 0% in 231 worker individuals]**35**
- 30a** Standing setae on area below propodeal spiracle usually absent and setae on postocular head margin only few (nSt 0.34 ± 0.45 , nOcc 4.5 ± 1.3). Pronotal setae rather long (PnHL/CS 0.152 ± 0.007). Nest means of individual values of discriminant $0.403*nSt + 0.169*nHT + 0.165*nOcc + 0.056*nGu - 52.07*PnHL + 11.89*GuHL + 4.938 < 0$ [error 1.1% in 87 nest samples]. (Figs. 41–42, Tab. 5)**alienus**
- 30b** At least single standing setae on area below propodeal spiracle present and setae numbers on postocular head margin higher (nSt 3.2 ± 1.4 , nOcc 8.0 ± 2.9). Nest means of individual values of discriminant > 0 [error 0.9% in 214 nest samples]**31**
- 31a** Terminal segment of maxillary palp and scape shorter, eye smaller. Frontal pubescence longer (PLF $> 26 \mu\text{m}$). Discriminant $59.35*MP6 + 35.04*SL - 44.09*CL + 76.324*EYE - 19.41 < 0$ [error 0% in 484 individuals]**32**
- 31b** Terminal segment of maxillary palp and scape long, eye larger. Frontal pubescence very short (PLF $< 23 \mu\text{m}$). Discriminant > 0 [error 0% in 6 individuals]. Large (CS $> 900 \mu\text{m}$). In contrast to poorly developed pilosity on other body parts, frontal clypeal margin with a conspicuous row of setae, only moderately decreasing their length laterad. Tunisia. (Figs. 83–84, Tab. 8)**tunisius sp. nov.**
- 32a** Clypeal pubescence distance low and terminal segment of maxillary palps short (sqPDCL 4.10 ± 0.57 , MP6/CS 0.172 ± 0.013). Pronotal setae usually significantly longer than gular setae (PnHL/CS 0.146 ± 0.017 , GuHL/CS 0.098 ± 0.017). Number of mandibular dents larger (MaDe 8.33 ± 0.34). Discriminant $0.93*sqPDCL + 24.96*MP6 - 55.28*PnHL + 66.71*GuHL - 0.359*nHT - 7.77 < 0$ [error 1.1% in 181 individuals]**33**
- 32b** Clypeal pubescence distance higher and terminal segment of maxillary palps longer (sqPDCL 5.45 ± 0.57 , MP6/CS 0.198 ± 0.011). Pronotal setae not much longer than gular setae (PnHL/CS 0.127 ± 0.012 , GuHL/CS 0.122 ± 0.018). Number of mandibular dents lower (MaDe 7.50 ± 0.55). Discriminant > 0 [error 0.7% in 298 individuals]**34**
- 33a** Clypeal pubescence distance larger (sqPDCL 4.40 ± 0.43), terminal segment of maxillary palp longer (MP6/CS 0.177 ± 0.011). Discriminant $1.934*sqPDCL - 58.58*GuHL + 51.21*MP6 - 0.126*nOcc - 8.288 > 0$ [error 3.8% in 132 individuals] N Iran. (Figs. 23–24, Tab. 3)**obscuratus**
- 33b** Clypeal pubescence distance small (sqPDCL 3.43 ± 0.23), terminal segment of maxillary palp shorter (MP6/CS 0.160 ± 0.009). Discriminant < 0 [error 0% in 50 individuals]. Potentially occurring in the northeast of the reference area. (Figs. 35–36, Tab. 4)**bombycina**
- 34a** Usually supercolonial. Absolute size small (CS $773 \pm 47 \mu\text{m}$), number of mandibular dents small (MaDe 7.27 ± 0.49), gular setae slightly shorter and less numerous (GuHL/CS 0.117 ± 0.021 , nGu 2.5 ± 0.5). Discriminant $17.512*CL + 11.91*SL + 35.919*GuHL - 17.52*PoOc - 93.04*EYE + 0.353*nGu - 0.356*nOcc + 0.004*nGen - 4.599 < 0$ [error 0% in 56 nest sample means]. (Figs. 13–14, Tab. 2)**neglectus**
- 34b** Supercoloniality unknown so far, usually monodomous. Absolute size larger (CS $855 \pm 64 \mu\text{m}$), number of mandibular dents larger (MaDe 7.68 ± 0.54), gular setae slightly longer and more numerous (GuHL/CS 0.125 ± 0.014 , nGu 3.52 ± 1.4). Discriminant > 0 [error 1.3% in 77 nest sample means]. (Figs. 17–18, Tab. 2)**turcicus**
- 35a** Israel and Jordan. Scape without or very few standing setae (nSc 1.1 ± 1.2). Number of mandibular dents lower (MaDe 7.67 ± 0.49). Torulo-clypeal distance smaller (dClAn/CS $4.16 \pm 0.37\%$, dClAn $35.9 \pm 2.6 \mu\text{m}$). (Figs. 21–22, Tab. 2)**israelicus sp. nov.**
- 35b** Scape with numerous standing setae (nSc 19.6 ± 7.7). Number of mandibular dents higher (MaDe 8.57 ± 0.46).

- Torulo-clypeal distance larger ($dCIAn/CS 5.16 \pm 0.52\%$, $dCIAn 49.5 \pm 6.5 \mu m$)**36**
- 36a** Humid broad-leaved forest of northern Iran. Clypeal pubescence distance and postocular distance larger, terminal segment of maxillary palps shorter ($sqPDCL 5.10 \pm 0.45$, $PoOc/CS 0.239 \pm 0.009$, $MP6/CS 0.191 \pm 0.012$). Discriminant $1.266*sqPDCL+38.697*CW-62.393*CL+73.402*PoOc-19.803*MP6+31.648*PnHL+1.690 > 0$ [error 0% in 25 individuals]. (Figs. 73–74, Tab. 7)*persicus* sp. nov.
- 36b** Unknown from Iran and Middle East. Clypeal pubescence distance and postocular distance smaller, terminal segment of maxillary palps longer ($sqPDCL 4.29 \pm 0.51$, $PoOc/CS 0.220 \pm 0.008$, $MP6/CS 0.208 \pm 0.016$). Discriminant < 0 [error 0% in 198 individuals]**37**
- 37a** Introduced to the Canary Islands. Discriminant $82.736*MP6-52.319*EYE-28.836*CL + 38.406*dCIAn+16.587*GuHL-0.046*nSc-0.107*nHT+0.161*nGen+0.391nSt-0.704*sqPDCL-1.335 < 0$ [error 0.8% in 124 individuals]. (Figs. 65–66, Tab. 7)*grandis*
- 37b** Canary Islands and N Africa. Discriminant > 0 [error 1.4% in 74 individuals]**38**
- 38a** Discriminant $0.148*nSc+0.113*nOcc+0.237*nSt-21.293*SL+52.263*PoOc-35.858*GuHL +8.448 < 0$ [error 0% in 21 individuals]. (Figs. 81–82, Tab. 8)*tebessae*
- 38b** Discriminant > 0 [error 0% in 54 individuals]. (Figs. 67–68, Tab. 7)*mauretanicus* sp. nov.
- 39a** Gular setae very long ($GuHL/CS 0.133 \pm 0.011$). Hind tibia with a moderate number of standing setae ($nHT 4.2 \pm 4.1$). Eye very large ($EYE/CS 0.267 \pm 0.008$). West Tianshan between 1400 and 2400 m. (Figs. 47–48, Tab. 5)*uzbeki*
- 39b** Character combination strongly deviating. If gular setae are long, then number of setae on hind tibia much larger ($nHT 23.2 \pm 5.0$, *flavescens* and *platythorax*) or much smaller ($nHT 0.5 \pm 0.9$, *neglectus* and *obscuratus*)**40**
- 40a** Less hirsute, nest means of $nGen+nGu+nSc+nHT +nSt < 25$ [error 0% in 195 nest samples]**41**
- 40b** More hirsute, nest means of $nGen+nGu+nSc+nHT +nSt > 25$ [error 0% in 260 nest samples]**44**
- 41a** Use nest means. Clypeal pubescence distance large ($sqPDCL 5.54 \pm 0.34$). Pronotal setae not much longer than gular setae ($PnHL/CS 0.127 \pm 0.010$, $GuHL/CS 0.117 \pm 0.016$). Number of mandibular dents low ($MaDe 7.26 \pm 0.37$). Body size small ($CS 773 \pm 40 \mu m$). Supercolonial invasive species. (Figs. 13–14, Tab.2)*neglectus*
- 41b** Use nest means. Clypeal pubescence distance smaller ($sqPDCL 4.37 \pm 0.36$). Pronotal setae significantly longer than gular setae ($PnHL/CS 0.145 \pm 0.013$, $GuHL/CS 0.071 \pm 0.034$). Number of mandibular dents higher ($MaDe 8.29 \pm 0.37$). Body size often larger**42**
- 42a** Scape long but terminal segment of maxillary palps short ($SL/CS 1.022 \pm 0.013$, $MP6/CS 0.158 \pm 0.009$). Clypeal pubescence more dilute ($sqPDCL 5.08 \pm 0.47$). A number of setae on dorsal plane of scape present but these rather short, many of these protruding close to counting threshold of $20 \mu m$ ($nSc 4.2 \pm 3.7$). Discriminant $25.991*SL-26.223 CW+49.767*PoOc-61.95*MP6+0.711*sqPDCL +0.519*nSc-7.106 > 0$ [error 0% in 12 individuals]. Hot steppe of E Kazakhstan. (Figs. 31–32, Tab. 3).....*brevipalpus* sp. nov.
- 42b** Scape shorter and terminal segment of maxillary palps usually longer ($SL/CS 0.962 \pm 0.021$, $MP6/CS 0.181 \pm 0.012$). Clypeal pubescence more dense ($sqPDCL 4.22 \pm 0.40$). Number of setae on dorsal plane of scape lower ($nSc 0.34 \pm 0.88$). Discriminant < 0 [error 0.4% in 238 individuals]**43**
- 43a** Setae numbers very low, pronotal setae a little longer. Discriminant $0.26*nOcc+0.35*nGu+0.662*nSt-32.945 *PnHL-0.237 GuHL-1.019 < 0$ [error 1.1% in 87 nest sample means]. (Figs. 41–42, Tab. 5)*alienus*
- 43b** Setae numbers higher but pronotal setae a little shorter. Discriminant > 0 [error 5.2% in 58 nest sample means]. (Figs. 23–24, Tab. 3)*obscuratus*
- 44a** At least mesosoma pale yellowish brown. Discriminant $0.646*sqPDCL+0.133*nHT+0.325*nSt-121.26*d CIAn-30.76*MP6-30.82*PnHL+4.943 > 0$ [error 0% in 42 specimens]. NE Afghanistan, Tian Shan. (Figs. 61–62, Tab. 5) ...
.....*flavescens*
- 44b** Concolorous dark brown, mesosoma occasionally a little lighter with a yellowish color component. Discriminant < 0 [error 0.8% in 263 individuals].....**45**
- 45a** Nest means of pronotal and gular setae length and clypeal pubescence distance large ($PnHL/CS 0.163 \pm 0.009$, $GuHL/CS 0.134 \pm 0.010$, $sqPDCL 4.96 \pm 0.53$). Discriminant $55.029*PnHL+47.808*GuHL+1.498*sqPDCL-58.86 EYE -5.818 > 0$ [error 0% in 111 individuals]. (Figs. 57–58, Tab. 6)*platythorax*
- 45b** Nest means of pronotal and gular setae length and clypeal pubescence distance smaller ($PnHL/CS 0.124 \pm 0.008$, $GuHL/CS 0.092 \pm 0.009$, $sqPDCL 3.54 \pm 0.30$). Discriminant < 0 [error 0% in 152 individuals]**46**
- 46a** Southern parts of East Siberia between 106 and $134^\circ E$ (Ussuri). Differs from *niger* by a combination of more numerous metapleural setae, less numerous scape setae and less dense clypeal pubescence. Discriminant $4.378*CW -1.640*sqPDCL+0.164*nSc -0.349*nSt+3.458 < 0$ [error 0% in 7 workers]. (Figs. 51–52, Tab. 6)*vostochni* sp. nov.
- 46b** From $10^\circ W$ to $108^\circ E$. Discriminant > 0 [error 0% in 155 workers]. (Figs. 49–50, Tab. 6)*niger*
- 47a** Whole body very hirsute ($nGen 20.5 \pm 3.3$, $nGu 19.8 \pm 5.3$, $nHT 32.1 \pm 3.6$). Gular setae very long ($GuHL/CS 0.154$

- ± 0.010). Scape long (SL/CS 1.018 ± 0.022). SW flank of Himalayas above 2000 m. (Figs. 91–92, Tab. 9) *hirsutus*
47b Much less hirsute (nGen < 12.5, nGu < 14). Gular setae usually shorter.....**48**
- 48a** Very large body size (CS 1153 ± 108 μm). Clypeal pubescence distance very large (sqPDCL 6.85 ± 0.88). Paramedian pubescence hairs on posterior dorsum of gaster tergites directed caudomedial or even medial. Pronotal setae short (PnHL/CS 0.119 ± 0.011). Number of mandibular dents low (MaDe 7.22 ± 0.67 M). Southern flank of Himalayas between 1700 and 3100 m. (Figs. 85–86, Tab. 9) *magnus*
48b Character combination strongly deviating**49**
- 49a** Setae numbers on whole body strongly reduced (nOcc + nGen = 1.2 ± 0.9). Pubescence on whole body and appendages very smooth, appressed and short. Dorsal and posterior profile of propodeum linear and forming a distinct, obtuse angle. Number of mandibular dents low (7.25 ± 0.49). Rather large (CS 1003 ± 82 μm). Scape short (SL/CS 0.900 ± 0.024). Pronotal setae short, PnHL/CS 0.108 ± 0.011 . SW flank of the Himalayas at elevations between 2300 and 2800 m. (Figs. 5–6, Tab. 1) *himalayanus*
49b Character combination strongly deviating**50**
- 50a** Terminal segment of maxillary palp and scape long (MP6/CS 0.201 ± 0.014 , SL/CS 1.021 ± 0.025). Clypeal pubescence distance large (sqPDCL 5.05 ± 0.47). Discriminant 41.753*MP6+13.0*SL+1.481*sqPDCL-0.244*nSt-45.071 * PnHL- 19.61 >0 [error 2.9% in 68 individuals]. Eastern margin of Tibetan Plateau. (Figs. 101–102, Tab. 10) *longipalpus* sp. nov.
50b Terminal segment of maxillary palp and scape shorter. Clypeal pubescence distance often smaller. Discriminant < 0 [error 1.9% in 159 individuals]**51**
- 51a** Southern flank of Himalayas**52**
- 51b** Tibetan Plateau**53**
- 52a** Eye small (EYE/CS 0.221 ± 0.008). Number of genal and gular setae lower (nGen 2.3 ± 1.4 , nGu 3.1 ± 1.4). Discriminant 199.63*EYE-56.58*CL+108.61*PnHL-4.236 < 0 [error 0% in 13 individuals]. (Figs. 87–88, Tab. 9) *lawarai*
52b Eye larger (EYE/CS 0.245 ± 0.006). Number of genal and gular setae larger (nGen 6.2 ± 2.6 , nGu 7.9 ± 3.3). Discriminant > 0 [error 0% in 12 individuals]. (Figs. 89–90, Tab. 9) *wittmeri*
- 53a** Standing setae on extensor profile of hind tibia more numerous and extending over the whole profile (nHT 10.8 ± 0.9). (Figs. 93–94, Tab. 9) *schaeferi*
53b Setae on extensor profile of hind tibia much fewer and concentrated to the proximal half of profile (nHT 2.5 ± 2.0). (Figs. 23–24, Tab. 9) *obscuratus*
- 54a** Terminal segment of maxillary palp and scape extremely long (MP6/CS 0.267 ± 0.008 , SL/CS 1.131 ± 0.031). Discriminant 34.93*SL-23.33*CW-15.45 > 0 [error 0% in 17 specimens]. Japan. (Figs. 103–104, Tab. 11) *productus*
54b Terminal segment of maxillary palp and scape much shorter. Discriminant < 0 [error 0% in 375 specimens]**55**
- 55a** Mesosoma with very flat propodeal dome and convex to angulate-convex posterior propodeal slope that is transversally carinulate. Petiole scale in lateral view thick, low and with a blunt apex; in anterior view rather narrow, with convex to nearly straight subparallel sides. Whole body very hirsute (nSt 12.2 ± 2.2). Discriminant 0.464*nSt-15.38*CL+20.00*SL-23.77*PoOc-23.98*GuHL-0.727 > 0 [error 0% in 12 individuals]. May form supercolonies. Japan. (Figs. 109–110, Tab. 11) *sakagamii*
55b Mesosoma and petiole of differing morphology. Number of standing setae on area below propodeal spiracle lower (nSt 3.3 ± 2.5). Discriminant < 0 [error 0.7% in 269 individuals]**56**
- 56a** Microsculpture between the frontal carinae rather deep, with the margins of meshes developed as elevated ridges and their inner part developed as a rather deep foveola which centrally carries the base of a pubescence hair; short fragments of microcarinulae are irregularly dispersed over the surface. Frontal pubescence short (PLF 25.4 ± 1.9 μm). Body size small (CS 819 ± 41 μm). Head elongated (CL/CW 1.104 ± 0.015). Scape short (SL/CS 0.973 ± 0.023). North Korea. (Figs. 105–106, Tab. 10) *koreanus*
56b Character combination different**57**
- 57a** Small (CS 826 ± 49 μm). Number of setae on surface below propodeal spiracle larger than number of genal setae (nSt 6.8 ± 1.7 , nGen 4.7 ± 2.7). Clypeal pubescence distance low (sqPDCL 3.97 ± 0.42). Scape and pronotal setae rather short (SL/CS 0.976 ± 0.008 , PnHL/CS 0.128 ± 0.005). Reddish color components absent. Ussuri region. (Figs. 51–52, Tab. 6) *vostochni* sp. nov.
57b Character combination strongly different**58**
- 58a** Clypeal pubescence distance large (sqPDCL 5.78 ± 0.27). Terminal segment of maxillary palp short (MP6/CS 0.176 ± 0.007). Pronotal setae long (PnHL/CS 0.160 ± 0.008). High mountain range of Sichuan 3000–3500 m. Discriminant 1.614*sqPDCL+0.229*nSt-43.39*MP6+23.468*PnHL-5.68 > 0 [error 0% in 12 individuals] *kabaki* sp. nov.
58b Clypeal pubescence distance frequently smaller, terminal segment of maxillary palp frequently longer. Discrimi-

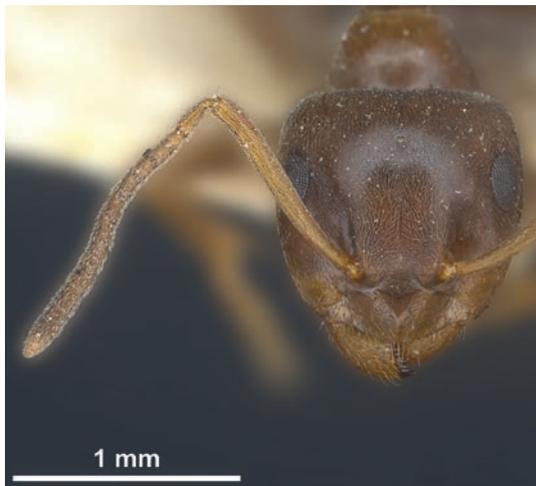
- minant < 0 [error 0% in 243 individuals]**59**
- 59a** Setae number on whole body low (nHT 4.2 ± 4.1 , nSt 0.4 ± 0.5). Eye large (EYE/CS 0.251 ± 0.007). Clypeal pubescence distance large (sqPDCL 5.05 ± 0.47). Torulo-clypeal distance low (dCIAn/CS $4.47 \pm 0.37\%$). Discriminant $0.089 \cdot \text{nHT} - 1.095 \cdot \text{sqPDCL} - 82.69 \cdot \text{EYE} + 70.50 \cdot \text{dCIAn} + 17.58 \cdot \text{PnHL} + 5.123 \cdot \text{CW} + 10.933 < 0$ [error 0% in 68 individuals]. (Figs. 101–102, Tab. 10)***longipalpus* sp. nov.**
- 59b** Setae numbers and torulo-clypeal distance larger, clypeal pubescence distance lower and eye larger. Discriminant > 0 [error 3.4% in 175 individuals].....**60**
- 60a** Sculpture on metapleuron and lower propodeum with regular, slightly curved and dense longitudinal carinulae and very delicate linear microstructures within the meshes of the microreticulum. This produces a matt overall surface appearance at lower magnifications. Chinese regions Yunnan, Sichuan, Shaanxi and Taiwan**61**
- 60b** Metapleuron and lower propodeum without or only very few suggested carinulae; usually only with a very delicate microreticulum and overall more shining**62**
- 61a** Scape longer (SL/CS 1.010 ± 0.027). Clypeal pubescence distance and torulo-clypeal distance larger (sqPDCL 4.61 ± 0.49 , dCIAn 5.26 ± 0.52). Setae longer and more numerous (PnHL/CS 0.156 ± 0.019 , GuHL/CS 0.101 ± 0.014 , nSc 27.6 ± 7.2 , nGu 6.9 ± 1.5). Discriminant $0.353 \cdot \text{nGu} - 64.932 \cdot \text{EYE} + 0.138 \cdot \text{nSc} + 9.961 > 0$ [error 0% in 34 individuals]. (Figs. 95–96, Tab. 10)***coloratus***
- 61b** Scape shorter (SL/CS 0.976 ± 0.030). Clypeal pubescence distance and torulo-clypeal distance smaller (sqPDCL 4.14 ± 0.54 , dCIAn 4.94 ± 0.54). Setae shorter and less numerous (PnHL/CS 0.135 ± 0.010 , GuHL/CS 0.083 ± 0.018 , nSc 11.2 ± 6.9 , nGu 3.4 ± 1.8). Discriminant < 0 [error 0% in 29 individuals]. (Figs. 97–98, Tab. 10)***sichuense* sp. nov.**
- 62a** Head capsule homogenously yellowish brown. Head short (CL/CW 1.028 ± 0.013) and usually with concave posterior margin. Scape rather short (SL/CS 0.958 ± 0.016). Eye rather small (EYE/CS 0.224 ± 0.007). Petiole sides more convex. Shady deciduous woodland in Japan, Korea, Kuriles. (Figs. 107–108, Tab. 11)***hayashi***
- 62b** Head capsule not homogenously yellowish brown; vertex dark or blackish brown; if reddish or yellowish pigmentation is present then restricted to clypeus. Head longer (CL/CW 1.062 ± 0.026) and without concave posterior margin. Scape longer (SL/CS 1.002 ± 0.028). Eye larger (EYE/CS 0.238 ± 0.009). Petiole sides less convex**63**
- 63a** Number of setae on whole body less large (nGu 9.0 ± 3.0 , nSt 3.1 ± 1.2). Discriminant $0.21 \cdot \text{nGu} + 0.739 \cdot \text{sqPDCL} + 0.528 \cdot \text{nSt} - 37.83 \cdot \text{EYE} + 0.133 < 0$ [error 0% in 59 individuals]. NE China, Korea, Russian Far East, Japan. (Figs. 53–54, Tab. 6)***japonicus***
- 63b** Number of setae twice as large (nGu 18.7 ± 4.6 , nSt 6.2 ± 1.5). Discriminant > 0 [error 4.9% in 41 individuals, 0% in 13 sample means]. E Tibet to NE China. (Figs. 55–56, Tab. 6)***chinensis* sp. nov.**



Figs. 1 and 2: *Lasius brunneus*; neotype



Figs. 3 and 4: *Lasius silvaticus* sp. nov.; holotype



Figs. 5 and 6: *Lasius himalayanus*; specimen from syntype series



Figs. 7 and 8: *Lasius excavatus* sp. nov.; holotype



Figs. 9 and 10: *Lasius lasioides*; CASENT0906077, photo S. Hartman



Figs. 11 and 12: *Lasius austriacus*; paratype



Figs. 13 and 14: *Lasius neglectus*; paratype



Figs. 15 and 16: *Lasius precursor* sp. nov.; holotype



Figs. 17 and 18: *Lasius turcicus*; CASENT0906080, photo S. Hartman



Figs. 19 and 20: *Lasius tapinomoides*; paratype



Figs. 21 and 22: *Lasius israelicus* sp. nov.; holotype Figs.



Figs. 23 and 24: *Lasius obscuratus*



Figs. 25 and 26: *Lasius psammophilus*; CASENT0179885, photo E. Prado



Figs. 27 and 28: *Lasius piliferus*; holotype



Figs. 29 and 30: *Lasius creticus* sp. nov.; holotype



Figs. 31 and 32: *Lasius brevipalpus* sp. nov.; holotype



Figs. 33 and 34: *Lasius paralienus*; CASENT0906118, photo E. Ortega .



Figs. 35 and 36: *Lasius bombycina*



Figs. 37 and 38: *Lasius casevitzi*; paratype



Figs. 39 and 40: *Lasius kritikos* sp. nov.; holotype



Figs. 41 and 42: *Lasius alienus*; CASENT0179927, photo E. Prado



Figs. 43 and 44: *Lasius karpinisi*; holotype



Figs. 45 and 46: *Lasius schulzi*; holotype



Figs. 47 and 48: *Lasius uzbeki*; holotype



Figs. 49 and 50: *Lasius niger*; CASENT0179897, photo E. Prado



Figs. 51 and 52: *Lasius vostochni* sp. nov.; holotype



Figs. 53 and 54: *Lasius japonicus*; CASENT0280450, photo W. Ericson



Figs. 55 and 56: *Lasius chinensis* sp. nov.; holotype



Figs. 57 and 58: *Lasius platythorax*; CASENT0179887, photo Erin Prado



Figs. 59 and 60: *Lasius cyperus* sp. nov.; holotype



Figs. 61 and 62: *Lasius flavescens*; paratype, CASENT0911048, photo Z. Lieberman



Figs. 63 and 64: *Lasius flavoniger*; paratype, CASENT0903218, photo W. Ericson



Figs. 65 and 66: *Lasius grandis*; CASENT0906079, photo S. Hartman



Figs. 67 and 68: *Lasius mauretanicus* sp. nov.; holotype



Figs. 69 and 70: *Lasius cinereus*; holotype



Figs. 71 and 72: *Lasius balearicus*; paratype



Figs. 73 and 74: *Lasius persicus* sp. nov.; holotype



Figs. 75 and 76: *Lasius emarginatus*



Figs. 77 and 78: *Lasius illyricus*; CASENT0914255, photo M. Esposito



Figs. 79 and 80: *Lasius maltaeus* sp. nov.; holotype



Figs. 81 and 82: *Lasius tebessae*; holotype



Figs. 83 and 84: *Lasius tunisius* sp. nov.; holotype



Figs. 85 and 86: *Lasius magnus*; paratype



Figs. 87 and 88: *Lasius lawarai*; paratype



Figs. 89 and 90: *Lasius wittmeri*; holotype



Figs. 91 and 92: *Lasius hirsutus*; holotype



Figs. 93 and 94: *Lasius schaeferi*; holotype, CASENT0912296, photo Z. Lieberman



Figs. 95 and 96: *Lasius coloratus*; CASENT0906278, photo E. Ortega



Figs. 97 and 98: *Lasius sichuense* sp. nov.; holotype



Figs. 99 and 100: *Lasius kabaki* sp. nov.; holotype



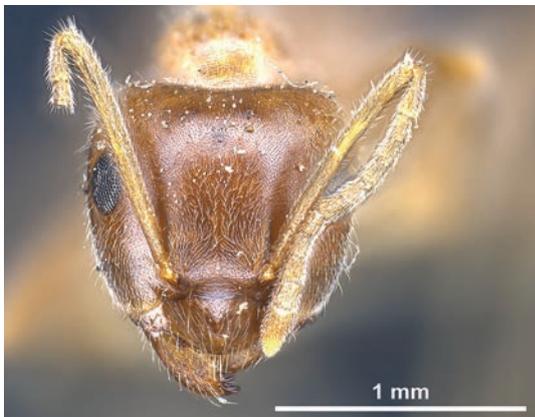
Figs. 101 and 102: *Lasius longipalpus* sp. nov.; holotype



Figs. 103 and 104: *Lasius productus*; paratype, CASENT0903217, photo W. Ericson



Figs. 105 and 106: *Lasius koreanus*; holotype, CASENT0912292, photo Z. Lieberman



Figs. 107 and 108: *Lasius hayashi*; paratype



Figs. 109 and 110: *Lasius sakagami*; paratype

4.4 Treatment by species

4.4.1 *Lasius brunneus* (Latreille 1798)

Formica brunnea Latreille 1798 [conception of Mayr (1861) and neotype fixation] Both the original description and that of Latreille (1802) do not allow a species identification. The locus typicus is Brive/France. The first unambiguous description was presented by Mayr (1861) that has been adopted by most of the European authors since then. A neotype is fixed herewith in three worker specimens collected near Brive, labelled "FRA: 44.9125°N, 1.4769°E, Souillac–1.7 km N, 120 m, tree row, leg. Galkowski 2008.09.07" and "Neotype (top) *Lasius brunneus* (Latreille 1798) des. Seifert 2019"; depository: SMN Görlitz.

Lasius pallidus (Latreille 1798)

Formica pallida Latreille 1798 [indirect indication] This taxon is not identifiable from data in the original description. Yet, as the synonymization with *Lasius brunneus* was established by Latreille himself (Latreille 1802), I follow his decision.

Lasius timidus (Foerster 1850)

Formica timida Foerster 1850 [original description] This taxon was described from near Aachen /Germany. The reported morphology (coloration, length of frontal line, pilosity) in combination with zoogeography strongly suggests a synonymy with *L. brunneus*.

Lasius alienobrunneus Forel 1874

Lasius niger var. *alienobrunneus* Forel 1874 [type specimens]

Forel did not mention a locus typicus. Five workers stored in MHN Genève, labelled as "Typus" and "L. alienobrunneus For. / Vaux" do not show any notable deviation from the normal morphology of *L. brunneus* both by NUMOBAT data and subjective impression (pictures in www.antweb.org under CASENT0911044).

All material examined. A total of 32 nest samples with 67 workers were subject to NUMOBAT investigation. These originated from Austria (1 sample), Bulgaria (1), England (1), France (3), Germany (11), Greece (1), Italy (1), Spain (2), Sweden (1), Switzerland (2), and Turkey (8). For details see supplementary information SII.

Geographic range. Eurocaucasian, submeridional and temperate. From S England and Iberia across Central Europe, the Apennine and the Balkans to Asia Minor and the Caucasus. In Scandinavia north to 60°N, absent from Finland. In N Tyrol ascending to 1410 m and in Anatolia at 37°N to 2000 m.

Diagnosis (Tab. 1, Figs. 1–2; images in www.antWeb.org with specimen identifiers CASENT0172717, CASENT0172745, CASENT0172746, CASENT0179886, CASENT0179917, CASENT0179917, CASENT0911044:

The species is rather easily identified by a combination

of short scape (SL/CS_{900} 0.874), broad head (CL/CW_{900} 1.041), reduced setae numbers on all body parts ($nOcc_{900}$ 2.0, $nGen_{900}$ 0.1, nGu_{900} 1.3, nSC_{900} 0.0, nHT_{900} 0.1, nSt_{900} 1.1) a very smooth pubescence surface on scape and tibiae, and reduced number of mandibular dents ($MaDe_{900}$ 7.06). The dorsal and posterior profile of propodeum are linear and form a distinct, obtuse angle. The petiole is in antero-caudal view rather rectangular or slightly converging dorsad but typically with straight sides and forming a sharp, weakly emarginate dorsal crest. A typical coloration of medium-sized to large specimens is mesosoma, petiole and appendages light yellowish brown, head a little darker bronze brown and gaster dark to blackish brown. However, small workers from initial colonies may show a homogeneously dark coloration as seen in *L. lasioides* or *L. neglectus* but can easily be separated by RAV-corrected NUMOBAT data.

Biology. See Seifert (2018).

Comments. For separation from the eastern sister species *L. silvaticus* sp. nov. and *L. himalayanus* see there and Tab. 1.

4.4.2 *Lasius silvaticus* sp. nov.

Etymology. The species name refers to the woodland habitat.

Type material. Holotype plus 2 paratype workers labelled "IRAN: 36.7198°N, 54.5813°E, Gorgan 19SE, 853 m, Caspian mild and wet, A.B. Yazdi 2016.06.15 -9" and "Holotype (bottom) and paratypes *Lasius silvaticus* Seifert"; 3 paratype workers "IRAN: 36.7198°N, 54.5813°E, Gorgan 19SE, 853 m, Caspian mild and wet, A.B. Yazdi 2016.06.15 -24" and "Paratypes *Lasius silvaticus* Seifert"; 3 paratype workers "IRAN: 37.367°N, 55.817°E, Golestan NP, Galesha canyon, 594 m, forest, nest on tree, Paknia 2007.05.23- 1420"; 3 paratype workers "IRAN: 37.367°N, 55.817°E, Golestan NP, Galesha canyon, 594 m, forest, nest under stone, Paknia 2007.05.23- 1427"; all material stored in SMN Görlitz.

All material examined. A total of 9 nest samples with 24 workers from seven localities in the Iran were subject to NUMOBAT investigation. For details see supplementary information SII.

Geographic range. S Caspian; known so far only from a rather small area between 36.7 and 37.4° N, 54.4 and 55.8°E, and 160 to 900 m a.s.l.

Diagnosis (Tab. 1, Figs. 3–4; key; image in www.antWeb.org with specimen identifier CFH000052): Showing all diagnostic characters of the *L. brunneus* species complex. The main difference to *L. brunneus* is the less sparse and longer pilosity on pronotum ($PnHL/CS_{900}$ 0.130), underside of head (nGu_{900} 3.6, $GuHL/CS_{900}$ 0.125), propodeum and hind tibia (nHT_{900} 1.6, nSt_{900} 2.9).

Accessory differences are the longer head and smaller postocular distance (CL/CW₉₀₀ 1.059, PoOc/CS₉₀₀ 0.235). The coloration is fully comparable to *L. brunneus*.

Biology. Habitat selection appears to be similar to its sibling species *Lasius brunneus*: Seven samples were found in wet and humid Caspian broad-leaved forest and one sample in a city park with trees. The nests were both in the wood of trees, under stones, in litter and (in a clearcutting) in soil.

Comments. *L. brunneus*, *L. silvaticus* sp. nov. and *L. himalayanus* are hypothesized here to represent three cryptic species with different geographic distribution. They are clearly clustered on the sample level as different entities by exploratory data analyses using the 16 standard NUMOBAT characters unselectively. The classification error relative to the controlling LDA is 0% in a PCA and a TSCA using the first four principal components. NC-Ward, NC-part.kmeans, NC-part.hclust and NC-NMDS-kmeans misclassify one *L. brunneus* sample from Aksehir / Turkey as *L. himalayanus* (=error 2.9% in 34 samples). A mean classification error of 1.9% within six exploratory data analyses is in agreement with the heterospecificity threshold of the GAGE species concept. The three cryptic species seem to be parapatric or allopatric according to the poor information currently available and it will be interesting to see if the current taxonomic assessment would change after investigations in the putative contact zone of *L. brunneus* and *L. silvaticus* sp. nov. near the Turkish-Iranian border will have been done. The allopatric data currently available provide a strong signal for species separation: the discriminant $D(8) = 40.81*SL - 38.9*CW + 71.2*PnHL + 0.866*nHT - 0.674*sqPDCL + 0.246*nSt - 2.392$ is $D(8) = -1.885 \pm 0.956 [-4.75, 0.00]$ in 56 workers of *L. brunneus* and $D(8) = 4.390 \pm 1.098 [2.63, 6.56]$ in 24 workers of *L. silvaticus*.

4.4.3. *Lasius himalayanus* Bingham 1903

Lasius himalayanus Bingham 1903 [first available use of *Lasius niger* r. *brunneus* var. *himalayanus* Forel 1894; type investigation]

Type material: 2 syntype workers labelled "L. brunneus v. himalayana Forel, Himalaya LX/9) (Smythies)", "Typus", "ANTWEB CASENT 0911043"; 8 syntype workers labelled "L. brunneus v. himalayana Forel, Himalaya 9000' (Smythies), XXX/22", "Cotypus"; all these syntypes stored in MHN Genève.

All material examined. A total of 11 nest samples with 37 workers were subject to NUMOBAT investigation. These originated from NE Pakistan (7 samples) and NW India (4). For details see supplementary information SII.

Geographic range. Known so far only from the SW flank of the Himalayas at elevations between 2300 and 2800 m, along a line delimited by 35.7°N, 71.6°E and 32.2°N, 77.2°E.

Diagnosis (Tab. 1, Figs. 5–6; key; images in www.antWeb.org with specimen identifiers CASENT0911043):

Showing all diagnostic characters of the *L. brunneus* species complex. *L. himalayanus* is most similar to *L. brunneus* but differs by narrower head (CL/CW₉₀₀ 1.072), longer scape (SL/CS₉₀₀ 0.921) and denser clypeal pubescence (sqPDCL₉₀₀ 4.66). Coloration is on average darker than in *L. brunneus* or *L. silvaticus* sp. nov., with head, mesosoma and coxae usually dark brown and gaster blackish brown.

Biology. Unknown.

Comments. For separation from the western sister species *L. silvaticus* sp. nov. and *L. brunneus* see above.

4.4.4 *Lasius excavatus* sp. nov.

Etymology. The species name refers to the shape of posterior head margin.

Type material. Holotype plus 2 paratype workers labelled "IRAN: 30.229°N, 55.375°E, Shar-e-babak: Maymand, on trees in garden, 2220 m, O. Paknia 2004.06.11 -169"; 3 paratype workers labelled "IRAN: 30.900°N, 51.419°E, Sisakht, Kharidun, 2500 m, oak steppe forest, on tree, O. Paknia 2007.07.10 -1727"; all material stored in SMN Görlitz.

All material examined. A total of two nest samples with 6 workers from two localities in the Iran were subject to NUMOBAT investigation. For details see supplementary information SII.

Geographic range. Only known so far from the two type localities in the highland desert of S Iran at elevations of 2200–2500 m.

Diagnosis (Tab. 1, Figs. 7–8): The low number of mandibular dents (MaDe₉₀₀ 7.00), the linear profile lines of the dorsum and posterior slope of propodeum, the sharp dorsal crest of petiole scale, the very smooth pubescence on scapes and tibiae, the strongly reduced pilosity, the short pronotal setae (PnHL/CS₉₀₀ 0.102) and the short frontal pubescence (PLF₉₀₀ 23.2 μm) place *L. excavatus* sp. nov. within the *Lasius brunneus* species complex. The main difference to the three related species *L. brunneus*, *L. silvaticus* sp. nov. and *L. himalayanus* are the longer scape (SL/CS₉₀₀ 0.974), the shorter postocular index (PoOc/CL₉₀₀ 0.222) and a suggested excavation of posterior head margin. The coloration is similar to the situation in *L. brunneus*, yet with two of the six type specimens a little darker.

Biology. The climatic conditions within the highland desert of Iran are harsh due to high aridity, high summer temperatures and very cold winters. The species was found in rare spots with less extreme conditions allowing growth of trees: a light *Quercus* woodland and a light stand of broad-leaved trees in the ancient settlement

of Maymand. *L. excavatus* sp. nov. appears to be arboricolous and is probably an Iranian endemic.

Comments. None.

4.4.5 *Lasius lasioides* (Emery 1869)

Prenolepis lasioides Emery 1869 [type investigation]

Type material: Lectotype, an alate gyne, labelled by Mayr "Neapel Emery", "Collect. G.Mayr", "L.fumatus m., lasioides m., det. Emery" and "lectotype, des. E.O.Wilson"; 1 paralectotype worker labelled by Mayr "Neapel Col. G.Mayr", "L.fumatus m., lasioides m., det. Emery" and "Typus"; both specimens in NHM Wien. Emery (1869) produced confusion in naming this species which was described "from the environs of Napoli". In the verbal description on page 6 he described the species under the name *Prenolepis lasioides* and gives a reference to Fig. 3a, but in the caption for Fig. 3a on page 26 he suddenly presents the name *Lasius fumatus*. Accordingly, *L. fumatus* is an objective synonym because it refers to the same material

Lasius fuscus (Emery 1869)

Prenolepis fuscula Emery 1869 [original description, investigation of type-compared material]

One worker, deposited in NHM Wien and labelled by Gustav Mayr "Emery Neapel 1874", "*Lasius fuscus* Emery Neapel" and "*Lasius fuscus* E. det. G.Mayr" was apparently sent by Emery to Mayr in 1874. *Lasius fuscus* was described from workers running over a balcony at Portici near Napoli. The rather detailed description of Emery and the fact that there is only one *Lasius* species in Italy matching this description strongly suggests a synonymy with *L. lasioides*. Emery reported a minute total length of 2–2.5 mm and only 5–6 mandibular dents which both is typical for nanitic workers of *L. lasioides*. It appears possible that the specimen sent to Mayr really belongs to original material of *L. fuscus* as it has MaDe 6.0 and CS 601 µm. The workers of both *Lasius lasioides* and *L. fuscus* Emery had at hand when describing these species were nanitic workers with a reduced number of mandibular dents. The latter character apparently prompted him to allocate both taxa to *Prenolepis*.

Lasius nigrobrunneus (Donisthorpe 1926)

Acanthomyops brunneus var. *nigrobrunneus* Donisthorpe 1926

This taxon was reported by Donisthorpe to occur at Ospedaletti, Bordighera and Monte Nero in N Italy and has been unexplained synonymized by Wilson (1955) and Baroni Urbani (1971) with *Lasius brunneus*. The complete morphological description of Donisthorpe is "head quite black, and the rest of the body dark brown; but there are no outstanding hairs on the tibiae" and he

reported to have found the three nests under stones. This information does not suggest an arboricolous ant related to *Lasius brunneus* but may refer to at least four different species expected to occur in the area: *L. alienus*, *L. paralienus*, *L. psammophilus*, and *L. lasioides*. There is a worker stored in BMNH London and pictured in antweb.org with specimen identifier CASENT0903216, labelled "Ospedaletti 6.II. 25.", "ex coll. Donisthorpe B.M. 1934-4" and "Type". This type specimens belongs to either *L. lasioides* or *L. alienus*. The short pronotal setae and scale shape more strongly suggest a synonymy with *L. lasioides* which is hypothesized here. The specimen was not directly investigated.

Lasius barbarus Santschi 1931

Lasius alienus var. *barbarus* Santschi 1931 [type investigation]

The taxon has been first described under the unavailable name *Lasius niger lasioides* v. *barbara* Santschi 1921. Type material: Lectotype and 3 paralectotypes on the same pin labelled "Type", "Sidiyech 141", "*Lasius niger* st. *lasioides* Em v. *barbara* Sants T. Santschi det. 1921", and "lectotype uppermost worker desig. by E.O.Wilson"; depository NHM Basel. Three paralectotype workers on one pin labelled "Sidiyech 141", "83", "MUSEUM PARIS AFRIQUE DU NORD A.THÉRY 1919 1923", "*Lasius niger* st *alienus* For v. *barbarus* Sants"; depository MNHN Paris. For synonymization with *L. lasioides* see under Comments.

All material examined. A total of 106 nest samples with 306 workers were subject to NUMOBAT investigation. These originated from Algeria (4 samples), Cyprus (4), France (14), Greece and Crete (15), Iran (1), Israel (3), Italy (15), Malta (4), Morocco (17), Spain (16), Syria (1), Tunisia (4), Turkey (8). For details see supplementary information SII.

Geographic range. *L. lasioides* is a Holomediterranean species – the missing of records from Libya and Egypt are caused by absence of sampling activities. The most southwestern site is in Morocco at 30.8°N, 8.8° W. The northern distributional border runs along 43.5° N in France, 44.6° N in Italy, 40.5°N in Greece and Turkey whereas the easternmost truly Mediterranean site is at 35.6°N, 36.2°E in Syria. The distribution farther east is poorly known. Samples from two sites in the East Anatolian highland (PR_N 502, 39.43°N, 39.88°E, 1800 m; PR_N 460, 38.63°N, 43.45°E, 2300 m) might possibly represent a separate population or even species with special adaptation to wintercold climate. The sample from Ghaemshar / Iran (36.46°N, 52.86°E, 49 m) represents the easternmost known site and raises the question if there is a continuous distribution from Syria and Israel east to the northern Iran. The highest site in the Moroccan Atlas Mountains is at 33.00°N, 5.07°W, 2240 m. It may be

expected to have colonized all sufficiently large islands in the Mediterranean Sea which have some tree stands.

Diagnosis (Tab. 1, Figs. 9–10; key; images in www.antWeb.org with specimen identifiers CASENT0906077, CASENT0912293): *L. lasioides* shows all diagnostic characters of the *L. brunneus* species complex. It can be separated from its semipatric relatives *L. brunneus* and *L. silvaticus* sp. nov. by smaller head width, longer scape and larger torulo-clypeal distance. With all measurements in mm, the discriminant

$$222.5 * dCIAn + 29.75 * SL - 35.6 * CW$$

is <0.8 in *L. brunneus* and *L. silvaticus* sp. nov. but >0.9 in *L. lasioides* (error 0% in 288 individuals). Confusion with *L. himalayanus* is excluded by zoogeography. The potentially sympatric Iranian desert species *L. excavatus* sp. nov. differs by head shape and coloration. Coloration in *L. lasioides*: head, mesosoma, gaster, femora and tibiae dark to medium brown; tibio-femoral joint region, scape and (frequently) anterior margin of clypeus pale yellowish-brown.

Biology. *Lasius lasioides* is apparently dependent from the presence of trees. It inhabits diverse types of broad-leafed or coniferous forest, both such with closed canopies or more open stands, as well as urban areas, gardens, pastures and road sides with at least a few scattered trees. The nests may be found under bark of the trees or on ground in dead logs or under stones. The behavior is similar to *L. brunneus*: it is fugitive and not aggressive and workers prefer runways in crevices of bark or other surface structures. Development of alates differs throughout the whole geographic range in dependence from latitude and altitude. Eleven observations of alates occurred 30 April – 29 July, ten of these before 8 July.

Comments. The Holomediterranean population of *L. lasioides* is polymorphic; there is in particular an extreme variance in scape length (Tab. 1). This polymorphism shows a rather clear geographic structuring. Exclusively the long-scaped morph, which corresponds to the types of *L. lasioides*, was found in Italy and Greece and the islands of Mallorca, Malta, and Sardinia. Only the short-scaped morph, which corresponds to the types of *L. barbarus*, was found in the Spanish mainland and on Cyprus. Sympatric occurrence of both morphs is observed in Morocco, Algeria, Tunisia, Syria, and Israel. The Iberian short-scaped population and the Italian long-scaped population are in contact in southern France. This structure and a seemingly mutually exclusive occurrence on islands aroused suspicion on heterospecificity of *L. lasioides* and *L. barbarus*. However, attempts to show heterospecificity with exploratory data analyses – different forms of NC-clustering as well as PCA or TSCA – led to contradictory results. The overall error rate remained clearly above the 4% threshold required by the GAGE species concept.

4.4.6 *Lasius austriacus* Schlick-Steiner 2003

Lasius austriacus Schlick-Steiner 2003
[type investigation]

Type material: 3 paratype workers from holotype nest labelled "AUS: 15.51 E, 48.40 N, Feldberg bei Pulkau, leg. Schlick & Steiner, 2002.08.06 – 10982"; 3 paratype workers labelled "AUS: 16.57 E, 48.09 N, Braunsberg bei Hainburg, leg. Schlick & Steiner, 2002.07.02 – 10445"; 3 paratype workers labelled "AUS: 16.57 E, 48.09 N, Braunsberg bei Hainburg, leg. Schlick & Steiner, 2002.07.02 – 10449; 3 paratype workers labelled "CZE: S Moravia: Hnanice 1.5 NNE, armer Steppenrasen mit Calluna auf Fels, 1997.09.18 -44"; all material deposited in SMN Görlitz.

All material examined. A total of 13 nest samples with 40 workers were subject to NUMOBAT investigation. These originated from Austria (9 samples), Czechia (2) and Turkey (2). For details see supplementary information S11.

Geographic range. In Europe known so far from only five sites in a 6500 km² area in the planar and colline region of east Austria and south Moravia (here north to 48.9°N). A single very remote site from outside this area was confirmed for Anatolia (38.9°N, 36.8°E, 1900 m). Due to hidden life style and misidentification as "*L. alienus*" in the past it is certainly underrecorded throughout its range.

Diagnosis (Tab. 2, Figs. 11–12; key; images in www.antWeb.org with specimen identifiers CASENT0916646): *Lasius austriacus* is an unmistakable combination of, in terms of *Lasius*. s.str., extremely small eye (EYE₉₀₀ 0.198), short terminal segment of maxillary palp (MP6₉₀₀ 0.144) and extremely small torulo-clypeal distance (dCIAn₉₀₀ 2.61%). Low scape length is another rare character (SL/CS₉₀₀ 0.892). Body size very small (CS 705 μm). Mean number of mandibular dents low (MaDe₉₀₀ 7.4). Petiole scale in lateral view thin and forming an acute tip. Clypeal pubescence dilute (sqPDCL₉₀₀ 5.51). Mean length of pubescence hairs on frons rather short (PLF₉₀₀ 30.5 μm). Dorsum of scape without or few, occasional setae. Coloration: Head, mesosoma and gaster dark brown; antennae, tibiae and tarsae yellowish.

Biology. See the short summary in Seifert (2018).

Comments. The almost completely subterranean foraging lead to a significant reduction of eye size (EYE/CS₉₀₀ 0.198 ± 0.009, n=40). This value is, however, larger than in the most large-eyed species of the entirely subterranean subgenus *Cautolasius*: *Lasius alienoflavus* Bingham 1903 with EYE/CS₉₀₀ 0.145 ± 0.006 (n=44) and *L. flavus* (Fabricius 1782) with EYE/CS₉₀₀ 0.147 ± 0.010 (n=200).

4.4.7 *Lasius neglectus* Van Loon et al. 1990

Lasius neglectus Van Loon, Boomsma & Andrasfalvy 1990 [type investigation]

Type material: 7 paratype workers from the holotype colony labelled "HUNGARY Budapest 1. VII 1988"; depositories: BMNH London, SMN Görlitz.

All material examined. A total of 69 nest samples with 207 workers were subject to NUMOBAT investigation. These originated from Belgium (3 samples), Bulgaria (1), Georgia (5), France (6), Great Britain (1), Germany (4), Greece (5), Hungary (1), Iran (1), Israel (1), Italy (1), Kyrgyzstan (6), Poland (1), Romania (2), Spain (5), Turkey (25), Uzbekistan (1). For details see supplementary information SII.

Geographic range. Highly invasive species having spread from a center most probably situated in Asia Minor. Currently known distribution: Tenerife, Iberia, France, Switzerland, Corsica, Italy, S England, Netherlands, Belgium, Germany, Poland, Hungary, Balkans, Ukraine, Cis- and Transcaucasia, Asia Minor, Iran, Uzbekistan, Kyrgyzstan (75°E), Israel. Invasion of Europe and Middle Asia started in about 1973. The northernmost known site in Europe by the year 2013 is Rostock (54.1°N). There is a clear potency for spreading to S Scandinavia because some Asian populations survive in regions with mean January temperatures of -5°C. In Asia Minor most abundant below 1000 m but some populations also ascend to 1900 m.

Diagnosis (Tab. 2, Figs. 13–14; key; images in www.antWeb.org with specimen identifiers CASENT0173143, CASENT0280447, CASENT0903220):

Body size small (CS 772 µm). Number of mandibular denticles low (MaDe₉₀₀ 7.3). Clypeal pubescence dilute (sqPDCL₉₀₀ 5.39). Pronotal setae rather short (PnHL/CS₉₀₀ 0.127), not much longer than gular setae (GuHL/CS₉₀₀ 0.115). Petiole scale in lateral view thin and forming an acute tip. Pubescence hairs on frons rather long (PLF 34.1 µm). Dorsum of scape and hind tibiae without or few, occasional setae. Coloration: Head, mesosoma and gaster dark brown; mandibles, antennae, tibiae and tarsae light yellowish-brown. For separation from *L. turcicus* and *L. precursor* sp. nov. see key.

Biology. See the short summary in Seifert (2018).

Comments. This invasive species has been issue of perhaps a hundred publications during the last three decades. The determination in the introduction areas, where no *L. turcicus* or *L. precursor* sp. nov. are present, is usually easy because of its impressive colony structure but initial colonies might be confused with *L. psammophilus* and *L. obscuratus*. The latter species differ from *L. neglectus* by longer pronotal setae, shorter maxillary palps and higher number of mandibular denticles.

The separation from the sister species *L. turcicus* and *L. precursor* sp. nov. is most challenging and requires complex character combinations. Using 15 standard characters (MP6/CS₉₀₀ excluded) in exploratory data analyses, 55 nest samples of *L. neglectus* are separated from 128 nest samples of *L. turcicus* and *L. precursor* sp. nov. with the following error rates: 3.8% in NC-Ward, 2.2% in NC-part.kmeans, and 3.3% in NC-NMDS-kmeans – in the mean 3.1%. This is below the 4% error threshold accepted here to indicate heterospecificity. Reducing the number of characters to 10 (CS, CL/CW₉₀₀, SL/CS₉₀₀, nHT₉₀₀, nOcc₉₀₀, nGU₉₀₀, GuHL/CS₉₀₀, nSt₉₀₀, dCIAn/CS₉₀₀, EYE/CS₉₀₀) the performance is slightly improved: 3.8% in NC-Ward, 1.6% in NC-part.kmeans, and 2.2% in NC-NMDS-kmeans, giving a total mean of 2.5%.

4.4.8 *Lasius precursor* sp. nov.

Etymology. From an evolutionary perspective, colony demography and behavior this species can be considered as a precursor of the situation in *L. neglectus* (Seifert 2010). *L. precursor* sp. nov. probably represents a rather recent split-off from *L. turcicus* and may probably serve as a genetic model for transition from monogyny in *L. turcicus* to true supercoloniality.

Type material. Holotype worker plus 4 paratype workers and 3 alate gynes labelled "TUR:39.795° N, 26.681°E, Üzümlü-1.1 km N, 167 m, rural grassland, leg. Cremer et al. 2004.06.08 -712"; 5 paratype workers plus 2 males labelled "TUR:39.795° N, 26.682°E, Üzümlü-1.1 km N, 160 m, rural grassland, leg. Cremer et al. 2004.06.08-710"; depository SMN Görlitz.

All material examined. A total of 51 nest samples with 180 workers from Greece (1 sample) and 14 localities in Turkey (50 samples) were subject to NUMOBAT investigation. For details see supplementary information SII.

Geographic range. So far only known from Anatolia between 26°E and 31°E and the Island of Kos (36.85°N, 27.08°E) close to coast of West Anatolia. The altitudinal distribution of 51 samples ranges from 5 to 1116 m with the median at 237 m and 86% of all findings below 400 m. This differs significantly from the situation in 77 sympatric *L. turcicus* samples with the median at 1007 m, 74% of all samples above 400 m and a range from 1 to 1170 m (one-tailed Mann-Whitney U-test p<0.0005). The situation in East Anatolia is not studied.

Diagnosis (Tab. 2, Figs. 15–16; key):

Body size small (CS 769 µm). Number of mandibular denticles low (MaDe₉₀₀ 7.6). Clypeal pubescence dilute (sqPDCL₉₀₀ 5.13). Pronotal setae rather short (PnHL/CS₉₀₀ 0.127), very little longer than gular setae (GuHL/CS₉₀₀ 0.125). Petiole scale in profile view rather thin with

an acute dorsal tip. Pubescence hairs on frons rather long (PLF₉₀₀ 34.5 µm). Dorsum of scape and hind tibiae without or few, occasional setae. It differs from *L. neglectus* by shorter scape (SL/CS₉₀₀ 0.946), larger postocular distance (PoOc/CL₉₀₀ 0.238), smaller torulo-clypeal distance (dCIAn/CS₉₀₀ 3.61%) and fewer setae on posterior margin of head (nOcc₉₀₀ 5.8). The most significant differences to *L. turcicus* are smaller absolute size, shorter scape, larger postocular distance and smaller torulo-clypeal distance. Coloration: Head and gaster dark brown, mesosoma often suggested lighter; mandibles, antennae, lateral part of clypeus, tibiae and tarsae light yellowish-brown.

Biology. Cremer et al. (2008) found the following differences in the biologies of *L. precursor* sp. nov. and *Lasius turcicus*: Gynes of *L. precursor* sp. nov. show a trend to mate within colonies and reduced dispersal rates compared to *L. turcicus* which is in line with the smaller absolute size and shorter wings of the former. Gynes of *L. turcicus* are larger and longer-winged, never showed intranidal mating in 106 nest box trials, and are better dispersers. Combining *L. turcicus* gynes with males of *L. precursor* sp. nov. resulted in 38% matings in 29 tests. In contrast, *L. turcicus* males never mated *L. precursor* sp. nov. gynes in 51 tests, suggesting that the males of *L. turcicus* need to fly before being able to copulate. This suggests that part of the *L. precursor* sp. nov. populations are propagated by intra-nest mating and colony budding, but without being invasive. Intraspecific aggression among workers of different nests was high in *L. turcicus*, lower but still significant in *L. precursor* sp. nov. and absent in *L. neglectus*. Relatedness was moderately high (0.392 ± 0.070) in nests of *L. precursor* sp. nov., whereas it reached in *L. turcicus* levels consistent with territorial colonies headed mostly by a single queen (0.561 ± 0.034). *L. precursor* sp. nov. shows an intermediate social structure between the supercolonial invasive *L. neglectus* and the highly structured *L. turcicus* populations: in *L. precursor*, several 'small-scale supercolonies' coexist in most populations, but without coming close to the sizes of the extensive *L. neglectus* supercolonies. Long-chain hydrocarbons were relatively frequent in *L. precursor* sp. nov. and rare in *L. turcicus*. The less volatile long-chain hydrocarbons have been hypothesized to be less informative as recognition cues which is consistent with the lower aggression levels in *L. precursor* sp. nov. compared to *L. turcicus*.

Comments. Based on investigation of cuticular hydrocarbon patterns, nuDNA (microsatellite data), Cremer et al. (2008) unambiguously supported the separate species identity of *L. neglectus* from *L. turcicus*. This finding is in line with the results of NC-clustering reported above. Yet, Cremer et al. also reported that *Lasius turcicus* in the conception of Seifert (2000)

can be divided into two entities which they called the highland form (= *L. turcicus* Santschi) and the lowland form (= *L. precursor* sp. nov. introduced here). They found clear differences between the two entities in cuticular hydrocarbons and microsatellite data. The material used here in NC-clustering, altogether 127 samples, is identical for 122 samples with the material evaluated by Cremer et al. Five samples – the type series of *L. turcicus* plus 4 samples from the islands of Kos and Rhodos – were added here. Using the 10 standard characters CS, CL/CW₉₀₀, SL/CS₉₀₀, nGen₉₀₀, nGu₉₀₀, sqPDCL₉₀₀, dCIAn/CS₉₀₀, PoOc/CL₉₀₀, EYE/CS₉₀₀) and MP6/CS₉₀₀, 51 nest samples of *L. precursor* are separated from of 77 nest samples of *L. turcicus* with the following error rates: 4.7% in NC-Ward, 4.7% in part.hclust (plus 4.7% outliers) 0.8% in NC-part.kmeans, and 0.8% in NC-NMDS-kmeans – in the mean of all four analyses 2.8%. This is below the 4% error threshold and justifies describing *L. precursor* sp. nov. as a separate species. Figure 111 shows the data of NC-Ward NC-part.hclust and NC-part.kmeans. If run as wild-cards in a linear discriminant analysis, the type sample of *L. turcicus* and the holotype sample of *L. precursor* sp. nov. are allocated to corresponding clusters with $p=0.999$ and 1.000. The classification error by the LDA was 7.6% in 396 worker individuals which is a normal value for cryptic species.

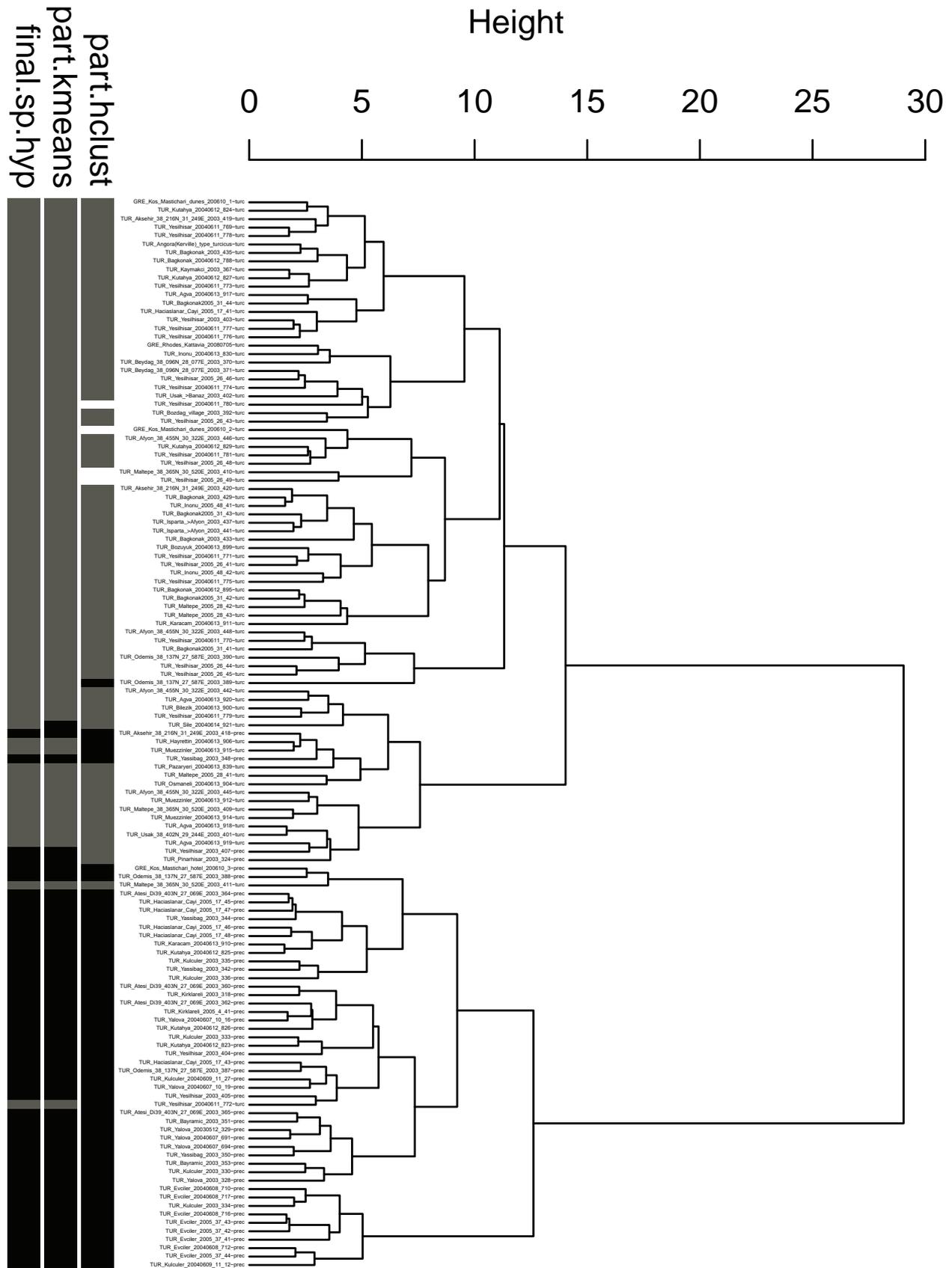
4.4.9 *Lasius turcicus* Santschi 1921

Lasius niger st. *turcica* Santschi 1921 [type investigation]

Type material: Lectotype worker on the same pin with a *Prenolepis* gyne, labelled "Asie min. Angora G.d.Kerville", "Lasius turcicus Sant SANTSCHI det. 1920", "lectotype € desig. by E.O.Wilson", ANTWEB CASENT 0912297; 2 paralectotype workers on another pin labelled "Asie min. Angora G.d.Kerville", "Lasius turcicus Sant type SANTSCHI det.1920", "K. 201"; depository NHM Basel.

All material examined. The full set of 16 standard NUMOBAT characters was available in 77 nest samples with 332 workers from Greece (3 samples) and Turkey (74). This refers largely to the material collected by Cremer et al. (2008). For details see supplementary information S11. In further 43 samples no data of PoOc, EYE, dCIAn, MP6, nGen and nSt were available making a safe separation from *L. neglectus* and *L. precursor* sp. nov. impossible.

Figs. 111: NC-clustering of 51 nest samples of *Lasius precursor* sp. nov. (black bars) and 77 nest samples of *L. turcicus* (grey bars) from the East Aegean and Asia Minor. The hierarchical algorithms, NC-Ward (tree shown) and NC-part.hclust, showed a classification error of 4.7% whereas the non-hierarchical algorithms, NC-part.kmeans and NC-NMDS-k.means (not shown), misclassified only 0.8% of the samples giving an overall mean error of 2.8%. Outliers in NC-part.hclust are indicated by white bars (gaps).



However in a number of these samples, large absolute worker size allowed a sufficiently credible determination and conclusions on geographic distribution east and south of the investigation area of Cremer et al. (2008).

Geographic range. From the Aegean islands Andros (37.83°N, 24.87°E, westernmost site), Kos and Rhodos over Anatolia east to the N Iran (36.8°N, 54.4° E). The southernmost known site is Wadi Barad in Syria (33.58°N, 36.20°E). The altitudinal distribution in West Anatolia ranges from 1 to 1170 m.

Diagnosis (Tab. 2, Figs. 17–18; key; images in www.antWeb.org with specimen identifiers CASENT0906080, CASENT09122972):

Body size larger than in sister species (CS 855 µm). Number of mandibular dents low (MaDe₉₀₀ 7.7). Clypeal pubescence dilute (sqPDCL₉₀₀ 5.34). Pronotal setae rather short (PnHL/CS₉₀₀ 0.127) as long as gular setae (GuHL/CS₉₀₀ 0.127). Petiole scale in profile view rather thin with an acute dorsal tip. Pubescence hairs on frons rather long (PLF 34.7 µm). Dorsum of scape and hind tibiae without or occasional setae. It differs from *L. neglectus* by larger size, more developed gular pilosity (nGu₉₀₀ 3.96 vs. 2.92, GuHL/CS₉₀₀ 0.127 vs. 0.115) and less developed pilosity on posterior margin of head (nOcc₉₀₀ 6.88 vs. 9.77). For the most significant differences to *L. precursor* sp. nov. see there and Tab. 3. Coloration: In medium sized specimens head and gaster dark brown, mesosoma often suggested lighter; mandibles, antennae, lateral part of clypeus, tibiae and tarsae light yellowish-brown. Large specimens often show more yellowish-reddish color components on mesosoma and lateral clypeus.

Biology. See statements under *Lasius precursor* sp. nov.

Comments. Preliminary investigations of Iranian samples show significant character differences to the Anatolian population. Assessment of the taxonomic status of the former needs a special, more extensive study.

4.4.10 *Lasius tapinomoides*

Salata & Borowiec 2018

Lasius tapinomoides Salata & Borowiec 2018
[type investigation]

Type material: Holotype worker labelled "GREECE, Crete, Rethymno Antonios Spilia Gorge 35°15.245 N/24°34.220 E 11 V 2013, 342 m L. Borowiec" and "CASENT0845075"; one paratype worker labelled "GREECE, Crete, Rethymno Orthes Gorge, 318 m 35,3336 N/ 24,6848 E 28 IV 2014, S. Salata"; one paratype worker labelled "GREECE, Crete, Rethymno Kato Malaki 15 V 2013, 235 m, L. Borowiec 35,28333 N /24,4 "; depository DBET Wrocław.

All material examined. Only the 3 type specimens were available.

Geographic range. Endemic species of Crete.

Diagnosis (Tab. 2, Figs.19–20; key; images in www.antWeb.org with specimen identifiers CASENT0845075):

Body size extremely small (CS 631 µm). Scape rather long (SL/CS₉₀₀ 0.994). Number of mandibular dents low (MaDe₉₀₀ 7.1). Pubescence on head sides ventral of the eyes and on clypeus very sparse (sqPDCL₉₀₀ 5.34). Pubescence hairs on frons long (PLF₉₀₀ 36.9 µm). Pronotal setae long (PnHL/CS₉₀₀ 0.154), longer than gular setae (GuHL/CS₉₀₀ 0.126). Dorsum of scape and hind tibiae without or very few fine setae (nSc₉₀₀ 1.1, nHT₉₀₀ 2.5). Posterior margin of head and metapleuron below spiracle with rather many and long setae (nOcc₉₀₀ 10.6, nSt₉₀₀ 6.9). Metanotal groove nearly absent; as result the dorsal profile of mesosoma approaches a linear condition. Petiole scale in profile view rather low and thick. Coloration: head, petiole and gaster dark to blackish brown; mesosoma, coxae and femora suggested lighter; antennae, lateral part of clypeus, tibiae and tarsae light yellowish-brown; mandibles light reddish brown.

Biology. According to Salata & Borowiec (2018) the species inhabits moist, closed canopy forests, which are most often located in stream valleys. Nests were in wet soil, under shallow and small rocks. Colonies seem to be monogynous.

Comments. The separate species status of *L. tapinomoides* against *L. neglectus*, *L. precursor* sp. nov. and *L. turcicus* is indicated by the following arguments: (i) The constantly very small CS over all nests reported by Salata & Borowiec (2018) – such a small size is only achieved by dwarf workers of *L. precursor* sp. nov. and *L. neglectus*. (ii) The metanotal groove in *L. tapinomoides* is very shallow; as result the dorsal profile of mesosoma is more or less linear. Such an extreme mesosoma profile is not found in dwarf workers of *L. precursor* sp. nov. and *L. neglectus* though having, compared to larger conspecific workers, a reduced relative depth of the metanotal groove, lower height of the propodeum and weaker convexity of mesonotal profile due to allometric shape variance. (iii) The longer pronotal setae compared to small workers of the other species. (iv) The more numerous metapleural setae compared to small workers of the other species. (v) Extreme reduction of pubescence density on head sides ventral of the eye. (vi) The habitat selection reported by Salata & Borowiec. The CL/CW and PoOc/CL data in Tab. 2 are not reliable due to deformations of the head capsule in two of the three specimens.

4.4.11 *Lasius israelicus* sp. nov.

Etymology. The name refers to the terra typica.

Type material. Holotype plus 2 paratype workers on one pin labelled "ISRAEL Nahal ,Ammud 32°58.50N

35°28.00E 28.v.1981 F. KAPLAN“; ”18.“; 1 male and 1 alate gyne paratype with the same labelling on another pin; 3 paratype workers labelled ”ISRAEL Hazbani 33°14.50N, 35°40.00E 24.iv.1982 J. KUGLER“; 2 paratype workers labelled ”ISRAEL Elon Nahal Keziv [Wadi Karkara] 33°04.00 N, 35°13.00E 3.iv. 1944 H. BYTINSKI-SALZ“; 3 paratype workers labelled ”ISRAEL Monfort 33.048N, 35.220E 10.iii. 1981 J. KUGLER“; depository SMN Görlitz.

All material examined. A total of 5 nest samples with 13 workers from Israel (4 samples) and Jordan (1) were subject to NUMOBAT investigation. For details see supplementary information SII.

Geographic range. So far only known from a small area of 6000 km² in north Israel and Jordan (West bank) at elevations between 205 and 662 m.

Diagnosis (Tab. 3, Figs. 21–22; key):

Belonging to the *L. turcicus* species complex. Body size rather large (CS 865 µm). Number of mandibular dents low (MaDe₉₀₀ 7.7). Clypeal pubescence dilute (sqPDCL₉₀₀ 5.44). Petiole scale in profile view rather thin with a sharp dorsal crest. Cuticular surface of head and mesosoma shining, with reduced microsculpture. Pubescence hairs on frons very long (PLF 38.4 µm). Not to confuse with other species of the *L. turcicus* species complex because of longer and much more numerous setae on all body parts with exception of scape (e.g., PnHL/CS₉₀₀ 0.147, nHT₉₀₀ 18.0) and much longer scape and terminal segment of maxillary palps (SL/CS₉₀₀ 0.996, MP6/CS₉₀₀ 0.216). Coloration variable: in bicolored specimens head and gaster dark brown; mesosoma, mandibles, antennae, lateral and anterior part of clypeus, tibiae and tarsae light yellowish-reddish; in more concolorous specimens head, mesosoma and gaster medium brown with a yellowish-reddish tinge.

Biology. Unknown.

Comments. No comments.

4.4.12 *Lasius obscuratus* Stitz 1930

Lasius brunneus var. *obscuratus* Stitz 1930 [type investigation]

Type material: Lectotype worker labelled “West-Pamir VII.X. 28 leg.Reinig”, ”Dschaingan 7 x. 1800m“. ”LECTOTYPE designated by E.O.Wilson 1954“, “*Lasius brunneus obscuratus* Stitz lectotype”, “Type”, “GBIF-D/FoCol 2739 specimen and label data documented”; 3 paralectotype workers labelled “West-Pamir VII.X. 28 leg.Reinig”, ”Dschaingan 7 x. 1800 m“ “*Lasius brunneus* Latr. *obscuratus* St.”; depository ZM Berlin.

***Lasius gebaueri* Seifert 1992 syn. nov.**

[type investigation]

Lasius gebaueri Seifert 1992

Type material: Holotype and 5 paratype workers on the same pin labelled ”Qinhai: Xining 101.53 E, 36.34

N 18.7.1990 leg. Gebauer Trocken Canon“; 3 paratype workers on the same pin labelled ”Quinghai Chaka 99.16 E, 36.49 N 13.6.1990 Wermutsteppe“; depository SMN Görlitz.

All material examined. A total of 58 nest samples with 167 workers were subject to NUMOBAT investigation. These originated from Armenia (1 sample), Georgia (13), China (12), Iran (3), Mongolia (21), Russia (3), Tadjikistan (1) and Turkey (4). For details see supplementary information S1.

Geographic range. Huge range in Asia between 27°E to 115°E and 34.5°N to 53.2°N. Known from entire Asia Minor, Great Caucasus, Armenia, N Iran (Elburs Mountains), Tadjikistan, Mongolia and NE Tibet. The altitudinal distribution ranges from 900 to 2600 m in Asia Minor and Great Caucasus, from 1900 to 3160 m in Elburs Mountains and W Pamirs, from 1300 to 3400 m in NE Tibet and Gansu, from 700 to 2100 m in Mongolia, and from 536 to 620 m near Lake Baikal.

Diagnosis (Tab. 3, Figs. 23–24; key; images in www.antWeb.org with specimen identifiers ANTWEB1008435, FOCOL0749, FOCOL2738, FOCOL 2739):

Absolute size rather small (CS 840 µm). Scape and head length indices and number of mandibular dents medium (SL/CS₉₀₀ 0.956, CL/CW₉₀₀ 1.065, MaDe₉₀₀ 8.4). Clypeal pubescence moderately dense (sqPDCL₉₀₀ 4.35). Pronotal setae of medium length (PnHL/CS₉₀₀ 0.140), significantly longer than gular setae (GuHL/CS₉₀₀ 0.091). Dorsum of scape and extensor profile of hind tibia without or only very few semierect setae. It differs from the sister species *L. psammophilus* by longer terminal segment of maxillary palps (MP6/CS₉₀₀ 0.173 vs. 0.145). Coloration: head, mesosoma and gaster dark brown, mandibles, antennae, and legs light yellowish-brown.

Biology. It prefers habitats with xerothermous conditions such as open steppe habitats with diverse phytoassociations, short-grassy pastures and light steppe forest. It was also found in less dry habitats such as cut meadows, floodplain pastures, sunny willow stands or montane stunted- growth forest at the tree line. Nest were found in soil, preferentially under stones.

Comments. The morphology of *L. obscuratus* shows a significant structuring in dependence from geography. 69 specimens from the Baikal region, Mongolia and northeast Tibet (*L. gebaueri* in my conception of 1992) differ from 63 specimens of the remaining western population (*L. obscuratus* in my former conception) by shorter pronotal setae (PnHL/CS₉₀₀ 0.134 vs. 0.152), larger eyes (EYE/CS₉₀₀ 0.248 vs. 0.240) and smaller postocular distance (PoOc/CL₉₀₀ 0.229 vs. 0.239). All these differences are significant for p < 0.0001 if tested in a one-tailed ANOVA. A LDA considering all 16 standard characters classified 97.0% of 132 individuals in agreement with

geography whereas only 90.2% were confirmed by a LOOCV-LDA. Furthermore, a two-step cluster analysis classified 93.2% of the individuals in agreement with geography. These data appear problematic. The final decision to synonymize *L. gebaueri* with *L. obscuratus* is based on the very incongruent results of different forms of NC-clustering: NC-part.kmeans could only recognize a single cluster whereas NC-part.hclust distinguished three clusters with a geographic distribution hardly to believe. NC-Ward presented two clusters but grouped two Mongolian-Tibetan samples together with samples from Asia Minor and three samples from Asia Minor together with Mongolian-Tibetan samples – this means 10.2% disagreement with the geographic hypothesis in 49 evaluated nest samples. NC-NMDS-k.means also showed 10.2% disagreement to expectations from geography.

4.4.13 *Lasius psammophilus* Seifert 1992

Lasius psammophilus Seifert 1992 [type investigation]

Type material: Holotype plus 4 paratype workers labelled “GER: Kr. Weißwasser 4 km N Steinbach: N 135 30.7.1991, leg. Seifert”; 26 paratype workers from the same locality and date labelling but with nest 082, sample numbers N 005, N 023, N 027, N 029, N 048, N N 206, N 215; depository SMN Görlitz.

All material examined. A total of 150 nest samples with 528 workers were subject to NUMOBAT investigation. These originated from Belgium (1 sample), Georgia (1), Czechia (3), Denmark (5), England (3), Finland (2), France (10), Germany (86), Greece (7), Italy (14), Norway (2), Slovenia (1), Spain (1), Sweden (7), Switzerland (4), Turkey (3). For details see supplementary information S1.

Geographic range. European, temperate-submeridional. From British Isles and France across Central and East Europe. Rapid postglacial immigration into North Central Europe via sand dunes and the outwash plains of big ancient river valleys is highly probable. In Central Europe and S Fennoscandia most abundant in sandy regions of the planar and colline zone but penetrating also mountain areas along river valleys: in the S Schwarzwald ascending to 1000 m and in the Alps to 2030 m (in S Tyrol at 46.5°N). Competing with *L. paralienus* in the High Apennine grasslands. Absent from Iberia and probably also the S Balkans, in N Greece at 40°N between 1600 and 1900 m. Main border of northern distribution in Sweden and Finland at 63.5°N but ranging north to 65.8° along the shores of the Gulf of Bothnia. Sympatric occurrence with *Lasius obscuratus* in Asia Minor and Great Caucasus, here easternmost known site at 52.52°N, 44.94°E. Sympatric occurrence with *L. piliferus* occurs in the Pyrenees.

Diagnosis (Tab. 3, Figs. 25–26; key; images in www.antWeb.org with specimen identifiers CASENT0172733, CASENT0179885, FOCOL0752):

Absolute size rather small (CS 826 µm). Scape and head length indices and number of mandibular dents medium (SL/CS₉₀₀ 0.960, CL/CW₉₀₀ 1.057, MaDe₉₀₀ 8.3). Clypeal pubescence rather dilute (sqPDCL₉₀₀ 4.56). Pronotal setae of medium length (PnHL/CS₉₀₀ 0.146), significantly longer than gular setae (GuHL/CS₉₀₀ 0.097). Dorsum of scape and extensor profile of hind tibia without or only few semierect setae. It differs from the eastern sister species *L. obscuratus* by the shorter terminal segment of maxillary palps (MP6/CS₉₀₀ 0.145 vs. 0.173) and from the western sister species *L. piliferus* by longer scape (SL/CS₉₀₀ 0.960 vs. 0.929), larger eye (EYE/CS₉₀₀ 0.238 vs. 0.220) and lower seta numbers. Coloration: head brown, mesosoma a little lighter brown with a yellowish tinge, gaster dark brown; petiole, coxae and femora yellowish brown; mandibles and anterior clypeal border yellowish-reddish, scape yellowish.

Biology. See Seifert (2018).

Comments. There is little morphological variation of *L. psammophilus* throughout its range except for significantly larger values of nSc₉₀₀, nGen₉₀₀, and PnHL/CS₉₀₀ in the population from Olympos and Smolikas mountains in north Greece. The separation of *L. psammophilus* from *L. obscuratus* by NC-clustering was clear in the 120 samples with MP6 data available. Considering the standard characters CL/CW₉₀₀, SL/CS₉₀₀, MP6/CS₉₀₀, PoOc/CL₉₀₀, EYE/CS₉₀₀, nGu₉₀₀, nSc₉₀₀, nHT₉₀₀, and nSt₉₀₀, the disagreement with the final species hypothesis was 1.7% in NC-part.kmeans, 3.3% in NC-Ward, and 1.7% in NC-NMDS-kmeans. NC-part.hclust showed an error of 2.5% and 6.7% of outliers. These data are a clear indication to accept heterospecificity according to the criteria of the GAGE species concept. The classification error of the controlling LDA was 2.7% in 331 worker individuals.

4.4.14 *Lasius piliferus* Seifert 1992

Lasius piliferus Seifert 1992 [type investigation]

Type material: Holotype plus 4 paratype workers labelled “Sierra de Gredos, 1600 m 13.5.91-8, 3 km S Hoyos de Espina”; 10 paratype of 2 other nest samples from the same location with date and sample label “13.5.91-27” and “13.5.91-S”; depository SMN Görlitz.

All material examined. A total of 11 nest samples with 53 workers were subject to NUMOBAT investigation. These originated from France (1 sample) and Spain (10). For details see supplementary information S1.

Geographic range. Iberian species. So far only known

from 8 sites in the Sierra de Gredos, Sierra de Guadarrama and NE Pyrenees at elevations between 1250 and 1950 m.

Diagnosis (Tab. 3, Figs. 27–28; key; image in www.antWeb.org with specimen identifiers FOCOL0753): Absolute size small (CS 812 μm). Head length index and number of mandibular dents medium (CL/CW₉₀₀ 1.061, MaDe₉₀₀ 8.2). Clypeal pubescence rather dilute (sqPDCL₉₀₀ 4.63). Pronotal setae of medium length (PnHL/CS₉₀₀ 0.150), significantly longer than gular setae (GuHL/CS₉₀₀ 0.114). Dorsum of scape without or only single semierect setae. Extensor profile of hind tibia with very few semierect setae (nHT₉₀₀ 3.2). It differs from the parapatric sister species *L. psammophilus* by the shorter scape (SL/CS₉₀₀ 0.929 vs. 0.960), smaller eye (EYE/CS₉₀₀ 0.220 vs. 0.238) and slightly larger seta counts. Coloration: not differing from situation in *L. psammophilus*.

Biology. Main habitats are semidry grasslands (pastures grazed by cattle, horse or sheep or S-facing meadows). However, more mesophilic conditions were not avoided. Nest were found under stones.

Comments. *L. piliferus* and *L. psammophilus* show significant differences in a number of characters. In 243 specimens with the full set of standard characters available, this is most clearly expressed in EYE/CS₉₀₀ (univariate ANOVA $F_{1,241} = 205.9$, $p < 0.0001$), SL/CS₉₀₀ ($F_{1,241} = 61.9$, $p < 0.0001$) and nSt₉₀₀ ($F_{1,241} = 56.7$, $p < 0.0001$). Considering the characters SL/CS₉₀₀, EYE/CS₉₀₀, GuHL/CS₉₀₀, nGen₉₀₀ and nSt₉₀₀, nest sample means of both species are fully separated in a plot of the first two factors of a PCA. Using both all 16 standard characters or the five selected ones, NC-Ward clustering misclassified only 1.2% of 83 samples in disagreement with the final species hypothesis. On the other hand, NC-part.kmeans, NC-part.hclust and NMDS-kmeans could not confirm the existence of two clusters both in the full or reduced character set. Problems are mainly caused by the two Pyrenean samples: one *L. psammophilus* sample from near Seu de Urgell (42.366°N, 1.262°E, 1600 m) and one *L. piliferus* sample from near La Tour de Carol (42.466°N, 1.89°E, 1500m). Considering 10 Spanish and 11 French samples of these species, these two samples are placed in an intermediate position if run as wild cards in an LDA. This may indicate hybridization in the Pyrenean contact zone of both taxa and reminds to the Pyrenean hybrid zone of the grasshoppers *Chorthippus parallelus* (Zetterstedt 1821) and *C. erythropus* Faber 1958. The zoogeographies and postglacial spreading of these grasshoppers (Hewitt 1993) appear analogous to those of *L. psammophilus* and *L. piliferus* respectively. In case of synonymization of both taxa by future authors, the least confusion in literature would arise if priority is given to *L. psammophilus* or if *piliferus* is ranked as subspecies of the former.

4.4.15 *Lasius creticus* sp. nov.

Etymology. The name refers to the island of Crete.

Type material. Holotype plus 5 paratype workers on two pins labelled "GREECE: 24.04—04.05.1992 Kreta, 1 km NW Melambos, 600–700 mH 626 leg. Schulz"; 6 paratype workers on two pins labelled "GR- Kreta 1 km NW Ano Meros 1000 m 658 Platanen an Fluß 90% Leg: Schulz 24.-04.05.92"; depository SMN Görlitz. All material examined. A total of 7 nest samples with 26 workers from Greece (3 samples), Turkey (2) and Iran (1) were subject to NUMOBAT investigation. For details see supplementary information S11.

Geographic range. The islands of Crete and Rhodes, Anatolia east to north Iran (35.83°N, 50.94°E). All seven localities are situated at latitudes of 35 to 41°N and altitudes of 25 to 1900 m.

Biology. One sample was collected from a Platanus stand of 90% canopy cover near a river at 1000 m and another one from an Abies stand of 70% canopy cover at 1900 m.

Diagnosis (Tab. 3, Figs. 29–30; key):

The allocation to the *L. obscuratus* complex is given by rather small absolute size (CS 859 μm), moderate scape and head length indices (CL/CW₉₀₀ 1.083, SL/CS₉₀₀ 0.965), medium number of mandibular dents (MaDe₉₀₀ 8.2), relatively large length of frontal pubescence hairs (PLF₉₀₀ 33.9), dilute clypeal pubescence (sqPDCL₉₀₀ 5.19) and reduced pilosity on dorsal plane of scape and extensor profile of hind tibia (nSc₉₀₀ 0.7, nHT₉₀₀ 2.6). It is outstanding within this complex by long maxillary palps (MP6/CS₉₀₀ 0.196), short postocular index (PoOc/CL₉₀₀ 0.229) and very long setae on hind margin of head and gula (GuHL/CS₉₀₀ 0.125). Coloration: varying from concolorous light reddish-brown to concolorous medium brown with reddish tinge.

Comments. All explorative data analyses clearly clustered *L. creticus* sp. nov. separate from any similar species.

4.4.16 *Lasius brevipalpus* sp. nov.

Etymology. The name refers to the short terminal segment of maxillary palp.

Type material. Holotype plus 5 paratype workers on three pins labelled "KAZ: 47.42.21N, 85.00E 496 m, feucht-salzige Artemisia-Steppe leg. Seifert 2001.07.25 -81", 12 paratype workers on four pins with the same locality label but sample No 73, 73b and 212; depository SMN Görlitz.

All material examined. A total of 5 nest samples with 12 workers from Kazakhstan were subject to NUMOBAT investigation. For details see supplementary information S11.

Geographic range. Only known from the type locality at 47.7058°N, 85.3000°E, 496 m.

Biology. The type locality is a staggered array of very shallow sand dunes with very poor herb layer that change with rather humid *Artemisia* steppe in deeper parts of the area. Four samples were collected from sandy soil in humid parts of the site and one sample from a sand dune.

Diagnosis (Tab. 3, Figs. 31–32; key):

Small-sized (CS 812 µm). Large head and scape length indices are contrasted by a small palp length index (CL/CW₉₀₀ 1.084, SL/CS₉₀₀ 1.004, MP6/CS₉₀₀ 0.153). Torulo-clypeal distance and number of mandibular dents medium (dCIAn₉₀₀ 4.46, MaDe₉₀₀ 8.53). Length of frontal pubescence hairs rather large (PLF₉₀₀ 32.1), clypeal pubescence dilute (sqPDCL₉₀₀ 4.99). Setae numbers on whole body small but pronotal setae long (nOcc₉₀₀ 9.0, nGen₉₀₀ 2.3, nGu₉₀₀ 2.3, nSc₉₀₀ 4.6, nHT₉₀₀ 6.2, PnHL/CS₉₀₀ 0.162). Setae on dorsal plane of scape rather short, most of these protruding close to counting threshold of 20 µm which explains the variance of nSc counts. Coloration: whole body concolorous medium brown to light yellowish-brown; antennae, tibiae and tarsae pale yellowish brown.

Comments. The next relatives of this species are unclear due to its controversial character combination. There is no species in Asia combining long scape, short terminal segment of maxillary palps, long pronotal setae and low gular setae numbers.

4.4.17 *Lasius paralienus* Seifert 1992

Lasius paralienus Seifert 1992 [type investigation]

Type material: Holotype plus 4 paratype workers labelled “Germania: Kr. Bautzen, 2km S Weißenberg: N 066, 11. 7. 1991, leg Seifert; 15 paratype workers with same collecting data but nest sample numbers ”N 005“, ”N 038“, and ”N 221“; 5 paratype workers labelled ”Germania: Kr. Bautzen, 1 km S Niedergurig, 28. 7. 1991, N 086“; 10 Paratype workers with same collecting data but nest sample numbers ”N 223“ and ”N 240“; depository SMN Görlitz.

All material examined. A total of 74 nest samples with 188 workers were subject to NUMOBAT investigation. These originated from Austria (2 samples), Bosnia-Herzegovina (1), Bulgaria (1), Czechia (1), France (1), Germany (45), Greece (1), Italy (18), Slovakia (1), Sweden (2), and Switzerland (2). For details see supplementary information S1. Further 18 samples from Austria (2), Germany (7), Sweden (8), and Switzerland (1) were assessed by simple eye-inspection.

Geographic range. North meridional and temperate zones of Europe. Postglacial invasion of Central Europe and S Scandinavia most probably from a refuge in the

Apennine. In the south ranging from S France (0.7°W) over entire Italy east to Bosnia-Herzegovina and Bulgaria (25°E). The main distribution in Central Europe reaches north to about 52.5°N. North of this line only isolated populations are known in Sweden: Södermanland (59.1°N), Öland (56.7°N) and Gotland (57.4°N). In Germany it ascends to 990 m (at 47.9°N), at the southern slope of the Alps to 1850 m. Sympatric with *L. bombycina* in the Balkans and with *L. casevitzi* in N Italy.

Diagnosis (Tab. 4, Figs. 33–34; key; images in www.antWeb.org with specimen identifiers CASENT0906118, FOCOL0751):

Absolute size rather small (CS 861 µm). Scape, head and maxillary palp length indices medium (SL/CS₉₀₀ 0.986, CL/CW₉₀₀ 1.067, MP6/CS₉₀₀ 0.183). Number of mandibular dents rather small (MaDe₉₀₀ 8.04). Clypeal pubescence dense (sqPDCL₉₀₀ 3.51). Pronotal setae relatively short (PnHL/CS₉₀₀ 0.135) but significantly longer than the few gular setae (GuHL/CS₉₀₀ 0.103, nGu₉₀₀ 2.3). Dorsum of scape and extensor profile of hind tibia without or with only few semierect setae. It differs from *L. bombycina* by longer scape and terminal segment of maxillary palp as well as shorter pronotal setae; from *L. casevitzi* by much shorter terminal segment of maxillary palps, shorter pronotal setae and much fewer setae on genae and hind tibia (nGen₉₀₀ 0.2 vs. 4.2, nHT₉₀₀ 1.8 vs. 8.6). Coloration: Scape, tibiae, tarsae and mandibles light yellowish brown, all remaining body parts dark to medium brown.

Biology. See Seifert (2018).

Comments. *L. paralienus* shows no outstanding characters but its character combination is separable by NC-clustering from the three other species of the *L. paralienus* complex with an error rate of 0%. The population from the Apennine Peninsula has a significantly larger body size and torulo-clypeal distance as well as shorter gular setae than the population from outside this area. It forms a separate cluster in NC-Ward (Fig. 112) but I refrain here from giving it a taxonomic status as the other three EDAs do poorly support it. The status of a sample from Sardinia (exposed as outlier in NC-part.hclust and separately listed in Tab. 4) appears problematic.

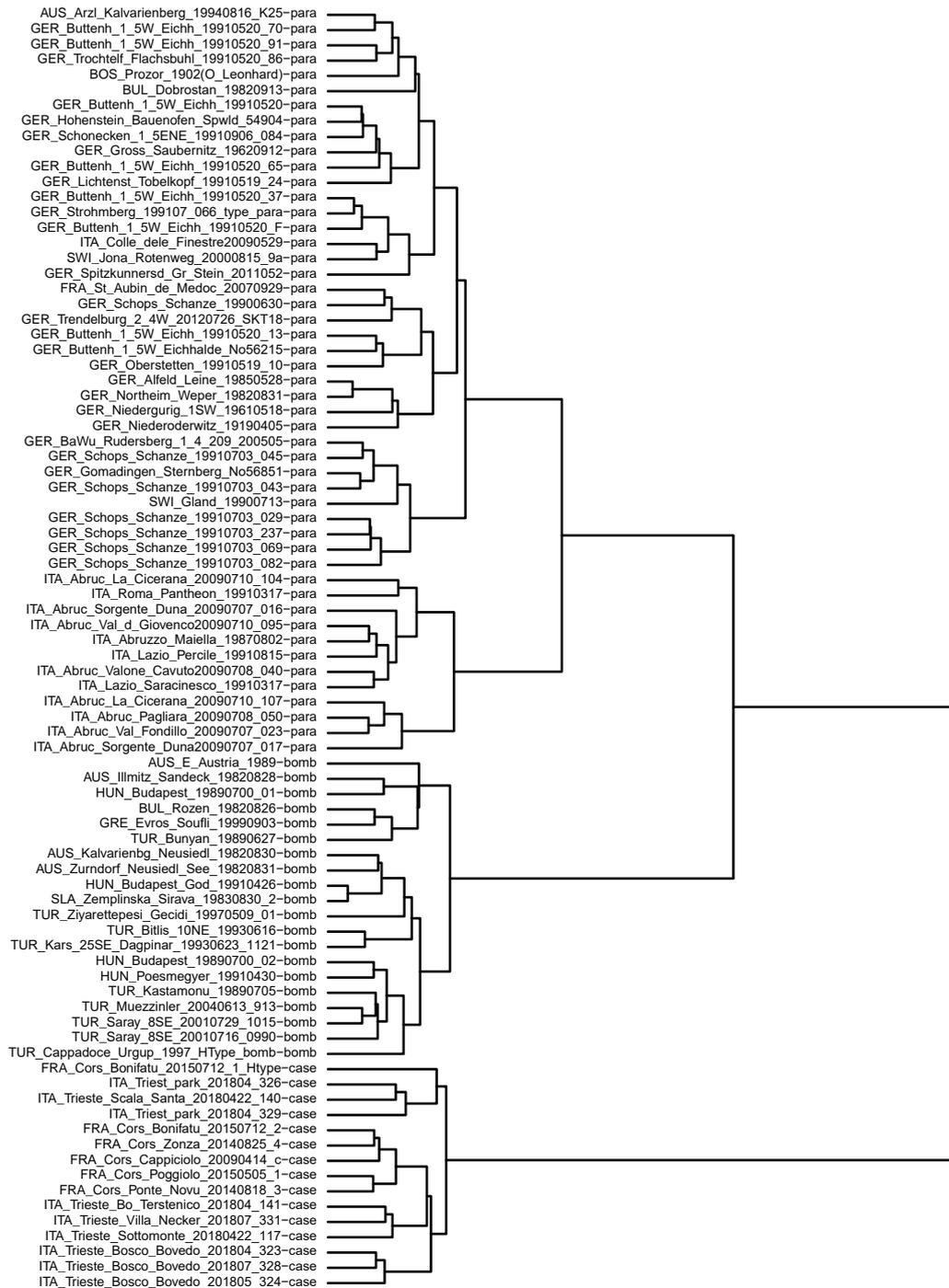
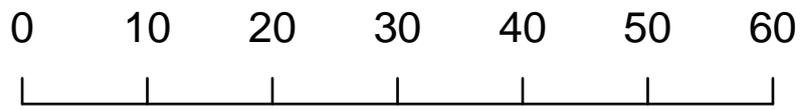
4.4.18 *Lasius bombycina* Seifert & Galkowski 2016

Lasius bombycina Seifert & Galkowski 2016 [type investigation]

Figs. 112: NC-clustering of 49 nest samples of *Lasius paralienus* (light grey bars), 20 nest samples of *L. bombycina* (black bars) and 15 samples of *L. casevitzi* (dark grey bars).

part.hclust
part.kmeans
final.sp.hyp

Height



Type material: Holotype plus four paratype workers labelled "TUR: 38.63°N, 34.91°E, 1060 m, Capadoce: Ürgüp, SSE-facing meadow, S. Aron 1990"; depository SMN Görlitz. Three paratype workers labelled "Türkei_26, Prov. Kayseri, Ziyarettepesi Gecidi (ca. 130 km E. Kayseri) , 1900mH, 09.05.1997, Leg. A.Schulz, K. Vock, M. Sanetra 01"; depository: NHM Wien.

All material examined. A total of 20 nest samples with 53 workers were subject to NUMOBAT investigation. These originated from Austria (4 samples), Bulgaria (1), Greece (1), Hungary (4), Slovakia (1) and Turkey (9). For details see supplementary information S1.

Geographic range. Balkan-Anatolian, meridional to submeridional. The most northwestern point of range is in E Austria (48.0°N, 16.7°E). In the south in entire Balkans and Asia Minor (here east to 44°E). The altitudinal range in Asia Minor is very wide: from sea level to 2350 m (at 40.6°N). Sympatric with *L. paralienus* in the NW Balkans and Bulgaria.

Diagnosis (Tab. 4, Figs. 35–36; key):

Medium-sized (CS 894 µm). Scape and maxillary palp length indices rather short (SL/CS₉₀₀ 0.968, MP6/CS₉₀₀ 0.160). Number of mandibular dents medium (MaDe₉₀₀ 8.20). Clypeal pubescence dense (sqPDCL₉₀₀ 3.42). Pronotal setae very long (PnHL/CS₉₀₀ 0.161). Dorsum of scape and extensor profile of hind tibia without or with only few semierect setae. It differs from *L. paralienus* by shorter scape and terminal segment of maxillary palp as well as longer pronotal setae and from *L. casevitzi* by much shorter terminal segment of maxillary palps (MP6/CS₉₀₀ 0.160 vs. 0.212). Coloration: whole body dark brown with a distinct blackish component. Scape, tarsae and mandibles a little lighter with a yellowish component.

Biology. See Seifert (2018).

Comments. *L. bombycina* is safely separable from the other three species of the *L. paralienus* species complex by different variants of NC-clustering (Fig. 112).

4.4.19 *Lasius casevitzi* Seifert & Galkowski 2016

Lasius casevitzi Seifert & Galkowski 2016
[type investigation]

Type material: Holotype plus three paratype workers labelled "FRA: 42.440°N, 8.868°E, 687 m Corse: Bonifatu, leg. Galkowski 2015.07.12 -1" and deposited in MNHN Paris. Three paratype workers from the holotype nest and four paratype workers from another nest at the holotype locality labeled "FRA: 42.440°N, 8.868°E, 687 m Corse: Bonifatu, leg. Galkowski 2015.07.12 -2" in SMN Görlitz.

All material examined. A total of 15 samples with 36 workers were subject to NUMOBAT investigation. These

originated from Corsica (6 samples) and NE Italy (9). For details see supplementary information S1.

Geographic range. So far only known from the Island of Corsica in altitudes between sea level and 800 m and from several localities in the urban region of Trieste /NE Italy.

Diagnosis (Tab. 4, Figs. 37–38; key; images in www.antWeb.org with specimen identifier CASENT1038019):

Absolute size rather small (CS 845 µm). Scape and maxillary palp length indices high (SL/CS₉₀₀ 0.999, MP6/CS₉₀₀ 0.212). Number of mandibular dents rather medium (MaDe₉₀₀ 8.20). Clypeal pubescence dense (sqPDCL₉₀₀ 3.39). Pronotal setae very long (PnHL/CS₉₀₀ 0.159). Dorsum of scape with single and extensor profile of hind tibia with several semierect to erect setae (nSc₉₀₀ 1.3, nHT₉₀₀ 8.6). *L. casevitzi* is an unmistakable combination of very dense clypeal pubescence, long terminal segment of maxillary palps, rather long scape, and significant setae numbers on genae, extensor profile of hind tibia and metapleuron below propodeal spiracle. Coloration: whole body dark brown but scape, tibiae and tarsae a little lighter with a yellowish component and mandibles lighter with a reddish component.

Biology. Both the data from Corsica and NE Italy indicate that it is no species of open xerothermous grassland and prefers semi-arboreal habitats and dry open forest. Nests are in soil, under trees or under stones. In Corsica it is absent from the coastal environment and from elevations above 1100 m. The altitudinal extremes within 50 records were 23 m and 1100 m, with the majority of nests found between 300 m and 800 m. Within the municipality of Trieste it occurs preferentially in city parks with trees. Alates were not observed in the nests during collecting in July and August. The ants behave aggressively during disturbance of the nest by the collector.

Comments. *L. casevitzi*, *L. bombycina* and *L. paralienus* are perfectly separated by NC-clustering (Fig. 112) for 84 nest samples with data on all 16 standard characters available. Furthermore, the classification error of the LDA is 0% in 192 individuals of the same sample after reducing the number of considered characters to 7 in order to avoid character overfitting.

4.4.20 *Lasius kritikos* sp. nov.

Etymology: Derived from the Greek masculine word Κρήτικός for an inhabitant of Crete.

Type material: Holotype plus 2 paratype workers on the same pin labelled "GREECE: 24.04—04.05.1992 Kreta, Ida Gebirge Nordseite, 1400-1500 mH, Leg. Schulz 640"; 3 paratype workers labelled "GREECE: 24.04—04.05.1992 Kreta, Ida Gebirge Nordseite, 1300 mH, Leg. Schulz 644"; 6 paratype workers on

two pins labelled "GR- Kreta, 3 km SW Omalos, 1400–1600m, Nordwesthang Eichenwald, Leg: Schulz 24.04—04.05.1992, 682"; depository SMN Görlitz.

All material examined. Only the 3 type samples with 12 workers were available for investigation. For details see supplementary information S11.

Geographic range. So far only known from the two type localities in Crete at elevations of 1300 to 1500 m.

Diagnosis (Tab. 4, Figs. 39–40; key):

Absolute size rather small (CS 866 μ m). Scape and maxillary palp length indices high (SL/CS₉₀₀ 1.007, MP6/CS₉₀₀ 0.217). Number of mandibular dents not recordable in the available material but MaDe₉₀₀ predictably > 8. Clypeal pubescence very dense (sqPDCL₉₀₀ 3.36). Pronotal setae long (PnHL/CS₉₀₀ 0.155). Dorsum of scape, extensor profile of hind tibia and metapleuron below propodeal spiracle without or with very few semierect to erect setae (nSc₉₀₀ 0.9, nHT₉₀₀ 2.2, nSt₉₀₀ 1.6). *L. kritikos* shares with *L. casevitzi* the large SL/CS₉₀₀ and MP6/CS₉₀₀ data but can be separated from the latter by the much lower setae numbers. Coloration: medium brown with a yellowish tinge, gaster a little lighter; mandibles antennae, tibiae and tarsae a pale yellowish brown.

Biology. Largely unknown. One sample was collected in a NW-facing *Quercus* forest.

Comments. Both NC-Ward and NC-UPGMA clustering place the three samples of *L. kritikos* sp. nov. as a branch separate from *L. casevitzi* and *L. paralienus* but in close proximity to the latter. NC-part.hclust and NC-part.kmeans do not confirm the separate identity of the *L. kritikos* sp. nov. branch which is a consequence of the low sample size. However, the distinct character combination of *L. kritikos* sp. nov. becomes clear from the data in Tab. 4 which justifies to consider it as a Cretan endemic species.

4.4.21 *Lasius alienus* (Foerster 1850)

Formica aliena Foerster 1850 [type investigation]

Type material: Neotype worker plus 10 workers from the neotype nest labelled "GER: Eifel, 7.9. 1991, 37 km SE Aachen, Schleiden"; depositories SMN Görlitz, BMNH London.

All material examined. A total of 237 nest samples with 706 workers were subject to NUMOBAT investigation. These originated from Andorra (1 sample), Austria (1), Bulgaria (5), China (3), Czechia (9), England (3), France (2), Georgia (2), Germany (133), Greece (9), Iran (5), Kazakhstan (14), Kyrgyzstan (5), Russia (1), Slovakia (7), Spain (6), Sweden (1), Turkey (29), and Ukraine (1). For details see supplementary information S1.

Geographic range. Huge Eurosiberian range, largely temperate to submeridional. From N Iberia and S England

east to Bogda Shan Mountains (43.9°N, 88.2°E). Northern border of distribution in Central Europe at 53.3°N. A finding in S Sweden (near Revinge, 57.7°N) seems isolated. The southern border in the W Palaearctic runs along the southern Turkish border to the Iranian Elburz Mountains (36.7°N, 50.3°E). The dependency of altitudinal distribution (ALT, in meters) latitude (LAT, in degrees) for 103 localities follows the rule $ALT = -93.1 \cdot LAT + 5172$ ($r = 0.701$, $p < 0.001$). The upper limit is 2400 m at 40.6°N in Asia Minor but it may occur at similarly low latitudes close to sea level given the habitat provides sufficient shade. For details see supplementary information S1.

Diagnosis (Tab. 5, Figs. 41–42; key; images in www.antWeb.org with specimen identifiers CASENT0179927, FOCOL0751):

Absolute size small (CS 823 μ m). Scape length index small, head and maxillary palp length indices medium (SL/CS₉₀₀ 0.946, CL/CW₉₀₀ 1.069, MP6/CS₉₀₀ 0.181). Number of mandibular dents medium (MaDe₉₀₀ 8.18). Clypeal pubescence moderately dense, intermediate between the situation in the *L. paralienus* and *L. obscuratus* species complexes (sqPDCL₉₀₀ 4.11). Pronotal setae relatively long (PnHL/CS₉₀₀ 0.152). Setae number on hind margin of head low (nOcc₉₀₀ 4.9). Gular setae absent or very few (nGu₉₀₀ 0.8). Dorsum of scape and extensor profile of hind tibia without or with very few semierect setae (nSc₉₀₀ 0.1, nHT₉₀₀ 0.9). The best separation from all other species with reduced scape and tibial pilosity is the strong setae reduction on metapleuron below propodeal spiracle (nSt₉₀₀ 0.3). Frequent coloration: Head, mesosoma, coxae and gaster medium brown; antenna, tibiae and tarsae light yellowish brown; mandibles light reddish brown.

Biology. See Seifert (2018).

Comments. *L. alienus* shows a weak morphological variation throughout its range stretching over 6600 km from the east to the west and 1900 km from the south to the north. Attempts to cluster geographic populations by NC-clustering showed error rates clearly above 4%. *L. alienus* cannot be allocated to a certain species complex based on morphological data and is safely separated from any similar species by different algorithms of NC-clustering in combination with an LDA.

4.4.22 *Lasius karpinisi* Seifert 1992

Lasius karpinisi Seifert 1992 [type investigation]

Type material: Holotype and 3 paratype workers labelled "GR: Evritania, Mt. Timfristos, 4 km E Karpinisi 11. VI. 1982 loc. 24 leg. R. Danielsson (DAYS)"; depository SMN Görlitz. The type locality is situated at approximately 38.92°N and 21.86°E.

All material examined. Only the type sample was available.

Diagnosis (Tab. 5, Figs. 43–44; key; images in www.antWeb.org with specimen identifiers FOCOL0744): Absolute size rather large (CS 912 μm). Scape length index large (SL/CS₉₀₀ 1.024) but head length index, in contrast, very small (CL/CW₉₀₀ 1.037). Terminal segment of maxillary palps moderately long (MP6/CS₉₀₀ 0.177). Number of mandibular dents medium (MaDe₉₀₀ 8.30). Clypeal pubescence moderately dense, intermediate between the situation in the *L. paralienus* and *L. obscuratus* species complexes (sqPDCL₉₀₀ 4.18). Pronotal setae very short (PnHL/CS₉₀₀ 0.108). Setae number on hind margin of head moderate (nOcc₉₀₀ 8.0). Gular setae few (nGu₉₀₀ 2.6). Dorsum of scape without and extensor profile of hind tibia with few semierect setae (nSc₉₀₀ 0.0, nHT₉₀₀ 4.2). Metapleuron below propodeal spiracle with few setae (nSt₉₀₀ 3.5). Coloration: Head and gaster medium brown with a reddish tinge; mesosoma, coxae and femora reddish brown; scape and tibiae reddish-yellowish, distal half of antennal funiculus darker.

Biology. Unknown.

Comments. As the type sample show no signs for morphological malformation and is unique in the character combination, it appears reasonable to hypothesize *L. karpinisi* as a good species endemic in the Pindos Mountains.

4.4.23 *Lasius schulzi* Seifert 1992

Lasius schulzi Seifert 1992 [type investigation]
Type material: Holotype worker labelled "Turkey: Alanya, 36.32 N 32.04 E 22.4.1988, leg. Schulz", "Machia in Bergland No 2448"; 7 paratype workers labelled "TUR: Gündogmus, 1800 m, 23.4. 1988, leg. A. Schulz, No 2475, 34 km N Alanya"; 3 paratype workers labelled "TR- Alanya, Gehweg in Stadt, leg. Schulz, 12.05.90"; depository SMN Görlitz.

All material examined. A total of 15 nest samples with 32 workers, all from Turkey, were subject to NUMOBAT investigation. For details see supplementary information S11.

Geographic range. Known so far only from 15 sites in Anatolia within an area of 120 000 km² delimited by 36.47°N, 40.40°N, 31.79°E and 34.78°E. Altitudinal distribution is from sea level to 1600 m, with 90% of the sites above 600 m.

Diagnosis (Tab. 5, Figs. 45–46; key; images in www.antWeb.org with specimen identifiers CASENT0903219):

Absolute size rather small (CS 854 μm). Scape and maxillary palp length indices large (SL/CS₉₀₀ 1.010, MP6/CS₉₀₀ 0.202). Postocular distance rather small (PoOc/CL₉₀₀ 0.224). Number of mandibular dents medium (MaDe₉₀₀ 8.26). Pubescence on clypeus and sides of head extremely dilute (sqPDCL₉₀₀ 6.43) – as result and

in combination with weak microsculpture these body surfaces very shining. Pronotal setae long (PnHL/CS₉₀₀ 0.157). Setae on hind margin of head long and numerous, contrasting with setae reduction on scape and tibiae (Occ₉₀₀ 15.0, nSc₉₀₀ 0.2, nHT₉₀₀ 1.5). Gular setae rather long and numerous (GuHL/CS₉₀₀ 0.121, nGu₉₀₀ 4.5). Coloration: Mesosoma, petiole, gaster and appendages bright yellow; head and gaster sometimes a littler darker with a brownish tinge.

Biology. Main habitats are humid, shaded places in forests or shrub but it also occurs in rural and urban habitats. The large eyes suggest substantial epigaeous foraging which is unusual for a *Lasius* with yellow pigmentation.

Comments. *Lasius schulzi* is an unmistakable combination of yellow color, long scape and maxillary palp, extremely dilute pubescence on clypeus and sides of head, long and numerous setae on hind margin of head and absence of setae on scape.

4.4.24 *Lasius uzbeki* Seifert 1992

Lasius uzbeki Seifert 1992 [type investigation]

Type material: Holotype and 7 paratype workers labelled "USSR-Uzbekistan, Chimgan near Tashkent, 6.5. 1978, 2400 m, J. Visa lgt."; depository SMN Görlitz.

All material examined. A total of 16 nest samples with 56 workers were subject to NUMOBAT investigation. These originated from Kazakhstan (5 samples) Kyrgyzstan (10) and Uzbekistan (1). For details see supplementary information S1.

Geographic range. Known so far only from West Tianshan between 70.0°E and 73.4°E, 39.7°N and 42.4°N at elevations of 1400 – 2400 m.

Diagnosis (Tab. 5, Figs. 47–48; key; images in www.antWeb.org with specimen identifiers FOCOL0747):

Absolute size rather small (CS 861 μm). Scape long but terminal segment of maxillary palp rather short (SL/CS₉₀₀ 0.994, MP6/CS₉₀₀ 0.172). Postocular distance very small (PoOc/CL₉₀₀ 0.219). Eye very large (EYE/CS₉₀₀ 0.264), even larger than in species related to *L. emarginatus*. Number of mandibular dents medium (MaDe₉₀₀ 8.14). Pubescence on clypeus dilute (sqPDCL₉₀₀ 5.01) but on postocular head sides and frons much denser than in *L. schulzi*. Setae on dorsum of scape and extensor profile of hind tibia thin and often difficult to distinguish from semierect pubescence which causes high variance in setae counts (see Tab. 5). Pronotal setae long (PnHL/CS₉₀₀ 0.163). Setae on underside of head very long and numerous (GuHL/CS₉₀₀ 0.132, nGu₉₀₀ 6.7). Coloration: polymorphous; the light morph, as represented by the type sample, has a light yellowish mesosoma with a brownish tinge, a pale yellowish-brown head, and a slightly

darker gaster; the dark morph, as represented by the majority of samples, typically shows a dirty brown mesosoma with a yellowish component, a dark brown head, and blackish brown gaster.

Biology. Nests were found under stones in open grassy habitats with bushes or alluvial habitats with trees or bushes.

Comments. The character combination of very large eye, rather short terminal segment of maxillary palp and long gular setae is not found in other Palaearctic species of the genus *Lasius*.

4.4.25 *Lasius niger* (Linnaeus 1758)

Formica nigra Linnaeus 1758 [type investigation]

Type material: Neotype worker plus 2 workers from the neotype nest labelled "S:B1. Johannishus 1 km NE k:a, RN-03F6f03, 10.08.74, P. Douwes DATA ZOOTAX"; depository ZMLU Lund.

All material examined. A total of 131 nest samples with 281 workers were subject to NUMOBAT investigation. These originated from Algeria (1 sample), Bulgaria (1), Czechia (14), Denmark (2), England (3), Finland (1), France (6), Germany (43), Italy (2), Kazakhstan (10), Kyrgyzstan (7), Mongolia (2), Poland (3), Portugal (1), Russia (15), Slovakia (6), Spain (4), Sweden (8), Turkey (1). For details see supplementary information S1.

Geographic range. Eurosiberian. Originally it was probably a species of the northern steppe zone and the transition zone from steppe to temperate forest but following the spread of human culture there was a strong range expansion even into the Mediterranean and S boreal zone. Total range from W Europe (10°W) to S Baikal region (108°E); going north to 63.6°N along the coast of Norway and to 64.5°N along the Gulf of Bothnia. Due to confusion with *Lasius grandis*, distribution in the Mediterranean region very poorly known, here probably rare and mainly above 700 m but occasionally found in humid coastal lowland habitats and even the town of Alger (here introduced?). In Central Europe planar to subalpine, in the Alps (Vorarlberg) up to 1900 m, in the Tian Shan at 42°N ascending to 2250 m. In SW Siberia a typical and abundant element of humid steppe, of river valleys, and cities.

Diagnosis (Tab. 6, Figs. 49–50; key; images in www.AntWeb.org with specimen identifiers CASENT0178773, CASENT0179897, CASENT0179929):

Absolute size rather large (CS 976 µm). Head, scape and maxillary palp length indices, postocular distance and eye size medium (CL/CW₉₀₀ 1.074, SL/CS₉₀₀ 0.979, MP6/CS₉₀₀ 0.180, PoOc/CL₉₀₀ 0.235, EYE/CS₉₀₀ 0.245). Number of mandibular dents medium (MaDe₉₀₀ 8.26). Pubescence on clypeus very dense (sqPDCL₉₀₀ 3.58). All

body parts with numerous standing setae but the length of setae is low (PnHL/CS₉₀₀ 0.123, GuHL/CS₉₀₀ 0.094). Coloration: Head, gaster, petiole, coxae, femora and tibiae dark brown; mesosoma dark brown to medium brown with a slight yellowish tinge; mandibles, scape, trochanter and tibio-femoral joint region yellowish-reddish brown.

Biology. See Seifert (2018).

Comments. *Lasius niger* is an unmistakable combination of very dense clypeal pubescence, numerous setae on all body parts but rather short setae length. It is safely separated from any Palaearctic species by different algorithms of NC-clustering. For separation from *Lasius vostochni* sp. nov. see below.

4.4.26 *Lasius vostochni* sp. nov.

Etymology. Derived from the Russian word восточный, meaning "eastern" and referring to the geographic range that is east of the range of the sister species *Lasius niger*.

Type material. Holotype plus 4 paratype workers on the same pin labelled "RUS: Ussuri: 42.97N, 133.52E, 160 m; Krivaya-Tal, Flussterrasse, Sandboden L. Kanter 1999.09.07-43a; 2 paratype workers labelled "RUS: 51.3528°N, 106.4800°E Gusinoosersk-4W, 604 m Pinus steppe forest under stone I.Antonov 2009.07.11-145"; depository SMN Görlitz.

All material examined. Only the two type samples with 7 workers were investigated. For details see supplementary information SII.

Geographic range. Apparently a species with distribution east of the Johannsen line (De Lattin 1967) with contact to *Lasius niger* in the South Baikal region.

Diagnosis (Tab. 6, Figs. 51–52; key):

Absolute size rather small (CS 826 µm). Scape length index rather small (SL/CS₉₀₀ 0.961), maxillary palp length index comparably large (MP6/CS₉₀₀ 0.192). Eye large (EYE/CS₉₀₀ 0.252). Number of mandibular dents not recordable in the available material but most probably similar to situation in *L. niger*. Clypeal pubescence rather dense (sqPDCL₉₀₀ 3.92). Pronotal setae short (PnHL/CS₉₀₀ 0.128). Setae number on dorsum of scape rather low (nSc₉₀₀ 6.1) but high on extensor profile of hind tibia and metapleuron below propodeal spiracle (nHT₉₀₀ 14.3, nSt₉₀₀ 8.0). Coloration: Head, gaster, petiole, coxae, femora and tibiae dark brown; mesosoma sometimes a little lighter; mandibles, scape, trochanter and tibio-femoral joint region pale yellowish-brown.

Biology. Largely unknown. The sample from the southern Sikhote-Alin range was collected on a sandy river terrace within an area of dense woodland and the South Baikal sample in a *Pinus* steppe forest from under a stone.

Comments. *Lasius vostochni* sp. nov. differs from its sibling species *L. niger* by a combination of more numerous metapleural setae, less numerous scape setae, less dense clypeal pubescence and a slightly longer terminal maxillary palp segment. Considering the full set of 16 standard characters in a PCA and calculating nest sample means of the PCA scores, the two samples of *L. vostochni* sp. nov. are placed separate from 67 samples of *L. niger* using the first three principal components. Reducing to the six characters CS, MP6/CS₉₀₀, dCIAn/CS₉₀₀, sqPDCL₉₀₀, nSc₉₀₀ and nSt₉₀₀, *L. vostochni* sp. nov. is placed separate from *L. niger* by a PCA on individual level as well as on nest sample level by NC-NMDS.kmeans, NC-Ward and NC-UPGMA clustering. However, conclusions based on such few individuals are problematic. A thorough study of the populations in the Russian Far East should be conducted to confirm the species hypothesis presented here.

4.4.27 *Lasius japonicus* Santschi 1941

Lasius emarginatus var. *japonicus* Santschi 1941
[type investigation]

Type material: Lectotype worker plus 4 paralectotype workers labelled "Japan. Tokiawa Hokkaido Teranishi"; "lectotype outer worker desig. by E.O.Wilson"; depository NHM Basel.

All material examined. A total of 32 nest samples with 104 workers were subject to NUMOBAT investigation. These originated from China (8 samples), Japan (19), Korea (1) and Russian Far East (4). For details see supplementary information SII.

Geographic range. NE China, Korea, Russian Far East, Japan. Extreme points of the known range are marked by Beijing (40.00°N, 116.34°E), Nukabira (43.36°N, 143.19°E), Kyushu (32.5°N, 130.9°E) and Khabarovsk (48.49°N, 135.11°E). The upper altitudinal limit seems to be at 1700 m on Mount Paekdusan (41.91°N, 128.10°E) and 2100 m in Honshu at 36°N.

Diagnosis (Tab. 6, Figs. 53–54; key; images in www.antWeb.org with specimen identifiers CASENT0217772, CASENT0280450, CASENT0912291):

Medium-sized (CS 950 µm). Scape and maxillary palp length indices and torulo-clypeal distance large (SL/CS₉₀₀ 1.012, MP6/CS₉₀₀ 0.205, dCIAn/CS₉₀₀ 5.50). Postocular distance and eye size medium (PoOc/CL₉₀₀ 0.240, EYE/CS₉₀₀ 0.244). Number of mandibular dents medium (MaDe₉₀₀ 8.11). Pubescence on clypeus moderately dense (sqPDCL₉₀₀ 4.33). All body parts with rather numerous and rather long standing setae (PnHL/CS₉₀₀ 0.150, GuHL/CS₉₀₀ 0.116). Coloration: polymorphous. The light morph with pale yellowish-reddish brown mesosoma, head and gaster with same tinge but darker; mandibles and anterior clypeal border (sometimes whole

clypeus) yellowish to bright orange. Dark morph with dark to blackish brown head, mesosoma, gaster, coxae, femora and tibiae; tarsae, scape, mandibles and anterior clypeal border paler yellowish brown.

Biology. Very euryptent species, occupying the ecological niche of *Lasius niger*. It inhabits all kinds of natural to anthropogenous, open to semi-shaded habitats, avoids very shady woodland and constructs the nests in most different substrates. According to Yamauchi (1978) the nests do not show conspicuous mounds of mineralic soil material as it is typical for *Lasius niger*. Nuptial flight takes place in early morning (Yamauchi et al. 1986).

Comments. *Lasius japonicus* is separable from all related species by exploratory and hypothesis-driven data analyses with error rates <1%. For separation from the most similar sister species *L. chinensis* sp. nov. see there.

4.4.28 *Lasius chinensis* sp. nov.

Etymology: The name refers to the terra typica China.

Type material: Holotype labelled "CHI: 36.0489°N, 103.8566°E Lanshou, 1522 m Universitätspark Seifert 2011.08.07-87"; 2 paratype workers from the holotype nest sample on another pin, 3 paratype workers from the same sample in ethanol; depository SMN Görlitz.

All material examined. A total of 13 nest samples with 41 workers, all originating from China, were subject to NUMOBAT investigation. For details see supplementary information SII.

Geographic range. Only NE China; from E Qinghai (36.6°N, 101.7°E) east to Shangdon (36.4°N, 117.4°N). The most southern and northern known sites are Chengdu (30.64°N, 104.05°E) and Yong Deng (36.7°N, 103.3°E). The altitudinal distribution ranges from 370 in Shaanxi to 3500 m in E Tibet.

Diagnosis (Tab. 6, Figs. 55–56; key):

Medium-sized (CS 965 µm). Scape and maxillary palp length indices and torulo-clypeal distance large (SL/CS₉₀₀ 1.017, MP6/CS₉₀₀ 0.199, dCIAn/CS₉₀₀ 5.63). Postocular distance and eye size medium (PoOc/CL₉₀₀ 0.237, EYE/CS₉₀₀ 0.240). Number of mandibular dents medium (MaDe₉₀₀ 8.33). Pubescence on clypeus moderately dense (sqPDCL₉₀₀ 4.14). All body parts with very numerous and long standing setae (nOcc₉₀₀ 21.6, nGu₉₀₀ 17.0, nSc₉₀₀ 26.2, PnHL/CS₉₀₀ 0.159, GuHL/CS₉₀₀ 0.121). Coloration: dark to blackish brown; antennal funiculus, tibio-femoral joint regions, tarsae and metatarsae, and anterior clypeal border paler with a yellowish tinge.

Biology. It was found at river banks, in open forest and in parks. It regularly occurs in concrete-sealed city centers provided there are few trees or some greenery. It is obviously a euryptent species with a niche comparable to *Lasius niger*.

Comments. *Lasius chinensis* sp. nov. is a western parapatric sibling species of *L. japonicus*. The contact zone of both species seems to be between 116 and 117° E, from about Beijing south to Shangdong, with syntopic occurrence of both species observed in one locality. The sister-species relation to *L. japonicus* is indicated by highly similar shape characters. The morphological separation from the latter is mainly given by the more profuse pilosity. Running exploratory data analyses with samples in which data of all standard characters were available, 13 nest samples with 41 workers in *L. chinensis* sp. nov. and 21 nest samples with 59 workers in *L. japonicus*, resulted in 0% classification error in NC-NMDS.kmeans clustering but in errors between 2.9 and 8.8% in the other algorithms of NC-clustering. In order to avoid overfitting of the controlling discriminant functions, the number of considered characters was reduced to seven: CL/CW_{900} , EYE/CS_{900} , $sqPDCL_{900}$, nGu_{900} , nSc_{900} , nHT_{900} , and nSt_{900} . With these input data, NC-Ward, NC-part.kmeans, NC-part.hclust and NC-NMDS.kmeans achieved a fully congruent clustering with an error of 0% on the nest sample level when checked by the controlling discriminant function. On the individual level, the LOOCV-LDA misclassified 2% of 100 workers.

4.4.29 *Lasius platythorax* Seifert 1991

Lasius platythorax Seifert 1991 [type investigation]

Type material: Holotype worker labelled "Oberlausitz, 1 km N Biesig bei Reichenbach 16.4.1988, leg. Seifert"; 5 paratype workers from the holotype nest on two separate pins labelled "1 km N Biesig Kr. Reichenbach, 1988, 16.4."; SMN Görlitz.

All material examined. A total of 109 nest samples with 222 workers were subject to NUMOBAT investigation. These originated from Bulgaria (2 samples), Croatia (1), Czechia (6), England (4), France (5), Germany (53), Greece (2), Ireland (1), Italy (6), Poland (1), Romania (3), Russia (17), Slovakia (1), Sweden (6), Turkey (1). For details see supplementary information S1.

Geographic range. Eurosiberian, largely temperate-subboreal. From Ireland and Scotland across continental Europe and Asia Minor to Central Siberia (east to 105°E). In the Mediterranean (Apennine, Corsica) usually in the montane zone but at 40.8°N even in lowland floodplain forest. In Norway reaching 64.7°N and in Sweden and Finland 66.3°N. In Central Europe from the planar to montane zone, ascending in Vorarlberg to 1500 m.

Diagnosis (Tab. 6, Figs. 57–58; key; images in www.AntWeb.org with specimen identifiers CASENT0172747, CASENT0172767, CASENT0179929, CASENT0179887, CASENT0179925, CASENT0913673, CASENT0915593):

Absolute size rather large (CS 970 μ m). Head length index low (CL/CW_{900} 1.051), scape moderately long (SL/CS_{900} 0.981), postocular distance rather large ($PoOc/CL_{900}$ 0.248); eye size medium (EYE/CS_{900} 0.236); terminal segment of maxillary palp rather short ($MP6/CS_{900}$ 0.176). Number of mandibular dents medium ($MaDe_{900}$ 8.18). Pubescence on clypeus very sparse ($sqPDCL_{900}$ 5.02). All body parts with long and numerous standing setae ($PnHL/CS_{900}$ 0.162, $GuHL/CS_{900}$ 0.135, nGu_{900} 11.6, nSc_{900} 20.0, nHT_{900} 20.1). Coloration: whole body homogeneously dark brown; scape, metatarsae and tarsi lighter with a yellowish tinge.

Biology. It is mainly a species of woodland habitats but may occur, in particular in regions with cool summer climate, also in open habitats. For details of its biology see Seifert (2018).

Comments. Being an unmistakable combination of low pubescence density, rather long frontal pubescence, long and profuse pilosity, broad head, rather short maxillary palps and moderately long scape, *Lasius platythorax* is separable by any variant of NC-clustering from the related species *L. niger*, *L. vostochni* sp. nov., *L. chinensis* sp. nov. and *L. japonicus* with an error of 0%. For separation from the endemic sister species *Lasius cyperus* sp. nov., see there.

4.4.30 *Lasius emarginatus* x *platythorax*

Lasius niger var. *nigro-emarginatus* Forel 1874

[type investigation]

Type material: 6 syntype workers labeled "Typus", "L. nigro-emarginatus W Mendrisio", "Coll. Forel.", among these one pin with 3 workers additionally labeled with "ANTWEB CASENT 0911046"; depository MNH Genève. NUMOBAT data were recorded in four workers.

Comments. Seifert (2019b) showed that the type series represent F_1 hybrids of *L. emarginatus* X *platythorax*. According to article 23.8 of ICZN, a species-group name established for an "animal" later found to be a hybrid must not be used as the valid name for either of the parental species, even if it is older than all other available names for them. Furthermore, article 1.3.3 excludes a name from the provisions of the code if proposed for "hybrid specimens as such".

4.4.31 *Lasius cyperus* sp. nov.

Etymology. The name refers to the terra typica Cyprus.

Type material. Holotype and two paratype workers on the same pin labelled "CYPERN – 11 Prov. Limassol, Platres 1200 mH Leg. Sanetra, 28.03.94"; 9 paratype

workers on three other pins from the holotype nest with the same labelling; depository SMN Görlitz.

Geographic range. Only the type sample from Cyprus is known.

Diagnosis (Tab. 6, Figs. 59–60; key):

Medium-sized (CS 894 μm). Head length index low (CL/CW₉₀₀ 1.058), scape short (SL/CS₉₀₀ 0.954), postocular distance rather small (PoOc/CL₉₀₀ 0.234); eye size rather small (EYE/CS₉₀₀ 0.229); terminal segment of maxillary of medium length (MP6/CS₉₀₀ 0.188). Number of mandibular dents medium (MaDe₉₀₀ 8.24). Pubescence on clypeus and on petiole scale extremely sparse (sqPDCL₉₀₀ 5.90). All body parts with very long and numerous standing setae (PnHL/CS₉₀₀ 0.172, GuHL/CS₉₀₀ 0.138, nGu₉₀₀ 17.3, nHT₉₀₀ 27.5), those on hind margin of vertex extremely long, those on scape shorter and less numerous. Coloration: head, mesosoma, and gaster brown with a yellowish component. Scape and tibiae (in particular fore tibiae) yellowish.

Biology. Unknown.

Comments. *Lasius cyperus* sp. nov. is a sister species of *L. platythorax* and probably endemic to Cyprus. It differs from *platythorax* by the smaller postocular distance, the shorter and fewer scape setae, the yellowish component of body color, the extremely long setae on posterior margin of vertex, and the much less pubescent petiole scale. Considering 15 standard NUMOBAT characters (nGen excluded because of incomplete data), a principal component analysis places five workers of the type sample of *L. cyperus* clearly separate from 111 *L. platythorax* workers. This result is repeated on the nest sample level by NMDS clustering.

4.4.32 *Lasius flavescens* Forel 1904

Lasius niger r. *flavescens* Forel 1904 [type investigation]
Type material: Two type workers labelled "Sardym, r. Gunt, Shugnan, v. Byx. Kaznak. 16VIII97" (printed label in Cyrillic), "L. niger flavescens For type Buchara", "ANTWEB CASENT 0911048"; depository: MHN Genève.

All material examined. A total of 17 samples with 45 workers were subject to NUMOBAT investigation. These originated from Afghanistan (2 samples), Kyrgyzstan (10) and Uzbekistan (4). For details see supplementary information S11.

Geographic range. Known so far only from an area of 200 000 km² covering NE Afghanistan (37°N, 71°E) and the western parts of the Tian Shan mountains north and south of the Ferghana Valley with the westernmost and easternmost points at 39°N, 67°E and 41.6°N, 75.0°E. The altitudinal records vary between 2040 and 3600 m.

Diagnosis (Tab. 5, Figs. 61–62; key; images in www.AntWeb.org with specimen identifiers CASENT0911048):

Absolute size rather small (CS 844 μm). Head length

index rather low (CL/CW₉₀₀ 1.068); scape short (SL/CS₉₀₀ 0.932); postocular distance medium (PoOc/CL₉₀₀ 0.238); torulo-clypeal distance low (dCIAn₉₀₀ 3.50); eye size medium (EYE/CS₉₀₀ 0.242); terminal segment of maxillary palp very short (MP6/CS₉₀₀ 0.161). Number of mandibular dents medium (MaDe₉₀₀ 8.23). Pubescence on clypeus very sparse (sqPDCL₉₀₀ 5.18); frontal pubescence long (PLF₉₀₀ 36.4). All body parts with very numerous standing setae of medium length (PnHL/CS₉₀₀ 0.139, GuHL/CS₉₀₀ 0.115, nGu₉₀₀ 14.1, nSc₉₀₀ 23.9, nHT₉₀₀ 27.9). Coloration: polymorphous but in overall impression always with a strong yellow component. The lighter specimens have the whole body more or less concolorous clear yellow to light yellowish brown. The darker specimens are more bicolored with head and gaster brown with a yellow component and have a lighter yellowish brown mesosoma.

Biology. Tarbinsky (1976), who apparently identified the species correctly, reported *L. flavescens* to be abundant in Kyrgyzstan, to occur there at elevations of 1600–3200 m in Ferula-Prangos steppes, high-grassy meadows in the fir forest zone and in meadows of the subalpine zone. The nests are populous and frequently found under stones. Tarbinsky called the species a "typical geobiont" but accessory epigaeous activity is indicated by eye size which is clearly larger than in subterranean species such as *L. austriacus* or much larger than in the subterranean subgenera *Chthonolasius*, *Cautolasius* or *Austrolasius*.

Comments. *L. flavescens* cannot be allocated to a certain species complex. It stands alone as an unmistakable combination of a very hirsute body and appendages, very sparse clypeal pubescence, small torulo-clypeal distance, short terminal segment of maxillary palps, short scape and a strong yellow component in mesosomal color. There is much variation in the material suggesting that more than one species could be involved. Bright yellowish specimens with a longer scape, smaller torulo-clypeal distance and more dilute frontal and genal pubescence were observed in more southwestern parts of the range whereas darker specimens with smaller SL/CS₉₀₀, larger dCIAn₉₀₀ and slightly denser pubescence show a more northwestern distribution. However, samples for which most standard characters have been recorded are too few, only four in the lighter and ten in the darker morph, to reliably run exploratory data analyses and a subjective inspection does also not speak a clear language. The problem has to be re-considered by future investigators after more samples are available.

4.4.33 *Lasius flavoniger* Seifert 1992

Lasius flavoniger Seifert 1992 [type investigation]
Type material: Lectotype (2nd specimen, by present designation) and two paralectotype workers on the

same pin labelled "TURKEY: S.Coastlands.Sogukolok. C. Kosswig. B.M.1948-400."; depository: SMN Görlitz.

All material examined. A total of 2 samples with 6 workers from Turkey were subject to NUMOBAT investigation.

Geographic range. Known so far from only two sites in SE Turkey: Sogukoluk (37.52°N, 27.92°E, 500 m) and from 5 km S of Altinözü (36.08°N, 36.25°E, 350 m).

Diagnosis (Tab. 5, Figs. 63–64; key; images in www.AntWeb.org with specimen identifiers CASENT0903218 and FOCOL0748):

Absolute size rather small (CS 872 µm). Head length rather large (CL/CW₉₀₀ 1.082); scape long (SL/CS₉₀₀ 1.002); postocular distance rather small (PoOc/CL₉₀₀ 0.228); torulo-clypeal distance medium rather large (dClAn₉₀₀ 4.71); eye size small (EYE/CS₉₀₀ 0.229); terminal segment of maxillary palp moderately long (MP6/CS₉₀₀ 0.196). Number of mandibular dents medium (MaDe₉₀₀ 8.00). Pubescence on clypeus very sparse (sqPDCL₉₀₀ 5.52); frontal pubescence, in contrast, rather dense and long (PLF₉₀₀ 35.2). All surfaces of head and mesosoma with numerous standing setae of medium to large length (PnHL/CS₉₀₀ 0.160, GuHL/CS₉₀₀ 0.128, nGu₉₀₀ 10.5, nOcc₉₀₀ 19.1, nGen₉₀₀ 10.2, nSt₉₀₀ 6.6). Dorsum of scape with a number of subdecumbent to suberect setae (nSc₉₀₀ 10.4), flexor profile of hind tibia with more numerous erect to suberect setae (nHT₉₀₀ 24.7). Coloration: Head and gaster yellowish brown, remaining body parts yellowish.

Biology. The sample from near Altinözü was collected from an orchard meadow 10 June 1993 with alates in the nest.

Comments. *L. flavoniger* is well separable from *L. flavescens* by a much longer and more flattened scape, a longer terminal segment of maxillary palp, and a larger torulo-clypeal distance. The main differences to *L. schulzi* are the much more numerous setae on scape, tibiae and genae and the rougher pubescence.

4.4.34 *Lasius grandis* Forel 1909

Lasius niger var. *grandis* Forel 1909 [type investigation] Type material: Lectotype (des. E.O. Wilson) plus 4 paralectotype workers on two pins labelled "L. niger v. grandis Forel type Ronda, Andalousie (C.Voigt)", "ANTWEB CASENT 0911047"; depository: MHN Genève.

All material examined. A total of 74 samples with 198 workers were subject to NUMOBAT investigation. These originated from Andorra (2 samples), France (34), Sardinia/Italy (2), Portugal (3) and Spain (33). For details see supplementary information SII.

Geographic range. Iberia, southernmost France (in Rhone valley north to 44°N), Corsica, Sardinia, introduced to Tenerife. Altitudinal records range from sea

level up to 2300 m in the Sierra Nevada at 37°N.

Diagnosis (Tab. 7, Figs. 65–66; key; images in www.AntWeb.org with specimen identifiers CASENT 0906079, CASENT 0911047):

Absolute size rather large (CS 984 µm). Head and scape length indices large (CL/CW₉₀₀ 1.095, SL/CS₉₀₀ 1.037); postocular distance low (PoOc/CL₉₀₀ 0.222); torulo-clypeal distance large (dClAn₉₀₀ 5.01); eye size medium (EYE/CS₉₀₀ 0.239); terminal segment of maxillary palp long (MP6/CS₉₀₀ 0.208). Number of mandibular dents large (MaDe₉₀₀ 8.62). Pubescence on clypeus moderately dense (sqPDCL₉₀₀ 4.53); frontal pubescence short (PLF₉₀₀ 27.2). All body parts with rather numerous standing setae of medium length (PnHL/CS₉₀₀ 0.145, GuHL/CS₉₀₀ 0.125, nGu₉₀₀ 9.8, nSc₉₀₀ 17.5, nHT₉₀₀ 19.4). Cuticular surface of dorsal head and mesosoma within the meshes of the microreticulum smooth and shining. There are two color morphs. The dark morph is rather homogeneously dark brown with the exception of pale yellowish-brown mandibles, scapes and tibiae. The light morph shows a distinct reddish color component with clypeus, mandibles, mesosoma, petiole and appendages light reddish-brown whereas vertex and gaster are darker reddish-brown. The light morph constitutes 90% of the samples from Corsica and Sardinia and the dark morph 95% of the samples from Iberia and southern France.

Biology. It is the most abundant species of the subgenus in Iberia and inhabits open habitats as well as deciduous and coniferous woodland habitats. It prefers medium to humid moisture conditions and occurs at lower altitudes typically in sheltered conditions (gorges or valleys with running waters). At sites with more precipitations, at altitudes above 2000 m or along the Atlantic coast of Iberia, it occurs in open grassland. Nests are under stones or in soil. Mound construction with mineral soil material, as it is typical for *Lasius niger*, is occasionally observed. *Lasius grandis* behaves as aggressively as *L. niger* after disturbance of the nest. Alates were observed between end of June and end of July.

Comments. *Lasius grandis* and *L. emarginatus* can be separated with an error rate of 0% by any variant of NC-clustering and the classification error on the worker individual level by an LDA is only 0.9%. This clear situation offers good conditions for identification of hybrid nests in the vectorial space (Bagherian et al. 2012; Kulmuni et al. 2010; Seifert 1999, 2006, 2019a, 2019b; Seifert et al. 2010). Occasional hybridization between Iberian *L. grandis* and *L. emarginatus* does in fact occur in the contact zone in southern France. A nest sample of five workers from Mount La Rhune (43.3079°N, 1.6318°W, 855 m) is placed exactly intermediate between the clusters of the parental species when run as wild-card in an LDA considering all 16 standard NUMOBAT

characters. The posterior probabilities of this sample are $p=0.404$ for *L. emarginatus* and $p=0.596$ for *L. grandis* whereas the most uncertain samples of *L. emarginatus* and *L. grandis* have posterior probabilities of 0.981 and 0.996 respectively. Morphological data exclude the involvement of *L. niger* and *L. platythorax* in this case and make involvement of *L. cinereus* most unlikely.

The Corsican population of *Lasius grandis* with lighter reddish specimens has been suspected of possibly representing an endemic island species but any attempt to show this by exploratory data analyses failed. Corsican and Iberian populations are not separable by structural characters, both subjectively and by the standard NUMOBAT characters. Furthermore, adding to the NUMOBAT data standardized pigmentation measurements performed in the RGB (Red-Green-Blue) channels did also not provide clusters interpretable as different species. The Corsican and Iberian populations differed significantly in the color-balanced (calibrated) R-values of dorsal pronotum (ANOVA $F_{1,140} = 7.277$, $p < 0.008$) and the geometric mean of the six absolute RGB-values of head and pronotum (ANOVA $F_{1,140} = 7.612$, $p < 0.007$) but the overlap of data is very large.

4.4.35 *Lasius mauretanicus* sp. nov.

Etymology. The name refers to "Mauritania", the Latin name for a region in the ancient Maghreb in which the new species is found.

Type material. Holotype and 5 paratype workers on two pins labelled " SPA:28.795°N, 17.803°W La Palma: Los Sauces -5 km W, Los Tilos, 830 m leg. Seifert 1995.07.15"; depository SMN Görlitz.

All material examined. A total of 19 samples with 60 workers were subject to NUMOBAT investigation. These originated from Morocco (8 samples) and the Canaric Islands (10). For details see supplementary information SII.

Geographic range. Morocco and the Canaric Islands, occurring here from sea level up to 2800 m.

Diagnosis (Tab. 7, Figs. 67–68; key):

A sister species of *L. grandis*. Absolute size medium to large (CS 943 μm). Head and scape length indices large (CL/CW₉₀₀ 1.086, SL/CS₉₀₀ 1.035); postocular distance low (PoOc/CL₉₀₀ 0.222); torulo-clypeal distance very large (dCIAn₉₀₀ 5.41); eye size medium (EYE/CS₉₀₀ 0.242); terminal segment of maxillary palp very long (MP6/CS₉₀₀ 0.224). Number of mandibular dents large (MaDe₉₀₀ 8.55). Pubescence on clypeus dense (sqPDCL₉₀₀ 3.92); frontal pubescence short (PLF₉₀₀ 27.5). All body parts with very numerous and rather long standing setae (PnHL/CS₉₀₀ 0.151, GuHL/CS₉₀₀ 0.123, nGu₉₀₀ 16.3, nSc₉₀₀ 21.4, nHT₉₀₀ 22.5). Coloration: rather homogeneously dark brown with the exception of the pale yellowish-brown mandibles, scapes and tibiae.

Biology. At altitudes from sea level to 1600 m it prefers

moist and sheltered places such as *Quercus*, *Salix*, *Castanea* and *Eucalyptus* forests, *Erica* heather forest, Laurel forest or *Pinus* stands. At elevations above 1900 m it occurs in open pastures or grassland with spiny xerophytes or shrubs. In cities it occurs in shady gardens with trees. *Lasius mauretanicus* behaves aggressively during disturbance of the nest. Alates were observed in the town of Agadir / Morocco in mid May.

Comments. *Lasius mauretanicus* sp. nov. differs from its sister species *L. grandis* by the longer terminal segment of maxillary palps, larger torulo-clypeal distance, higher clypeal pubescence density and more numerous genal and gular setae. The mean classification error of NC-Ward, NC-part.hclust and NC-part.kmeans is 1.5% in 65 nest samples when all 16 standard NUMOBAT characters were recorded. The classification error by an LDA is 0.6% in 176 worker individuals.

4.4.36 *Lasius cinereus* Seifert 1992

Lasius cinereus Seifert 1992 [type investigation]

Type material: Holotype plus 2 paratypes on the same pin labelled "45 km N Castellon 7.5.91,-116, 430 m 5 WSW Alcala de Chivert"; depository: SMN Görlitz.

All material examined. A total of 20 nest samples with 58 workers were subject to NUMOBAT investigation. These originated from France (3) and Spain (17). For details see supplementary information SII.

Geographic range. Iberia and southernmost France with the northern border running here approximately over points near Montpellier (43.63°N, 3.87°E), near Avignon (43.97°N, 4.60°E) and near Cannes (43.51°N, 6.91°E). Altitudinal records range from 70–200 m in southern France and 430–1950 m in Spain.

Diagnosis (Tab. 7, Figs. 69–70; key; images in www. AntWeb.org with specimen identifiers FOCOL0743):

A species related to *L. grandis*. Absolute size rather small (CS 860 μm). Head and scape length indices large (CL/CW₉₀₀ 1.091, SL/CS₉₀₀ 1.012); postocular distance low (PoOc/CL₉₀₀ 0.219); torulo-clypeal distance large (dCIAn₉₀₀ 5.01); eye size rather small (EYE/CS₉₀₀ 0.233); terminal segment of maxillary palp moderately long (MP6/CS₉₀₀ 0.197). Number of mandibular dents large (MaDe₉₀₀ 8.69). Pubescence on clypeus rather dense (sqPDCL₉₀₀ 4.37); frontal pubescence very short (PLF₉₀₀ 23.5). All body parts with rather numerous standing setae of medium length (PnHL/CS₉₀₀ 0.146, GuHL/CS₉₀₀ 0.116, nGu₉₀₀ 13.2, nSc₉₀₀ 22.6, nHT₉₀₀ 20.1). In difference to *L. grandis*, cuticular surface of dorsal head and mesosoma completely matt; this is caused by fine punctures ("ultrastructures") within the meshes of the microreticulum or in interspaces of microrugae. Coloration: head and gaster blackish brown; mesosoma

dark to medium brown with a yellowish-reddish tinge but even in the lightest specimens darker than in the light color morph of *L. emarginatus*. Mandibles, anterior clypeal margin and scape orange brown.

Biology. The majority of the sites are on limestone ground with habitats including xerothermous grassland, bare rocky ground with spiny shrubs, a sunny *Juniperus-Artemisia* phytoassociation, open broad-leaved forest or sunny *Pinus* forests. *L. cinereus* is distinctly more xerothermous than *L. grandis* and there seems to exist mutual spatial exclusion. Nest were under stones, in dead wood laying on ground, and in soil. The workers behave aggressively during disturbance of the nest.

Comments. Apart from the frequently diagnostic ultrastructure of cuticular surface, 46 nest samples of *Lasius cinereus* and *L. grandis* with the full set of standard NUMOBAT data available were separated by any of the four variants of NC-clustering with an error rate of 0%. The classification error by an LDA was 0.7% in 134 worker individuals of both species.

4.4.37 *Lasius balearicus*

Talavera & al. 2014

Lasius balearicus Talavera, Espadaler & Vila 2014
[type investigation]

Type material: 3 paratype workers from the holotype nest labelled "Col des Prat, Escorca, Mallorca Spain 39°48'29.86"N 2°51'4.52"E 1194 m 13.x.2008 code 08R384 R. Vila & G. Talavera leg."; depository: SMN Görlitz.

All material examined. Only the type sample was available.

Geographic range. Island endemic. Only known from the top summits of the island of Mallorca at elevations between 800 and 1400 m.

Diagnosis (Tab. 7, Figs. 71–72; key):

A species related to *L. cinereus* and *L. grandis*. Absolute size small (CS 850 µm; according to Talavera et al. (2014) ranging from 0.69–0.93 mm). Head and scape length indices large (CL/CW₉₀₀ 1.094, SL/CS₉₀₀ 1.011); postocular distance and torulo-clypeal distance higher than in Iberian sister species (PoOc/CL₉₀₀ 0.234, dClAn₉₀₀ 5.43); eye size rather small (EYE/CS₉₀₀ 0.236); terminal segment of maxillary palp rather short (MP6/CS₉₀₀ 0.186). Number of mandibular dents large (MaDe₉₀₀ 8.60). Pubescence on clypeus more dilute than in sister species (sqPDCL₉₀₀ 5.00); frontal pubescence very short (PLF₉₀₀ 23.0). All body parts with very numerous standing setae of medium length, number of genal setae in particular much larger than in Iberian sister species (PnHL/CS₉₀₀ 0.135, GuHL/CS₉₀₀ 0.133, nGen₉₀₀ 14.5, nGu₉₀₀ 17.8, nSc₉₀₀ 22.6, nHT₉₀₀ 20.1). As difference to *L. cinereus*,

the surface within the meshes of the microreticulum on lateral pronotum is perfectly smooth and shining. In contrast, and resembling the situation in *L. cinereus*, fine punctures (ultrastructures) within these meshes are present on dorsum of pronotum – as result the surface appears completely matt. Meshes of microreticulum on dorsum of head without or with only occasionally these ultrastructures. Coloration: the entire body is yellowish brown, with head and gaster slightly darker and antennae and tarsae slightly paler.

Biology. According to Talavera et al. (2014), it is typically found on limestone ground with a lot of bare rock and sparse and shrubby vegetation, frequently associated with endemic plants *Hypericum balearicum* and *Genista valdes-bermejoi*. Nests were under stones. The ants tended aphids. Restriction of the distribution to the top summits of Mallorca induces a risk of extinction by global warming.

Comments. According to mtDNA data it is supposed to have diverged from its sister species *L. grandis* and *L. cinereus* about 1.5 Ma b.p. (Talavera et al. 2014). The identification of *L. balearicus* should be clear by a combination of small size, very high setae numbers on basically all body parts, the shape characters reported above and the peculiar distribution.

4.4.38 *Lasius persicus* sp. nov.

Etymology: The name refers to the terra typica where the species has been found.

Type material: Holotype and 2 paratype workers on two pins labelled "IRAN:36.5006°N,51.9346°E Nur, Abpari forest, 318m, forest floor, in rotten log O.Paknia 2008.06.24 -2673"; 3paratype workers on one pin labelled "IRAN:36.5020°N,51.9322°E Nur, Abpari forest, 315m, forest floor, in rotten log Paknia 2008.06.23 -2795"; 3paratype workers on one pin labelled "IRAN:36.50067°N,51.9345°E Nur, Abpari forest, 318m, forest floor, in rotten log Paknia 2008.06.22 -2993"; depository SMNG Görlitz.

All material examined. A total of 11 nest samples with 25 workers were subject to NUMOBAT investigation. For details see supplementary information SII.

Geographic range. Only known from the small band of humid Caspian forest in the northern Iran between 37.7°N, 48.8°E and 36.1°N, 53.2°E at elevations between minus 26 and 1170 m.

Biology. The species is obviously closely connected to humid broad-leaved forest. The majority of nests were found in rotten logs and more rarely in soil.

Diagnosis (Tab. 7, Figs. 73–74; key; image in www.antWeb.org with specimen identifier CFH000014):

Shows similarities to both *Lasius grandis* and *L.*

emarginatus. Medium-sized (CS 908 μm). Head length index medium and scape length rather large (CL/CW₉₀₀ 1.064, SL/CS₉₀₀ 1.030). Outlines of head in dorsal view more rounded than in *emarginatus*, postocular distance significantly larger (PoOc/CL₉₀₀ 0.239), eye smaller (EYE/CS₉₀₀ 0.238). Toruloclypeal distance large (dClAn₉₀₀ 5.33). Terminal segment of maxillary palp of medium length (MP6/CS₉₀₀ 0.192). Number of mandibular dents above-average (MaDe₉₀₀ 8.70). Pubescence on clypeus very dilute (sqPDCL₉₀₀ 5.11) and on whole body smooth; frontal pubescence appressed and of medium length (PLF₉₀₀ 26.7 μm). Whole body and appendages with numerous long setae which are longer than in most of the related species (nOcc₉₀₀ 13.7, nGen₉₀₀ 9.8, nGu₉₀₀ 11.7, nSc₉₀₀ 23.3, nHT₉₀₀ 20.6, nSt₉₀₀ 3.8, PnHL/CS₉₀₀ 0.161, GuHL/CS₉₀₀ 0.140). Coloration: Mandibles, clypeus, antennae, legs, mesosoma, petiole, and frontal face of first gaster segment light orange brown; remaining gaster dark brown, vertex medium brown with orange tinge.

Comments. *Lasius persicus* sp. nov. is not to confuse with any species occurring in the area. The most similar sympatric species is *L. illyricus* from which it differs by much higher setae numbers (on scape and hind tibia in particular), longer setae, shorter scape and terminal segment of maxillary palps and smaller eye.

4.4.39 *Lasius emarginatus* (Olivier 1791)

Formica emarginata Olivier 1791 [description]

Type specimens are assumed to be lost but Olivier's description of specimens found in the Provence allows the following conclusions. The absolute length of males ("deux lignes" = 4.5 mm) and of gynes ("pres de quatre lignes" = nearly 9.0 mm) and petiole shape indicate a *Lasius* and exclude other genera of Formicinae occurring in this particular region. The rectangular, emarginate petiole scale, the dark reddish brown head, the lighter reddish brown ventral part of the mesosoma compared to its dark reddish-brown dorsal part, and the light (not infuscated!) wings in the gyne exclude species of the subgenus *Chthonolasius* with rectangular scales. The nuptial flight in the evening by the end of June is another reported trait. All these statements multiply to a fair probability that the interpretation of *Formica emarginata* applied by the myrmecologists during the last 150 years was correct. As there are four cryptic species close to *Lasius emarginatus* alone in the West-palaearctic, a neotype fixation in a specimen from France is indicated. Herewith I fix a neotype in the top worker on a pin with three workers labelled "FRA: Frankreich-06, Prov. Savoie, 12 km E Belley, im Rhonetal, 250 mH, 14.04.1996, 133 Leg. A. Schulz, K. Vock"; depository: SMN Görlitz.

***Lasius brunneoemarginatus* Forel 1874.**

Lasius emarginatus var. *brunneoemarginatus* Forel 1874 [description]

The full text of Forel's description is: "*L. brunneoemarginatus*, ou plutot *emarginatus brunneoides*. Formes de l'*emarginatus* plus claires et moins poilues, vivant sous l'écorce des arbres." and later, on page 217, he stated as collecting localities Lugano and Zurich. I investigated 6 specimens in MHN Genève which carry a printed "Typus" label and "L. brunneo emarginatus Forel Crimée" and "ANTWEB CASENT 0911045". According to disagreement with the published type localities these specimens cannot be considered as types. Furthermore, there is some doubt if the young Forel, who had little contacts to foreign collectors in 1873 has seen specimens from the Crimea so early. According to Ivan Löbl (former curator in MHN Genève) and the deceased former curator of NHM Basel, Walter Wittmer, Forel's wife placed printed type labels to many specimens in the collection after Forel's death and probably Forel himself has made this error in his later life. The original handwritten label of Forel does not contain an indication of a type status. The synonymization of *L. brunneoemarginatus* with *L. emarginatus* as it is stated here is based on the fact that the latter is the only species of the *Lasius emarginatus* complex occurring in Lugano or Zurich.

***Lasius brunneoides* Forel 1874**

Lasius emarginatus var. *brunneoides* Forel 1874 [description]

I agree with Wilson (1955) that *Lasius brunneoides* is an objective synonym of *L. brunneoemarginatus* because Forel applied two names on the same descriptive information.

All material examined. A total of 61 nest samples with 154 workers were subject to NUMOBAT investigation. These originated from Austria (6 samples), Bosnia (1), Bulgaria (3), Croatia (4), Czechia (2), England (1), France (3), Germany (13), Greece (17), Israel (1), Italy (7), Slovakia (1), Switzerland (1), and the Ukraine (1). For details see supplementary information SII.

Geographic range. Only European, meridional to south temperate. From S England and France across Central Europe to the Ukraine; Iberia, Apennine and entire Balkans south to 37°N. A single, extremely isolated finding from Israel (31.798°N, 35.146°E, leg. Besuchet & Löbl 1985.04.30) is interpreted here as anthropogenous introduction from Europe. The northern distributional limit in Central Europe was at 52.5°N in 1980, here planar to submontane, in Vorarlberg up to 600 m and in N Tyrol up to 1200 m. In Greece at 40°N ascending to 1700 m. Significant northern range expansion since 1980 particularly in W Europe: after the first finding in 1983 it has colonized entire Belgium, first records in the

Netherlands in 1996 and in S England in 2006. In 2017, 13 sites were known in S England and 7 in the Netherlands with a northern range border at 52.6°N. There is a large geographic overlap area with the sister species *L. illyricus* in the Balkans and south Ukraine.

Biology. See Seifert (2018).

Diagnosis (Tab. 8, Figs. 75–76; key; images in www.AntWeb.org with specimen identifiers CASENT0172762, CASENT0179933, CASENT0280445):

Absolute size rather large (CS 962 µm). Head and scape length indices large (CL/CW₉₀₀ 1.085, SL/CS₉₀₀ 1.067); postocular distance small, eye and torulo-clypeal distance large (PoOc/CL₉₀₀ 0.217, EYE/CS₉₀₀ 0.253, dCIAn₉₀₀ 5.38); terminal segment of maxillary palp long (MP6/CS₉₀₀ 0.221). Number of mandibular dents large (MaDe₉₀₀ 8.76). Pubescence on clypeus dilute (sqPDCL₉₀₀ 5.14); frontal pubescence short (PLF₉₀₀ 24.8). All body parts with standing setae of medium length, (PnHL/CS₉₀₀ 0.139, GuHL/CS₉₀₀ 0.126, nOcc₉₀₀ 12.2, nGen₉₀₀ 6.5, nGu₉₀₀ 6.8, nSc₉₀₀ 10.4, nHT₉₀₀ 18.1). The propodeal dome is (as in *Lasius illyricus*, *L. tebessae* and *L. maltaeus* sp. nov.) higher than in usually seen in *Lasius* s.str. Coloration: Two color morphs occur. The light morph has head, coxae, femora and tibiae medium reddish-brown to dark brown with a reddish tinge whereas mesosoma, anterior clypeal margin, scape, petiole and tarsae are orange. The dark morph is almost concolorous medium to dark brown, is restricted to the south Balkans and may occur sympatric with the light morph. Attempts to separate the light and dark color morph by exploratory or hypothesis-driven data analyses using the 16 standard NUMOBAT characters failed.

Comments. The Westpalaearctic species of the *L. emarginatus* complex are characterized by a combination of elongated head, long scape, long maxillary palps, large eyes, large torulo-clypeal distance, short frontal pubescence and the gular setae not being much shorter or equal in length to pronotal setae (Tab. 8). The only species of this complex occurring sympatric with *L. emarginatus* is *L. illyricus*. The mean classification errors for 52 and 39 samples of *L. emarginatus* and *L. illyricus* respectively, in which all standard NUMOBAT characters have been recorded, were 3.3% in NC-Ward, 2.2% in NC-part.hclust, 0% in NC-part.kmeans and 0% in NC-NMDS.kmeans. A mean error rate of 1.4% relative to the controlling discriminant function is a good confirmation of heterospecificity according to the GAGE species concept. The classification error by the LDA on the individual level was 2.2% for 232 workers of both species. For separation from the allopatric species *L. maltaeus* sp. nov. and *L. tebessae* see there.

4.4.40 *Lasius illyricus* Zimmermann 1935

Lasius alienus subsp. *illyricus* Zimmermann 1935

[type investigation]

Type material: Lectotype worker labelled "Mt. Petka Dubrovnik YUGOSLAVIA V-1928 S.Zimmerman", "type series *Lasius alienus illyricus* Zimmermann" (upperside 2nd label), "unlabelled type Le Tenrant 7.90" (underside 2nd label), "M.C.Z. CoType 30116", "LECTOTYPE desig. by E.O.Wilson", "Jan-Jun.2001 MCZ Image Database"; 3 paralectotype workers labelled "Mt. Petka Dubrovnik YUGOSLAVIA V-1928 S.Zimmerman", "*Lasius alienus illyricus* Zimmermann COTYPE", "M.C.Z. CoType 30116"; depository: MCZ Cambridge.

Lasius ponticus Stärcke 1944

Lasius alienus var. *pontica* Stärcke 1944 [description] Stärcke selected as types for *L. ponticus* 4 workers from the former syntype series of *L. alienobrunneus* Forel 1874 collected in Neu Atos (Novy Afron) / Caucasus after he fixed a lectotype of *L. alienobrunneus* on another pin with 4 specimens from Sierre / Switzerland. Types of *L. ponticus* were not available but the synonymization proposed here is most probable as *L. illyricus* is the only species occurring in the terra typica and matching Stärcke's description.

All material examined. A total of 39 nest samples with 94 workers were subject to NUMOBAT investigation. These originated from Austria (1 sample), Bulgaria (2), Croatia (1), Georgia (3), Greece (6), Iran (11), Turkey (14) and the Ukraine (1). For details see supplementary information SII.

Geographic range. From the Balkans (42.65°N, 18.07°E) over the southern Ukraine, the southern Caucasus and entire Asia Minor east to the eastern Elburs Mountains (36.867°N, 54.933°E). The altitudinal distribution ranges from sea level up to 1900 m.

Biology. There seem to exist no significant differences to *Lasius emarginatus* in habitat selection. In the sympatric area on the Balkans, both species prefer broadleaved forests, especially *Quercus* and *Platanus* forests, but there is some trend of *L. illyricus* to select more open and drier localities. It may occur in urban areas, in gardens and olive plantations. In regions with dryer macroclimate it is found in very shady woods along streams and in the North Iran it is typical for humid broad-leaved Caspian forest. A flight was observed shortly after sunset. Nest are in soil, under stones or in rotten logs. Zimmermann wrote in the original description of *L. illyricus* "...auch fehlt ihnen der *L. emarginatus* eigentümliche Geruch..." ["...even so, the peculiar odor of *L. emarginatus* is lacking..."]. It remains to be checked if this is a constant character or only an ephemeral impression due to the circumstances of observation.

Diagnosis (Tab. 8, Figs. 77–78; key; images in www.AntWeb.org with specimen identifiers CASENT0905686, CASENT0914255):

Absolute size large (CS 991 μm). Head and scape length indices large (CL/CW₉₀₀ 1.082, SL/CS₉₀₀ 1.073); postocular distance small, eye and torulo-clypeal distance large (PoOc/CL₉₀₀ 0.223, EYE/CS₉₀₀ 0.250, dCIAn₉₀₀ 5.45); terminal segment of maxillary palp long (MP6/CS₉₀₀ 0.217). Number of mandibular dents large (MaDe₉₀₀ 8.58). Pubescence on clypeus very dilute (sqPDCL₉₀₀ 5.71); frontal pubescence short (PLF₉₀₀ 22.9). All body parts with much fewer setae than in *L. emarginatus* but in length very similar (PnHL/CS₉₀₀ 0.137, GuHL/CS₉₀₀ 0.124, nOcc₉₀₀ 7.8, nGen₉₀₀ 4.1, nGu₉₀₀ 4.1, nSc₉₀₀ 2.1, nHT₉₀₀ 7.4). Coloration: similar to the light morph of *L. emarginatus*. Dark morph morphs were so far not observed – the darker, more concolorous pigmentation of the small-sized type specimens is probably due to the positive allometry of yellowish or reddish pigments usually observed in *Lasius* s.str. species.

Comments. A sample from a *Quercus pubescens* forest from Leopoldsberg near Vienna is determined with a posterior probability of 0.962 as *L. illyricus* when run as wild-card in a 2-class LDA with *L. emarginatus* as alternative hypothesis and this sample is allocated to *L. illyricus* in any exploratory data analysis tested. There are several Mediterranean floral and faunal elements at Leopoldsberg but the interpretation is of this case is problematic as the nearest known site of *L. illyricus* is 600 km south. In the North Iran, *L. illyricus* occurs in sympatry and syntopic with *L. persicus* sp. nov. – a species with a very similar pigmentation but strongly deviating structural characters (for morphological differences see there).

4.4.41 *Lasius maltaeus* sp. nov.

Etymology: The name refers to island of Malta where it is an endemic species.

Type material: Holotype and 5 paratype workers on two pins labelled "MALTA: 35.93°N, 14.35°E Ghajn Tuffieha, 40 m S.P. Schembri 1989.0503"; 3 paratype workers labelled "MALTA: 3.859°N, 14.399°E Buskett, 185 m col. Collingwood 1983.11.30"; 3 paratype workers labelled "MALTA: 35.897°N, 14.461°E Birkirkara, 35 m June 1978, No 55213"; 4 paratype workers labelled "MALTA: 38.9157°N, 14.4980°E, Sliema, 15 m, base of promenade wall, P. Attewell 2019.06.06"; depository SMN Görlitz.

All material examined. Identical with the 15 individuals of the four type samples.

Geographic range. Endemic species of Malta.

Biology. Unknown.

Diagnosis (Tab. 8, Figs. 79–80; key):

Absolute size medium to rather large (CS 948 μm). Head length index very large (CL/CW₉₀₀ 1.106), scape length index large (SL/CS₉₀₀ 1.067); postocular distance medium (PoOc/CL₉₀₀ 0.228), eye and torulo-clypeal distance large (EYE/CS₉₀₀ 0.247, dCIAn₉₀₀ 5.20); terminal segment of maxillary palp longest within the *L. emarginatus* species complex (MP6/CS₉₀₀ 0.241). Number of mandibular dents above average (MaDe₉₀₀ 8.44). Pubescence on clypeus dilute (sqPDCL₉₀₀ 5.11); frontal pubescence short (PLF₉₀₀ 24.6). Most hairy species of the *L. emarginatus* species complex; number of setae on genae, gula, dorsum of scape and flexor profile of hind tibia extremely high (nOcc₉₀₀ 18.2, nGen₉₀₀ 13.0, nGu₉₀₀ 17.4, nSc₉₀₀ 30.1, nHT₉₀₀ 26.9). Coloration: all body parts orange colored, with dorsum of head sometimes slightly darker orange brown, gaster always darker orange brown.

Comments. *L. maltaeus* sp. nov. shows by far the highest setae numbers within the *L. emarginatus* species complex and has the longest maxillary palp segment and largest head length index. The low sample size does not allow to run NC-clustering. Furthermore checking classifications by an LDA is unreliable due to unavoidable overfitting of character number. Yet, running a PCA with specimens in which the 16 standard NUMOBAT characters have been recorded (15 in *L. maltaeus* sp. nov., 22 in *L. tebessae* and 93 in *L. emarginatus*) and forming nest sample means of the first and second factor of PCA places the 3 samples of *L. maltaeus* sp. nov., 6 samples of *L. tebessae* and 39 samples of *L. emarginatus* clearly separate from each other.

4.4.42 *Lasius tebessae* Seifert 1992

Lasius tebessae Seifert 1992 [type investigation]

Type material: Holotype plus 8 paratype workers labelled "Algeria Tebessa 16.5. 1967, 950 m ex coll. Cagniant"; 8 paratype workers labelled "Algeria: 50 km S Alger, 17.6.1964, 1200 m ex coll. Cagniant"; depository SMN Görlitz.

All material examined. A total of 6 nest samples with 28 workers were subject to NUMOBAT investigation. These originated from Algeria (2 samples) and Morocco (4). For details see supplementary information S11.

Geographic range. Occurring from North Morocco (34.915°N, 5.393°W) to East Algeria (35.400°N, 8.117°E) at elevations between 888 and 1750 m.

Biology. The species is apparently bound to habitats with trees. Reported were *Quercus ilex*, *Pinus halepensis* and *Picea* forests and a open pasture with scattered trees.

Diagnosis (Tab. 8, Figs. 81–82; key):

Absolute size rather large (CS 966 μm). Head length index large (CL/CW₉₀₀ 1.090), scape length index large

(SL/CS₉₀₀ 1.037); postocular distance small (PoOc/CL₉₀₀ 0.218), eye and torulo-clypeal distance large (EYE/CS₉₀₀ 0.249, dCIAn₉₀₀ 5.20); terminal segment of maxillary palp long (MP6/CS₉₀₀ 0.230). Number of mandibular denticles of average level (MaDe₉₀₀ 8.13). Pubescence on clypeus denser than in *L. emarginatus* (sqPDCL₉₀₀ 4.07); frontal pubescence rather short (PLF₉₀₀ 27.6). Setae length slightly larger than in *L. emarginatus* but their number very similar (PnHL/CS₉₀₀ 0.155, GuHL/CS₉₀₀ 0.136, nOcc₉₀₀ 11.6, nGen₉₀₀ 6.3, nGu₉₀₀ 7.0, nSc₉₀₀ 8.8, nHT₉₀₀ 14.7). Coloration: variable from concolorous medium to dark brown to moderately bicolored with mesosoma lighter than head and gaster. The concolorous pale yellowish-reddish brown pigmentation of the type specimens is possibly caused by bleaching during 25 years of ethanol storage.

Comments. The separation of 21 specimens of *L. tebessae* from 53 specimens of sympatric *L. mauretanicus* sp. nov. is mainly given by the higher setae numbers in the latter. A PCA considering all 16 standard NUMOBAT characters provides a complete separation of these 74 specimens. This classification is confirmed by a LOOCV-LDA with an error of 0% in 74 specimens after character reduction to CL/CW₉₀₀, PoOc/CL₉₀₀, nOcc₉₀₀, nSc₉₀₀ and nSt₉₀₀ in order to prevent character-number overfitting. Furthermore all four variants of NC-clustering confirm the PCA classification.

4.4.43 *Lasius tunisius* sp. nov.

Etymology. The name refers to Tunisia where the species has been found.

Type material. Holotype and 5 paratype workers on two pins labelled "TUNESIEN-08, 10-15 km S. Ain Draham, Kroumirie, 600-800 mH, 02.10.1995 Leg. Schulz & Vock 932"; depository SMN Görlitz.

All material examined. Only the type series was available.

Geographic range. Only known from the type locality which is situated at about 36.712°N, 8.671°E, 700 m in a rather humid area fully covered by broad-leaved woodland.

Biology. Unknown. Apparently a woodland species.

Diagnosis (Tab. 8, Figs. 83–84; key):

Absolute size large (CS 994µm). Head length and scape length indices slightly smaller than in related species (CL/CW₉₀₀ 1.076, SL/CS₉₀₀ 1.018). Outlines of head in dorsal view more rounded than in *emarginatus*; postocular distance significantly larger (PoOc/CL₉₀₀ 0.238), eye large (EYE/CS₉₀₀ 0.247) and torulo-clypeal distance rather low (dCIAn₉₀₀ 4.41). In contrast to poorly developed pilosity on other body parts, frontal clypeal margin with a conspicuous row of setae, only moderately

decreasing their length laterad: the 3rd paramedian setae as long as 68–83% of the innermost (1st paramedian) setae; in other species this ratio is 43–65%. Median clypeal margin slightly truncate. Terminal segment of maxillary palp long (MP6/CS₉₀₀ 0.230). Pubescence on clypeus dilute (sqPDCL₉₀₀ 5.01); frontal pubescence extremely appressed and short (PLF₉₀₀ 19.0). Least hairy species of the *L. emarginatus* species complex; setae on dorsum of scape and flexor profile of hind tibia completely absent, pronotal hairs shorter than gular hairs (nOcc₉₀₀ 6.4, nGen₉₀₀ 3.1, nGu₉₀₀ 4.0, nSc₉₀₀ 0, nHT₉₀₀ 0, nSt₉₀₀ 4.1, PnHL/CS₉₀₀ 0.112, GuHL/CS₉₀₀ 0.123). Lateral profile of propodeum similar to *brunneus*: its slope very straight, meeting the dorsal profile at distinct angle of 95–100°. Petiole scale: rather high, subquadrate; dorsal crest wide, emarginate. Coloration: blackish head and gaster, mesosoma dark reddish brown, femora blackish brown, tibiae slightly lighter. Scape yellowish.

Comments. The character combination of *Lasius tunisius* sp. nov. appears unmistakable already under subjective inspection. When run in a PCA, the 6 available specimens cluster clearly separate from any African species.

4.4.44 *Lasius magnus* Seifert 1992

Lasius magnus Seifert 1992 [type investigation]

Type material: Holotype and 20 paratype workers labelled "Gogona, 3100 m 10.-12.6"; "Nat.-Hist.Museum Basel – Bhutan Expedition 1972"; depositories: holotype plus 16 paratypes NHM Basel, 4 paratypes SMN Görlitz.

All material examined. A total of 19 samples with 60 workers were subject to NUMOBAT investigation. These originated from Bhutan (10 samples), India (7) and Nepal (2). For details see supplementary information SII.

Geographic range. Known so far from 16 sites at the southern flank of the Himalayas at elevations between 1700 and 3100 m and along a line delimited by 27.9°N, 86.2°E and 27.4°N, 90.5°E. Two sites from the Meghalaya Mountains (25.45°N, 91.76°E, 1800m; 25.50°N, 91.90°E, 1900 m) are isolated from the main population.

Biology. The main habitats are woodland biomes, mainly evergreen broad-leaved and evergreen coniferous mountain forest with mesophilic to very moist conditions, that is just below or within the zone of cloud forests. The highest known site at 3100 m was in the lower zone of *Rhododendron*-conifer woodland.

Diagnosis (Tab. 9, Figs. 85–86; key; image in www.antWeb.org with specimen identifier CASENT0912294):

Largest species of the subgenus *Lasius* s.str. (CS 1153 µm). Head length index very large (CL/CW₉₀₀ 1.138, mean CL/CW without RAV 1.076). Scape length indices large (SL/CS₉₀₀ 1.034, mean SL/CS without RAV 0.978).

Postocular and torulo-clypeal distances rather large (PoOc/CL₉₀₀ 0.253, dCIAn₉₀₀ 4.90); terminal segment of maxillary palp of medium length (MP6/CS₉₀₀ 0.191). Number of mandibular dents very small (MaDe₉₀₀ 7.11). Pubescence on clypeus extremely sparse (sqPDCL₉₀₀ 7.24); frontal pubescence of medium length (PLF₉₀₀ 27.8). Pubescence on all surfaces smooth or rather smooth. Gaster tergites with a diagnostic pubescence pattern deviating from the strictly longitudinal orientation seen in other *Lasius* species: the paramedian pubescence hairs on posterior dorsum of tergites are directed caudomedial or even mediad. This unique pattern may be affected in case of polluted surfaces. Setae rather short and of medium numbers (PnHL/CS₉₀₀ 0.119, GuHL/CS₉₀₀ 0.080, nOcc₉₀₀ 10.0, nGen₉₀₀ 1.7, nGu₉₀₀ 3.4, nSc₉₀₀ 14.7, nHT₉₀₀ 16.7). Coloration: all body parts rather concolorous, varying from pale yellowish-reddish brown, over medium brown with yellowish tinge to dark brown.

Comments: The unique character combination of *Lasius magnus* should exclude a confusion with any species. Small workers can be clearly distinguished from equal-sized specimens of other species by a combination of elongated head, low number of mandibular dents, short pronotal setae, extremely dilute clypeal pubescence and the diagnostic pubescence pattern on gaster tergites. There are three samples in NHM Basel having no setae but only a fine pubescence on dorsal crest and sides of petiole scale whereas in the other samples the scale is fringed in frontal view by a number of setae. I assume intraspecific polymorphism but the issue should be checked for taxonomic significance. The exceptionally large size of workers and queens in *L. magnus*, the exceptionally large size in the temporary social parasite *Lasius (Chthonolasius) crinitus* (Smith 1858) and syntopic occurrence, strongly suggest the former to represent the host of the latter.

4.4.45 *Lasius lawarai* Seifert 1992

Lasius lawarai Seifert 1992 [type investigation]

Type material: Holotype and 5 paratype workers labelled "PAKISTAN. Dir, Lawarai-Pass 21e, 2700 m; 21. v. 1983 Besuchet-Löbl"; depositories: MHN Genève, 2 paratypes in SMN Görlitz.

Lasius breviscapus Seifert 1992 syn. nov.

Lasius breviscapus Seifert 1992 [type investigation]

Type material: Holotype and 4 paratype workers labelled "Chopal, 2400-2750m, 7.5.1977" and "Indien Him. Prad. Wittmer, Brancucci"; depository NHM Basel.

All material examined. A total of 10 nest samples with 29 workers were subject to NUMOBAT investigation. These originated from India (3 samples) and Pakistan (7 samples). For details see supplementary information SII.

Geographic range. Known so far only from the SW flank of the Himalayas at elevations between 2300 and 3100 m, along a line delimited by 35.8°N, 71.8°E and 30.8°N, 77.8°E.

Diagnosis (Tab. 9, Figs. 87–88; key; images in www.antWeb.org with specimen identifiers CASENT0911182, CASENT0912289):

Within the Himalayan-Tibetan species of the subgenus, the species is well separable as a combination of small eyes (EYE/CS₉₀₀ 0.214), large postocular index (PoOc/CL₉₀₀ 0.261) and short scape (SL/CS₉₀₀ 0.948). Seta counts (those of nSc and nHT in particular) are weakly reproducible because of unclear thickness differences between elongated pubescence hairs and setae. A frequent coloration is head, mesosoma petiole and gaster dark brown; mandibles, antennae, tibiae and tarsae light yellowish brown.

Biology. Unknown.

Comments. The synonymization of *Lasius breviscapus* is explained as follows. Based on a single sample of 5 workers, Seifert (1992) described *L. breviscapus* as a species because of very small body size and an extremely low RAV-corrected scape length. The sample means of CS and SL/CS₉₀₀ are 731 µm and 0.907 whereas these means vary in the nine samples of *L. lawarai* 789–870 µm and 0.936–0.981 – i.e., the data are clearly outside the normal distribution of *L. lawarai* known in that time. However, I was unaware in 1992 that nanitic, malnourished workers of *Lasius*, typically those reared first by a founding queen, may show a reduction of relative scape length in contradiction to the overall allometric rule that SL/CS increases with reduction of body size. Furthermore, considering all 16 standard characters, no exploratory data analysis could expose the *L. breviscapus* type series outside the *L. lawarai* cluster and both taxa share the rare characters of small eye size and large postocular index.

4.4.46 *Lasius wittmeri* Seifert 1992

Lasius wittmeri Seifert 1992 [type investigation]

Type material: Holotype and 5 paratype workers labelled "Kashmir, 1976, W. Wittmer" and "Pahalgam 7. 7. 2200-3100 m"; 6 paratype workers labelled "Pakistan 1974, C. Baroni Urbani" and "Naran 7900' Kagan Valley 25.V"; both samples deposited in NHM Basel.

All material examined. A total of 2 nest samples with 12 workers were subject to NUMOBAT investigation. These originated from Pakistan and India. For details see supplementary information SII.

Geographic range. The two known sites are situated at the southwestern flank of the Himalayas at 34.90°N, 73.75°E, 2400 m and 34.04°N, 75.33°E, 2650 m.

Diagnosis (Tab. 9, Figs. 89–90, key, images in www.

antWeb.org with specimen identifiers CASENT0912298): The most similar Himalayan species is *L. lawarai* from which it differs by larger eyes (EYE/CS₉₀₀ 0.240), smaller postocular index (PoOc/CL₉₀₀ 0.241), longer scape (SL/CS₉₀₀ 0.979) and smaller torulo-clypeal distance (dCIAn/CS₉₀₀ 3.60%). The Tibetan *L. schaeferi* differs by a much shorter frontal pubescence (PLF₉₀₀ 29.6 vs. 38.8 µm) and the presence of very distinct standing setae on hind tibia, the morphology of which differs clearly from neighboring pubescence hairs. Seta counts in *L. wittmeri* are not clearly reproducible because of unclear thickness differences between elongated semierect pubescence hairs and semierect setae. Yet, this missing differentiation may be used as accessory character to distinguish *L. lawarai* also from East Tibetan populations of *L. obscuratus*. Coloration: all body parts dark brown, mandibles and tarsae slightly lighter with a yellowish tinge.

Biology. Unknown.

Comments. 96% of 25 workers of *L. lawarai* and *L. wittmeri* for which data of the full character set were available were correctly classified in a LOOCV-LDA using the first three components of a PCA as input data.

4.4.47 *Lasius hirsutus* Seifert 1992

Lasius hirsutus Seifert 1992 [type specimens]

Type material: holotype plus 5 paratype workers labelled "PAKISTAN: Chitral, Madaglasht 2700 m, 26. V. 1983 27b, Besuchet–Löbl", depository: MHN Genève.

All material examined. Only the type series is known.

Geographic range. The type locality is situated at the southwestern flank of the W Himalayas at 35.78°N, 72.03°E and 2700 m.

Diagnosis (Tab. 9, Figs. 91–92; key): Among the Himalayan-Tibetan species it is easily identified as a combination of very long scape (SL/CS₉₀₀ 1.022), extremely long gular pilosity (GuHL/CS₉₀₀ 0.154), and very high seta counts on genae (nGen₉₀₀ 19.9), underside of head (nGu₉₀₀ 19.2) and hind tibiae (nHT₉₀₀ 31.2). Coloration: Dorsum of head blackish brown; genae and clypeus medium brown; mandibles and head capsule at mandibular angles yellowish; mesosoma, femora and tibiae medium brown; tibio-femoral and tibio-metatarsal joints and antennae yellowish.

Biology. Unknown.

Comments. There is no species known which appears to be closely related to *L. hirsutus*.

4.4.48 *Lasius nigrescens* Stitz 1930

Lasius emarginatus var. *nigrescens* Stitz 1930

[type investigation]

Type material: Lectotype (des. E.O. Wilson) and 4

paralectotype gynes labelled "West-Pamir, VII-IX 28, leg. Reinig, Maz, 3800 m, 15.-19. VIII"; depository ZM Berlin.

Comments. The types series consists of alate gynes obviously caught during nuptial flight. The missing knowledge on worker morphology in *Lasius nigrescens* and missing knowledge on gyne morphology in the Himalayan-Tibetan species makes the taxonomic assessment difficult. Considering the correlations that usually exist between gyne and worker morphology in *Lasius* (Seifert 1992), the worker of *L. nigrescens* is expected to have a long scape (SL/CS₉₀₀ perhaps 1.06), an average head length index (CL/CW₉₀₀ perhaps 1.07), and numerous setae on underside of head and hind tibiae. Pictures of the type gynes are shown in antweb.org under the specimen identifiers ANTWEB1008433 and ANTWEB1008434. I present here the data of 5 investigated type gynes: CS 1411 ± 17 [1392, 1432]; CL/CW 0.883 ± 0.010 [0.872, 0.896]; SL/CS 0.870 ± 0.010 [0.856, 0.879]; nGu 32.0 ± 5.6 [27, 40], nOcc 29.1 ± 1.6 [27, 31]; nGen 15.2 ± 4.2 [12.5, 20.0]; GuHL/CS 0.112 ± 0.005 [0.107, 0.16]; PnHL/CS 0.147 ± 0.005 [0.143, 0.152]; sqPDCL 4.68 ± 0.17 [4.49, 4.89]; ML/CS 2.168 ± 0.036 [2.130, 2.223]; MH/CS 1.146 ± 0.026 [1.122, 1.189]; MW/CS 1.329 ± 0.006 [1.322, 1.333].

4.4.49 *Lasius schaeferi* Seifert 1992

Lasius schaeferi Seifert 1992 [type specimens]

Type material: holotype plus 4 paratype workers labelled "II. Dolan Expedition Westchina/Tibet leg. E. Schäfer, 1934/36", "131"; depository: NHM Basel.

All material examined. Only the type series is known.

Geographic range. The label "131" refers to station 131 of Ernst Schäfer's expedition route which is situated at approximately 33.60°N, 96.58°E and 3900 m and was reached 4 August 1935.

Diagnosis (Tab. 9, Figs. 93–94; images in www.antWeb.org with specimen identifier CASENT0912296; key): The most similar species among the Himalayan-Tibetan species is *Lasius obscuratus*. *L. schaeferi* differs from the latter in particular by much more numerous setae on hind tibia (nHT₉₀₀ 12.7 vs. 2.8) which also occur on the distal half of extensor profile. The best separation from the Himalayan species *L. lawarai* and *L. wittmeri*, which show similar shape and setae data, is given by the shorter frontal pubescence (PLF₉₀₀ 29.6 µm; in *L. lawarai* and *L. wittmeri* 36.1 and 38.8 µm respectively) and the presence of very distinct erect to suberect setae on hind tibia, the morphology of which differs clearly from the neighboring appressed pubescence hairs. This clear differentiation between setae and pubescence is lost in *L. lawarai* and *L. wittmeri* where we observe unclear thickness differences between elongated semierect

pubescence hairs and semierect setae. Coloration: Head and mesosoma yellowish-brown, gaster in three specimens yellow, in one specimen yellowish brown.

Biology. Unknown. According to the geographic data of the type locality, it is possible that *L. schaeferi* lives under the harshest climatic conditions of all *Lasius* s. str. species worldwide.

Comments. Most probably belonging to *Lasius obscuratus* species complex.

4.4.50 *Lasius coloratus* Santschi 1937

Lasius niger st. *coloratus* Santschi 1937

[type investigation]

Type material: Lectotype (des. E.O. Wilson) and paralectotype worker labelled in Santschi's handwriting "Lasius niger coloratus Sant", "Musha Formosa K. Sato", "Type"; depository NHM Basel.

All material examined. A total of 13 samples with 36 workers were subject to NUMOBAT investigation. These originated from continental China (11 samples) and Taiwan (2). For details see supplementary information SII.

Geographic range. Distributed over the Chinese provinces Sichuan and Shaanxi from 28.82°N, 103.06°E to 34°N, 109°E. The two sites in Taiwan are at 23.5°N, 120.7°E and 24.0°N, 121.1°E. The elevation of 13 sites was 1388 ± 517 [583, 2490] meters.

Biology. The species was always connected to woodland both in continental China and in Taiwan.

Diagnosis (Tab. 10, Figs. 95–96; key; images in www.antWeb.org with specimen identifiers CASENT0906278 and CASENT0912290):

Rather large (CS 985 µm). Head and scape length indices rather large (CL/CW₉₀₀ 1.083, SL/CS₉₀₀ 1.029). Postocular and torulo-clypeal distances large (PoOc/CL₉₀₀ 0.250, dClAn₉₀₀ 5.23); terminal segment of maxillary palp long (MP6/CS₉₀₀ 0.209). Number of mandibular dents medium (MaDe₉₀₀ 8.28). Pubescence on clypeus moderately dense (sqPDCL₉₀₀ 4.69); frontal pubescence of medium length (PLF₉₀₀ 29.5). Pubescence surface on body and appendages rough. Setae of medium length and numerous (PnHL/CS₉₀₀ 0.156, GuHL/CS₉₀₀ 0.102, nOcc₉₀₀ 14.6, nGen₉₀₀ 5.5, nGu₉₀₀ 6.2, nSc₉₀₀ 24.6, nHT₉₀₀ 22.0). Sculpture on metapleuron, lower propodeum and often pronotum differing from the condition in species related to *Lasius niger* or *L. japonicus* in having regular, slightly curved, dense longitudinal carinulae and delicate microstructures within the meshes of the microreticulum. This produces a matt overall surface appearance at lower magnifications. Coloration: more or less bicolored. The lighter forms have the mesosoma pale yellowish-reddish brown, the dorsum of head slightly and the gaster notably

darker. The darker forms have the mesosoma medium reddish brown, the dorsum of head dark brown with a reddish tinge and the gaster blackish brown.

Comments: For differences to the sister species *Lasius sichuense* sp. nov., see there.

4.4.51 *Lasius sichuense* sp. nov.

Etymology. The name refers to the type locality in the Chinese province Sichuan.

Type material. Holotype and 2 paratype workers on one pin labelled "China, Sichuan, NW Jiuxiangzhen, N 29,562, E 102,336, 2615 m asl, 2009-07-10, leg. Kabak, Chi 2009 221a"; 3 paratype workers on one pin labelled "China, Sichuan, NW Jiuxiangzhen, N 29,564, E 102,336, 2710 m asl, 2009-07-10, leg. Kabak, Chi 2009 204"; depository SMN Görlitz.

All material examined. A total of 13 samples with 29 workers were subject to NUMOBAT investigation. These originated from continental China (12 samples) and Taiwan (1). For details see supplementary information SII.

Geographic range. Distributed over the Chinese provinces Yunnan, Sichuan and Shaanxi from 24.86°N, 98.76°E to 32.0°N, 109.1°E. The elevation of 13 sites was 2154 ± 357 [1400, 2710] m.

Biology. The species was always connected to woodland both in continental China and in Taiwan but occurs at significantly higher elevations than *L. coloratus* (ANOVA $F_{1,24} = 19.26$, $p < 0.0005$).

Diagnosis (Tab. 10, Figs. 97–98; key):

Sister species of *L. coloratus*. Rather large (CS 1005 µm). Head length rather large (CL/CW₉₀₀ 1.083), scape shorter than in *L. coloratus* (SL/CS₉₀₀ 0.999). Postocular distance large (PoOc/CL₉₀₀ 0.250), torulo-clypeal distance smaller than in *L. coloratus* (dClAn₉₀₀ 4.90); terminal segment of maxillary palp long (MP6/CS₉₀₀ 0.200). Number of mandibular low (MaDe₉₀₀ 7.93). Pubescence on clypeus denser than in *L. coloratus* (sqPDCL₉₀₀ 4.23); frontal pubescence of medium length (PLF₉₀₀ 29.1). Pubescence surface on body and appendages rough. Setae significantly shorter and fewer than in *L. coloratus* (PnHL/CS₉₀₀ 0.135, GuHL/CS₉₀₀ 0.084, nOcc₉₀₀ 10.2, nGen₉₀₀ 2.6, nGu₉₀₀ 2.9, nSc₉₀₀ 9.4, nHT₉₀₀ 12.1). Sculpture on metapleuron and lower propodeum similar to situation in *L. coloratus*. Coloration similar to *L. coloratus* but in the average slightly darker.

Comments. Any variant of NC-clustering separated the 26 samples of *Lasius sichuense* sp. nov. and *L. coloratus* with an error of 0% and the classification error by an LDA was 0% in 63 worker individuals. For separation of from *Lasius kabaki* sp. nov. and *L. longipalpus* sp. nov., see there.

4.4.52 *Lasius kabaki* sp. nov.

Etymology. The name refers to the collector of the type specimens, the Russian naturalist Ilya Igorevitch Kabak.

Type material. Holotype and 2 paratype workers on one pin labelled "China, S Sichuan, S Yanyuan, N 27,359, E 101,507, 3035 m asl, 2010-06-29, leg. Belousov & Kabak, Chi 2010 102"; 3 paratype workers labelled "China, S Sichuan, S Yanyuan, N 27,359, E 101,507, 3035 m asl, 2010-06-29, leg. Belousov & Kabak, Chi 2010 022"; 3 paratype workers labelled "China, S Sichuan, S Yanyuan, N 27,3461, E 101,5117, 3435 m asl, 2010-06-30, leg. Belousov & Kabak, Chi 2010 159"; 3 paratype workers labelled "China, S Sichuan, S Yanyuan, N 27,351, E 101,509, 3290 m asl, 2010-06-19, leg. Belousov & Kabak, Chi 2010 275"; depository SMN Görlitz.

All material examined. The 4 type samples with 12 workers were subject to NUMOBAT investigation. For details see supplementary information SII.

Geographic range. High mountain range about 10 km S of Yanyuan at elevations between 3035 and 3435 m which is clearly higher than in sympatric *L. sichuense* sp. nov. and *L. coloratus*.

Biology. Unknown but the coordinates suggest an affinity to woodland.

Diagnosis (Tab. 10, Figs. 99–100; key):

Related to *Lasius sichuense* sp. nov. and *L. coloratus*. Smaller (CS 921 μm). Head length comparably large, scape length index smaller than in the other two species (CL/CW₉₀₀ 1.093, SL/CS₉₀₀ 0.989). Postocular distance slightly smaller and eye slightly larger (PoOc/CL₉₀₀ 0.241, EYE/CS₉₀₀ 0.245). Torulo-clypeal distance comparably large and terminal segment of maxillary palp shorter (dClAn₉₀₀ 5.04, MP6/CS₉₀₀ 0.178). Number of mandibular denticles larger (MaDe₉₀₀ 8.67). Pubescence on clypeus much more dilute (sqPDCL₉₀₀ 5.80); frontal pubescence of medium length (PLF₉₀₀ 28.9). Setae of large to medium length (PnHL/CS₉₀₀ 0.160, GuHL/CS₉₀₀ 0.106) and overall rather numerous; on genae, underside of head and below propodeal spiracle more numerous than in *L. sichuense* sp. nov. (nGen₉₀₀ 7.6, nGu₉₀₀ 5.7, nSt₉₀₀ 4.9). Overall sculpture in comparison to *L. sichuense* sp. nov. and *L. coloratus* reduced and more shining. On dorsum of head a microreticulum is absent, the only elements of microsculpture are a number of very fine and short longitudinal carinulae and the shallow pits forming the bases of pubescence hairs. Sculpture on mesosoma reduced in comparison to sister species and metapleuron with much finer longitudinal carinulae. Lateral pronotum very shining. Scale in frontal view with more straight, dorsad less converging sides and straight or feebly emarginate dorsal crest. Coloration: homogeneously yellowish to chestnut brown.

Comments. After character reduction to CS, CL/CW₉₀₀, SL/CS₉₀₀, EYE/CS₉₀₀, sqPDCL₉₀₀, nGu₉₀₀, nSc₉₀₀ and MP6/CS₉₀₀, the four nest samples of *Lasius kabaki* sp. nov. are separated from the *Lasius sichuense* sp. nov. and *L. coloratus* cluster by NC-Ward, NC-part.hclust and NC-NMDS-kmeans with an error of 0% whereas NC-part.kmeans recognizes only one cluster. The separation of *L. kabaki* sp. nov. from the latter two species is supported by the more shining cuticular surface and by living in much higher altitudes. Using the characters sqPDCL, MP6, CW and EYE in a LDA, the 12 individual workers of *L. kabaki* sp. nov. are fully separated from the 62 workers of *L. sichuense* sp. nov. and *L. coloratus*.

4.4.53 *Lasius longipalpus* sp. nov.

Etymology. The name refers to the terminal segment of maxillary palps which is long compared to sympatric smaller-sized and weakly-haired species.

Type material. Holotype and 2 paratype workers on one pin labelled "China, Ganzu, Lanshou, street trees, 1500 m asl, E 103.85°, N 36.05° 2011-09-22, Chi 2011 140"; 3 paratype workers on one pin labelled "China, Ganzu, Lanshou, street trees, 1500 m asl, E 103.85°, N 36.05° 2011-09-22, Chi 2011 141a"; 2 paratype workers on one pin labelled "China, Ganzu, Lanshou, street trees, 1500 m asl, E 103.85°, N 36.05° 2011-09-24, Chi 2011 148b"; depository SMN Görlitz.

All material examined. A total of 27 samples with 72 workers were subject to NUMOBAT investigation. These originated from China (25 samples), Russian Far East (1) and Japan (1). For details see supplementary information SII.

Geographic range. Apparently widely distributed over the Chinese provinces E Qinghai, Gansu, Sichuan and Shaanxi at elevations between 1300 and 3155 m. A probably disjunct population, apparently separated by some 2000 km from the Chinese population, is found in the Russian Far East (42.9°N, 133.9°E, 35 m) and Hokkaido (42.9°N, 143.2°N, 77 m).

Biology. The species occurs in woodland areas and semi-open habitats such as city parks; in highest elevations also in more open situations. Details of biology is unknown but it appears to be rather euryoecious.

Diagnosis (Tab. 10, Figs. 101–102; key):

Probably related to *L. sichuense* sp. nov. but smaller (CS 888 μm) and longer-scaped (SL/CS₉₀₀ 1.019). Head moderately elongated (CL/CW₉₀₀ 1.086). Postocular distance smaller and eye significantly larger than in *L. sichuense* sp. nov. (PoOc/CL₉₀₀ 0.238, EYE/CS₉₀₀ 0.250). Torulo-clypeal distance smaller than in species of the *L. coloratus* complex (dClAn₉₀₀ 4.47). Terminal segment of maxillary palp long (MP6/CS₉₀₀ 0.200). Number of

mandibular dents medium (MaDe₉₀₀ 8.08). Pubescence on clypeus dilute (sqPDCL₉₀₀ 5.04) and frontal pubescence of medium length (PLF₉₀₀ 28.6). Setae rather short (PnHL/CS₉₀₀ 0.130, GuHL/CS₉₀₀ 0.088) and occurring on most body surfaces in low numbers reminiscent of the situation in the *L. obscuratus* group (nOcc₉₀₀ 7.1, nGen₉₀₀ 2.1, nGu₉₀₀ 2.4, nSc₉₀₀ 2.8; nHT₉₀₀ 4.2, nSt₉₀₀ 0.4). The surface sculpture on metapleuron and lower propodeum as it is seen in *L. coloratus* is basically present but the longitudinal carinulae are more delicate and reduced to shorter fragments. Coloration: head mesosoma and gaster either homogeneously medium to dark brown or head and gaster blackish brown and mesosoma less dark; head, mandibles, antennae, metatarsae and tarsae pale yellowish.

Comments. *L. longipalpus* sp. nov. is separable from *Lasius sichuense* sp. nov. by any algorithm of NC-clustering without classification error. The two apparently disjunct samples from Russian Primorye and Hokkaido do not form a separate branch in NC-Ward and are not exposed as outliers by NC-part.hclust or in a PCA. The classification error by an LDA in 97 individual workers of *L. longipalpus* sp. nov. and *L. sichuense* sp. nov. is 0%.

4.4.54 *Lasius productus* Wilson 1955

Lasius productus Wilson 1955 [description]

The extremely elongated appendages of this species are outstanding among the Holarctic *Lasius* of any subgenus. Wilson (1955) presented the following measurements for the holotype worker from Mt. Imano / Shikoku, leg. Okamoto: CL 1.17 mm, CW 1.04 mm and SL 1.17 mm. A scatterplot of SL and CW places the holotype within the cluster of the 16 conspecific specimens studied here and completely outside the clusters of any Palaearctic species. The holotype data translate into CS 1105 µm, CL/CW₉₀₀ 1.176 and SL/CS₉₀₀ 1.164.

All material examined. A total of 6 nest samples with 16 workers were subject to NUMOBAT investigation. These originated from Japan. For details see supplementary information SII.

Geographic range. Distributed over the Japanese islands Tsushima, Kyushu, Shikoku and Honshu. Three altitudinal records range from 50 to 1000 m.

Biology. Connected to broad-leaved deciduous forest. Nesting in rotten wood on ground or in dead parts of tree trunks. Nuptial flight in August and September.

Diagnosis (Tab. 11, Figs. 103–104; key; image in www.antWeb.org with specimen identifier CASENT0903217):

Large (CS 1050 µm). Head and scape length indices outstandingly large (CL/CW₉₀₀ 1.139, SL/CS₉₀₀ 1.169). Postocular distance rather small and eye rather large

(PoOc/CL₉₀₀ 0.235, EYE/CS₉₀₀ 0.248). Torulo-clypeal distance large (dCIAn₉₀₀ 5.65). Terminal segment of maxillary palp outstandingly long (MP6/CS₉₀₀ 0.293). Pubescence on clypeus moderately dense (sqPDCL₉₀₀ 4.35); frontal pubescence of medium length (PLF₉₀₀ 28.8). Scape densely covered with decumbent pubescence hairs. Gular setae rather long, only slightly shorter than pronotal setae (GuHL/CS₉₀₀ 0.117, PnHL/CS₉₀₀ 0.134); setae numbers rather low (nOcc₉₀₀ 9.8, nGen₉₀₀ 3.2, nGu₉₀₀ 3.1, nSc₉₀₀ 10.2, nHT₉₀₀ 6.7, nSt₉₀₀ 1.9). Coloration: varying from concolorous medium brown to bicolored with contrasting reddish brown mesosoma and dark brown head and gaster.

Comments: *Lasius productus* is unmistakable due to the extremely long scape and maxillary palp segments.

4.4.55 *Lasius koreanus* Seifert 1992

Lasius koreanus Seifert 1992 [type investigation]

Type material: Holotype worker labelled "Korea, Kaesong, Mts. Pakyon, 20 km NE from Kaesong, 30. Sept. 1971.", "No 254, leg. S. Horvatovich et J. Papp"; 5 paratype workers on separate pins labelled "North Korea Paekdusan 1.-18.8. 1989 Kozánek lgt."; depository SMN Görlitz.

All material examined. A total of 5 nest samples with 9 workers were subject to NUMOBAT investigation. These originated from North Korea. For details see supplementary information SII.

Geographic range. Only known so far from North Korea between 38.1 and 40.9°N and elevations between 10 and 1700 m.

Biology. Largely unknown. Alates were collected between 6 and 23 August.

Diagnosis (Tab. 10, Figs. 105–106; key; image in www.antWeb.org with specimen identifiers CASENT0912292 and FOCOL 0750):

Small size (CS 819 µm). Head moderately elongated and scape shorter than in other East Asian species (CL/CW₉₀₀ 1.085, SL/CS₉₀₀ 0.956). Postocular distance rather small and eye rather large (PoOc/CL₉₀₀ 0.236, EYE/CS₉₀₀ 0.252). Torulo-clypeal distance small (dCIAn₉₀₀ 4.38). Terminal segment of maxillary palp long (MP6/CS₉₀₀ 0.201). Pubescence on clypeus moderately dense (sqPDCL₉₀₀ 4.57); frontal pubescence rather short (PLF₉₀₀ 27.0). Gular and pronotal setae of medium length (GuHL/CS₉₀₀ 0.103, PnHL/CS₉₀₀ 0.137); overall setae numbers rather low (nOcc₉₀₀ 11.9, nGen₉₀₀ 1.1, nGu₉₀₀ 4.9, nSc₉₀₀ 2.6, nHT₉₀₀ 13.0, nSt₉₀₀ 4.8). Microsculpture on head and mesosoma more strongly developed than in other species. Microsculpture between the frontal carinae rather deep, with the margins of meshes developed as elevated ridges and their inner part developed as a rather deep

foveola which centrally carries the base of a pubescence hair; short fragments of microcarinulae are irregularly dispersed over the surface. Lateral metapleuron and lower lateral propodeum densely longitudinally carinate. Coloration: variable; head brown to dark reddish brown, mesosoma medium brown to light reddish brown, gaster varying between dark reddish brown and blackish brown.

Comments: Forming a combination of small size, short scape, large eyes and particular microsculpture, *Lasius koreanus* should not be confused with any other species.

4.4.56 *Lasius hayashi*

Yamauchi & Hayashida 1970

Lasius hayashi Yamauchi & Hayashida 1970

[type investigation]

Type material: one paratype worker from the holotype nest series labelled "Sapporo Hokkaido 27-VII-1967 K. Yamauchi"; depository SMN Görlitz.

All material examined. A total of 6 nest samples with 29 workers were subject to NUMOBAT investigation. These originated from Japan. For details see supplementary information SII.

Geographic range. Japan from 32°N to 45°N, Korea and Kuriles. The upper altitudinal limits are 600 m at 44°N in Hokkaido and 1600 m at 34°N in Shikoku.

Biology (according to Yamauchi 1979, Yamauchi, Ito & Suzuki 1986). Main habitat is shady deciduous woodland with large trees. The nests are mostly constructed within the root systems or in hollow trunks of trees and sometimes in rotten logs and may contain carton structures. Being active in Sapporo to mid November, *L. hayashi* has a longer foraging season than sympatric congeneric species. The foraging paths are almost completely covered by macerated plant and humus material both on tree trunks and on the ground near the tree where trophobiotic Homoptera are tended. Flights were observed from early July to late August and start in the late evening at light intensities of only 0–10 lux and air temperatures of 22–24°C. Air movements and rain stop the flight.

Diagnosis (Tab. 11, Figs. 107–108; key; image in www.antWeb.org with specimen identifier CASENT1041269):

Large (CS 994 µm). Head shorter than in other sympatric species (CL/CW₉₀₀ 1.049) and usually with concave posterior margin. Scape rather short (SL/CS₉₀₀ 0.978). Postocular distance medium and eye rather small (PoOc/CL₉₀₀ 0.241, EYE/CS₉₀₀ 0.230). Torulo-clypeal distance rather large (dCIAn₉₀₀ 5.07). Number of mandibular dents rather low (MaDe 7.95). Terminal segment of maxillary palp rather long (MP6/CS₉₀₀ 0.194). Pubescence on clypeus moderately dense (sqPDCL₉₀₀ 4.59); on frons rather short (PLF₉₀₀ 28.4); on scape subdecumbent to suberect and difficult to distinguish from shorter setae;

on hind tibia decumbent to appressed, contrasting the situation in the long, suberect to erect setae. Gular and pronotal setae long (GuHL/CS₉₀₀ 0.114, PnHL/CS₉₀₀ 0.154). Whole body covered by numerous standing setae (nOcc₉₀₀ 13.1, nGen₉₀₀ 5.1, nGu₉₀₀ 6.4, nSc₉₀₀ 18.3, nHT₉₀₀ 17.4, nSt₉₀₀ 4.9). Coloration: mesosoma, petiole, scape, femora and tibiae pale yellowish brown, head darker yellowish brown, gaster blackish brown or dark brown with yellowish tinge.

Comments: *Lasius hayashi* is separable from the sympatric similarly hirsute *L. japonicus* by the broader head, shorter scape, more convex petiole sides and the homogeneously yellowish brown head capsule.

4.4.57 *Lasius sakagami*

Yamauchi & Hayashida 1970

Lasius sakagami Yamauchi & Hayashida 1970

[type investigation]

Type material: one paratype worker from the holotype nest series labelled "Sapporo Hokkaido 30-VII-1966 K. Yamauchi"; depository SMN Görlitz.

All material examined. A total of 6 nest samples with 19 workers were subject to NUMOBAT investigation. These originated from Japan. For details see supplementary information SII.

Geographic range. Widely spread all over Japan from 33°N to 45°N from sea level to 500 m.

Biology (according to Yamauchi 1979, Yamauchi, Ito & Suzuki 1986). Main habitat are sun-exposed deposition areas of alluvial and aeolian sands with only sparse vegetation; these are river banks, dry river beds, sand dunes or road sides. Nests are usually constructed at spots with bare sand or under stones and have numerous distinct chambers usually reaching down to 60 cm. Nuptial flights were observed from early July to late September at warm evenings with air temperatures > 22°, high air humidity and no air movements. The species is polygynous and in many nests only males fly. Nuptial flight of gynes only takes place from nests without males, otherwise they mate intranidally with subsequent dispersal flight. It may form supercolonies dominating large habitat areas.

Diagnosis (Tab. 11, Figs. 109–110; key; images in www.antWeb.org with specimen identifiers CASENT0906279, CASENT1041276):

Medium-sized (CS 887 µm). Head moderately long (CL/CW₉₀₀ 1.071). Scape long (SL/CS₉₀₀ 1.034). Postocular distance small and eye medium-sized (PoOc/CL₉₀₀ 0.225, EYE/CS₉₀₀ 0.244). Torulo-clypeal distance large (dCIAn₉₀₀ 5.21). Number of mandibular dents large (MaDe 8.52). Terminal segment of maxillary palp rather long (MP6/CS₉₀₀ 0.194). Pubescence on clypeus dense (sqPDCL₉₀₀ 3.78) and on frons rather long (PLF₉₀₀ 33.0).

Gular and pronotal setae rather long (GuHL/CS₉₀₀ 0.110, PnHL/CS₉₀₀ 0.157). Whole body covered by extremely numerous standing setae (nOcc₉₀₀ 23.4, nGen₉₀₀ 16.1, nGu₉₀₀ 18.6, nSc₉₀₀ 32.0, nHT₉₀₀ 29.8, nSt₉₀₀ 12.6). Mesosoma with very flat propodeal dome and convex to angulate-convex posterior propodeal slope that is transversally carinulate. Petiole scale in lateral view thick, low and with a blunt apex; in anterior view rather narrow, with convex to nearly straight subparallel sides. Coloration: mesosoma medium brown with a yellowish-reddish tinge, head a little and gaster distinctly darker; sometimes whole body concolorous pale or dark brown.

Comments: *Lasius sakagamii* represents an unmistakable combination of extremely large setae numbers, flat propodeal dome, low petiole and low clypeal pubescence distance.

4.5. Nomina nuda and Incertae sedis

The following names which probably refer to the subgenus *Lasius* s.str. cannot be interpreted 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 the rationale that nobody can present counter-arguments because no information is available. Such solutions were chosen for example by Bolton (1995). The alternative is listing these names under Incertae Sedis. I prefer the latter solution and recommend future revisers not to synonymize these names as long as no reliably identified type specimens have been discovered. Taxonomy needs clear arguments and not speculative assertions. I present the unclear taxa in alphabetic order.

***Lasius alienoniger* Forel 1874**

Lasius niger var. *alieno-niger* Forel 1874

The short description of Forel is contradictory. The name should refer to either *Lasius alienus*, *L. psammophilus*, *L. paralienus* or setae-reduced specimens of *L. niger*.

***Lasius emarginatobrunneus* Ruzsky 1902**

Lasius brunneus var. *emarginato-brunneus* Ruzsky 1902

Ruzsky erroneously attributed this taxon to Forel who, however, has never published this name. Ruzsky gave no descriptive information and reported only the Caucasian collection sites Batumi, Novy Afon, Kutaisi, Bardat and Pjatigorsk.

***Lasius emeryi* Ruzsky 1905**

Lasius niger subsp. *emeryi* Ruzsky 1905

The taxon was described from the Pamirs and reported to have a yellowish-reddish mesosoma and short oblique

hairs on scapes and tibiae, with the hairs on scapes being sparser than on tibiae. It might possibly be related to one of the Himalayan species such as *L. lawarai* or *L. wittmeri*.

***Lasius longicirrus* Chang & He 2002**

Lasius longicirrus Chang & He 2002

The type series has been collected on Mount Jishi in Gansu / China at an elevation of 2100 m. The verbal description and figures are insufficient. A possible synonymy with either *L. coloratus*, *L. sichuense* sp. nov. or *L. longipalpus* sp. nov. is suggested by sympatric occurrence, the long maxillary palps and long scape. Types were not available from the Agricultural College of Ningxia University.

***Lasius minimus* Kuznetzov-Ugamsky 1928**

Acanthomyops niger var. *minimus* Kuznetzov-Ugamsky 1928

This taxon has been described from the Okeanskaya Railroad Station near Vladivostok. The description only mentions the very small size of the ants and might possibly refer to dwarf workers of *Lasius japonicus* or *L. vostochni* sp. nov.

***Lasius nigerrima* (Christ 1791)**

Formica nigerrima Christ 1791

The description reports nothing but body length, color and occurrence in gardens and could refer to either a *Lasius* s.str. or a *Tapinoma* species. Christ's paper considers ants on a worldwide scale but he gave no collecting locality for *Formica nigerrima*. Supposing that he meant a German garden, there is some likelihood for a synonymy with *Lasius niger*.

***Lasius nitidus* (Kuznetzov-Ugamsky 1927)**

Acanthomyops niger subsp. *nitidus* (Kuznetzov-Ugamsky 1927)

This taxon has been collected at the Kara Su river, 65 km NE Tashkent, Uzbekistan and was reported to differ from *Lasius niger* by a more shining cuticular surface. Considering which species potentially occur at the type locality, the description might possibly refer to dark color variants of *Lasius flavescens* or *L. uzbeki*.

***Lasius pallescens* (Schenck 1852)**

Formica pallescens Schenck 1852

Schenck observed a swarming nest at the trunk of an oak near Dillenburg /Hessen. He collected a gyne and a male and described the gyne to be 3.5 lines long, to have a pale yellowish head, mesosoma, petiole, antennae, mandibles and legs, a brown gaster, hirsute scapes and tibiae and hyaline wings. The male was reported to be 2 lines long, to have a brown head, brownish mandibles, a yellowish mesosoma with three brown longitudinal stripes, a

brownish scutellum and posterior part of mesosoma and hyaline wings. If Schenck meant Prussian lines, the gyne and male were 7.6 and 4.4 mm long – if referring to Hessian lines 8.8 and 5 mm. This description strongly indicates genus *Lasius* but I do not know a German species to which such a character combination might refer.

***Lasius pannonicus* Rösler 1942**

Lasius alienus var. *pannonica* Rösler 1942

The description of this ant, found in dense shady woodland near Budafok / Hungary, should refer to the subgenus *Lasius* s.str. but further conclusions are not possible. The whole text appears to be a mixture of phantasy and imprudent statements. I have never seen an ant combining the reported life-style, habitat selection and morphology.

***Lasius transylvanicus* Rösler 1943**

Lasius transylvanica Rösler 1943

Rösler claimed to have made intensive observations of nest construction and behavior of this ant in the floodplain of the Nyarad river / Romania. The morphological description reports a dense and erect scape pilosity as in *Lasius niger* in combination with complete absence of setae on legs as found in *Lasius alienus*. I have never seen such an ant in thousands of Palaearctic *Lasius* samples. The description of behavior also indicates involvement of phantasy, invention or cognitive failure.

4.6 Acknowledgements

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Tab. 1*: Members of the *Lasius brunneus* species complex (nOcc+nGu+nSt < 10). Data are given as arithmetic mean \pm standard deviation [lower extreme, upper extreme] number of individuals.

	<i>brunneus</i> (n=67)	<i>silvaticus</i> n.sp. (n=24)	<i>himalayanus</i> (n=37)	<i>excavatus</i> n.sp. (n=6)	<i>lasioides</i> (n=306)
CS [μ m]	930 \pm 115 [723,1134] 67	944 \pm 61 [818,1039] 24	1003 \pm 82 [749,1134] 37	900 \pm 31 [855, 937] 6	813 \pm 0.067 [601,991] 306
CL/CW ₉₀₀	1.041 \pm 0.012 [1.012,1.061] 67	1.059 \pm 0.009 [1.041,1.078] 24	1.072 \pm 0.012 [1.045,1.095] 37	1.028 \pm 0.012 [1.014,1.049] 6	1.054 \pm 0.017 [1.014,1.112] 306
SL/CS ₉₀₀	0.874 \pm 0.014 [0.838,0.905] 67	0.908 \pm 0.015 [0.873,0.934] 24	0.921 \pm 0.028 [0.874,0.978] 37	0.974 \pm 0.017 [0.950,0.990] 6	0.974 \pm 0.027 [0.909,1.038] 306
MP6/CS ₉₀₀	0.174 \pm 0.007 [0.158,0.188] 37	0.172 \pm 0.005 [0.163,0.183] 24	0.187 \pm 0.008 [0.174,0.202] 24	0.181 \pm 0.014 [0.159,0.193] 6	0.184 \pm 0.010 [0.163,0.218] 233
PoOc/CL ₉₀₀	0.244 \pm 0.007 [0.231,0.262] 56	0.235 \pm 0.006 [0.221,0.246] 24	0.242 \pm 0.007 [0.226,0.254] 26	0.222 \pm 0.003 [0.218,0.226] 6	0.239 \pm 0.009 [0.214,0.263] 288
EYE ₉₀₀	0.229 \pm 0.005 [0.219,0.239] 56	0.233 \pm 0.004 [0.227,0.240] 24	0.235 \pm 0.003 [0.229,0.242] 27	0.238 \pm 0.005 [0.234,0.244] 6	0.241 \pm 0.006 [0.226,0.256] 288
dClAn/CS ₉₀₀ [%]	3.49 \pm 0.33 [2.65,4.19] 56	3.36 \pm 0.36 [2.78,3.99] 24	3.84 \pm 0.32 [2.99,4.41] 26	4.34 \pm 0.25 [4.03,4.68] 6	4.49 \pm 0.38 [3.64,5.61] 288
MaDe ₉₀₀	7.06 \pm 0.28 [6.9,7.9] 15	7.27 \pm 0.55 [6.9,7.9] 3	7.19 \pm 0.46 [6.5,7.9] 10	7.00 \pm 0.00 [7.0,7.0] 2	7.13 \pm 0.52 [6.0,8.1] 164
sqPDCL ₉₀₀	5.31 \pm 0.53 [4.11,6.87] 67	4.59 \pm 0.28 [3.93,5.17] 24	4.66 \pm 0.61 [3.71,5.92] 36	5.51 \pm 0.43 [4.95,6.11] 6	5.56 \pm 0.64 [3.71,7.73] 306
PLF ₉₀₀	23.3 \pm 2.1 [18.7,27.5] 22	24.4 \pm 1.6 [21.9,27.3] 9	24.3 \pm 1.4 [21.6,26.8] 18	23.2 \pm 1.0 [22.1,24.6] 6	25.1 \pm 2.9 [20.7,34.1] 107
GuHL/CS ₉₀₀	0.094 \pm 0.042 [0.000,0.133] 67	0.125 \pm 0.014 [0.099,0.151] 24	0.018 \pm 0.030 [0.000,0.098] 37	0.021 \pm 0.034 [0.000,0.079] 6	0.042 \pm 0.041 [0.000,0.126] 306
PnHL/CS ₉₀₀	0.098 \pm 0.010 [0.081,0.122] 67	0.130 \pm 0.008 [0.113,0.150] 24	0.108 \pm 0.011 [0.079,0.125] 37	0.102 \pm 0.023 [0.064,0.120] 6	0.120 \pm 0.010 [0.088,0.149] 306
nOcc ₉₀₀	2.0 \pm 0.9 [0.0,4.2] 67	3.1 \pm 1.3 [1.1,5.1] 24	1.1 \pm 0.9 [0.0,3.2] 36	2.1 \pm 1.2 [0.5,3.6] 6	3.3 \pm 1.2 [0.5,6.9] 306
nGen ₉₀₀	0.1 \pm 0.3 [0.0,1.2] 58	0.8 \pm 0.8 [0.0,2.8] 24	0.1 \pm 0.2 [0.0,0.9] 27	0.1 \pm 0.2 [0.0,0.5] 6	0.2 \pm 0.5 [0.0,4.0] 288
nGu ₉₀₀	1.3 \pm 0.9 [0.0,3.4] 67	3.6 \pm 1.0 [1.6,5.5] 24	0.3 \pm 0.6 [0.0,2.9] 37	0.2 \pm 0.3 [0.00,0.50] 6	0.6 \pm 0.8 [0.00,3.6] 306
nSc ₉₀₀	0.0 \pm 0.0 [0.0,0.0] 67	0.1 \pm 0.3 [0.0,1.4] 24	0.0 \pm 0.0 [0.0,0.0] 37	0.0 \pm 0.0 [0.0,0.0] 6	0.0 \pm 0.1 [0.0,1.2] 306
nHT ₉₀₀	0.1 \pm 0.3 [0.0,1.7] 67	1.6 \pm 0.6 [0.5,2.7] 24	0.1 \pm 0.2 [0.0,0.8] 37	0.0 \pm 0.0 [0.0,0.0] 6	0.0 \pm 0.1 [0.0,1.1] 306
nSt ₉₀₀	1.1 \pm 0.9 [0.0,3.7] 56	2.9 \pm 0.9 [1.4,5.2] 24	0.4 \pm 0.5 [0.0,1.6] 27	1.2 \pm 0.6 [0.3,1.9] 6	2.2 \pm 1.4 [0.0,6.8] 288

* Tabs. 1-11 show an indicator of absolute body size (CS) whereas all other data are size-corrected – i.e., allometric variance is removed for the assumption of each individual having a head size CS of 900 μ m.

Tab. 2: Members of the *Lasius turcicus* species complex (nOcc+nGu+nSt > 10).

	<i>austriacus</i> (n=40)	<i>tapinomoides</i> (n=3)	<i>neglectus</i> (n=207)	<i>precursor</i> n.sp. (n=197)	<i>turcicus</i> (n=321)	<i>israelicus</i> n.sp. (n=13)
CS [μ m]	705 \pm 32 [648,775] 40	631 \pm 9 [622,640] 3	773 \pm 47 [606,901] 207	769 \pm 50 [642,887] 197	855 \pm 64 [669,1019] 321	865 \pm 56 [766,949] 13
CL/CW ₉₀₀	1.080 \pm 0.017 [1.048,1.123] 40	1.065 \pm 0.006 [1.059,1.069] 3	1.087 \pm 0.015 [1.027,1.123] 207	1.076 \pm 0.018 [1.034,1.124] 197	1.084 \pm 0.015 [1.025,1.133] 321	1.069 \pm 0.011 [1.058,1.094] 13
SL/CS ₉₀₀	0.892 \pm 0.021 [0.844,0.933] 40	0.994 \pm 0.015 [0.977,1.005] 3	0.967 \pm 0.015 [0.924,1.015] 205	0.946 \pm 0.017 [0.891,0.997] 171	0.964 \pm 0.017 [0.889,1.019] 304	0.996 \pm 0.013 [0.978,1.019] 13
MP6/CS ₉₀₀	0.144 \pm 0.015 [0.112,0.166] 13	0.177 \pm 0.017 [0.164,0.196] 3	0.193 \pm 0.007 [0.173,0.210] 63	0.183 \pm 0.010 [0.156,0.209] 160	0.192 \pm 0.009 [0.168,0.219] 249	0.216 \pm 0.007 [0.201,0.225] 8
PoOc/CL ₉₀₀	0.270 \pm 0.006 [0.260,0.281] 40	0.233 \pm 0.002 [0.231,0.234] 3	0.228 \pm 0.007 [0.211,0.251] 185	0.238 \pm 0.008 [0.219,0.261] 171	0.228 \pm 0.007 [0.210,0.258] 283	0.231 \pm 0.006 [0.222,0.242] 13
EYE ₉₀₀	0.198 \pm 0.009 [0.174,0.212] 40	0.240 \pm 0.002 [0.237,0.241] 3	0.240 \pm 0.006 [0.217,0.254] 185	0.235 \pm 0.005 [0.220,0.248] 173	0.234 \pm 0.006 [0.211,0.252] 283	0.232 \pm 0.005 [0.225,0.241] 13
dCIAn/CS ₉₀₀ [%]	2.61 \pm 0.45 [1.67,3.53] 40	4.07 \pm 0.32 [3.85,4.44] 3	4.23 \pm 0.36 [3.39,5.27] 185	3.61 \pm 0.34 [2.84,4.56] 172	4.01 \pm 0.42 [2.80,5.53] 283	4.17 \pm 0.39 [3.73,5.03] 13
MaDe ₉₀₀	7.41 \pm 0.49 [6.1,8.1] 32	7.10 \pm 0.00 [7.1,7.1] 2	7.31 \pm 0.51 [6.0,8.3] 111	7.64 \pm 0.43 [7.0,8.1] 64	7.72 \pm 0.54 [6.0,9.0] 136	7.68 \pm 0.48 [7.0,8.0] 12
sqPDCL ₉₀₀	5.51 \pm 0.50 [4.49,6.60] 40	5.25 \pm 0.25 [5.08,5.54] 3	5.39 \pm 0.54 [3.86,7.32] 205	5.13 \pm 0.48 [4.19,6.78] 171	5.34 \pm 0.55 [3.76,6.81] 302	5.44 \pm 0.32 [5.02,6.09] 13
PLF ₉₀₀	30.5 \pm 2.4 [25.6,36.9] 18	36.9 \pm 0.6 [36.3,37.3] 3	34.3 \pm 3.0 [28.7,42.5] 47	34.5 \pm 3.2 [28.2,40.6] 16	34.7 \pm 2.5 [29.2,38.9] 41	38.4 \pm 2.8 [35.6,44.8] 13
GuHL/CS ₉₀₀	0.108 \pm 0.029 [0.000,0.142] 40	0.126 \pm 0.013 [0.115,0.140] 3	0.115 \pm 0.022 [0.000,0.147] 205	0.125 \pm 0.011 [0.098,0.155] 194	0.127 \pm 0.011 [0.094,0.154] 310	0.136 \pm 0.013 [0.109,0.152] 13
PnHL/CS ₉₀₀	0.123 \pm 0.011 [0.098,0.149] 40	0.154 \pm 0.007 [0.146,0.159] 3	0.127 \pm 0.012 [0.094,0.164] 205	0.127 \pm 0.010 [0.089,0.152] 194	0.127 \pm 0.009 [0.100,0.146] 310	0.147 \pm 0.008 [0.136,0.159] 13
nOcc ₉₀₀	5.3 \pm 1.6 [2.4,9.5] 40	10.6 \pm 1.7 [8.8,12.1] 3	9.8 \pm 2.9 [0.0,17.5] 205	5.8 \pm 1.7 [1.7,9.7] 174	6.9 \pm 2.2 [2.3,15.0] 305	15.2 \pm 2.1 [11.6,19.3] 13
nGen ₉₀₀	1.0 \pm 1.0 [0.0,3.5] 40	2.4 \pm 1.8 [0.8,4.4] 3	2.0 \pm 1.4 [0.0,6.9] 197	1.3 \pm 0.9 [0.0,4.2] 164	1.8 \pm 1.1 [0.0,7.2] 280	5.8 \pm 1.8 [3.1,8.9] 13
nGu ₉₀₀	2.6 \pm 1.2 [0.0,4.9] 40	3.5 \pm 0.8 [2.5,4.0] 3	2.9 \pm 1.0 [0.0,5.6] 204	3.3 \pm 0.9 [1.2,6.5] 194	4.0 \pm 1.3 [0.0,8.6] 309	9.1 \pm 1.3 [7.2,11.5] 13
nSc ₉₀₀	0.1 \pm 0.2 [0.0,1.3] 40	1.1 \pm 0.5 [0.8,1.6] 3	0.1 \pm 0.4 [0.0,3.1] 205	0.1 \pm 0.3 [0.0,2.3] 174	0.1 \pm 0.4 [0.0,2.9] 302	1.2 \pm 1.3 [0.0,3.6] 13
nHT ₉₀₀	0.2 \pm 0.4 [0.0,2.2] 40	2.5 \pm 1.3 [0.0,4.8] 3	0.7 \pm 1.0 [0.0,4.8] 205	0.1 \pm 0.3 [0.0,1.4] 175	0.3 \pm 0.6 [0.0,4.4] 302	18.0 \pm 3.4 [11.3,24.2] 13
nSt ₉₀₀	3.5 \pm 1.4 [0.0,6.4] 40	6.9 \pm 0.4 [6.5,7.3] 3	3.6 \pm 1.2 [0.0,6.9] 188	3.8 \pm 1.1 [0.7,7.1] 194	4.2 \pm 1.2 [0.0,7.4] 291	5.2 \pm 0.8 [4.1,7.2] 13

Tab. 3: The *Lasius obscuratus* species complex & *L. brevipalpus* n.sp.

	<i>piliferus</i> (n=53)	<i>psammophilus</i> (n=528)	<i>obscuratus</i> (n=167)	<i>creticus</i> n.sp. (n=26)	<i>brevipalpus</i> n.sp. (n=12)
CS [μ m]	812 \pm 53 [656, 932] 53	826 \pm 67 [651, 1004] 528	840 \pm 64 [640, 989] 167	859 \pm 42 [783, 921] 26	812 \pm 95 [650, 937] 12
CL/CW ₉₀₀	1.061 \pm 0.015 [1.022, 1.095] 53	1.057 \pm 0.018 [1.009, 1.119] 310	1.065 \pm 0.016 [1.017, 1.112] 112	1.083 \pm 0.015 [1.060, 1.112] 26	1.084 \pm 0.013 [1.055, 1.103] 12
SL/CS ₉₀₀	0.929 \pm 0.018 [0.896, 0.977] 53	0.960 \pm 0.023 [0.885, 1.024] 528	0.956 \pm 0.019 [0.917, 1.012] 167	0.965 \pm 0.012 [0.941, 0.984] 26	1.004 \pm 0.017 [0.975, 1.030] 12
MP6/CS ₉₀₀	0.140 \pm 0.010 [0.118, 0.178] 37	0.145 \pm 0.010 [0.123, 0.166] 206	0.173 \pm 0.011 [0.149, 0.201] 132	0.196 \pm 0.007 [0.184, 0.211] 26	0.153 \pm 0.011 [0.130, 0.165] 12
PoOc/CL ₉₀₀	0.247 \pm 0.006 [0.234, 0.261] 37	0.241 \pm 0.007 [0.224, 0.260] 206	0.234 \pm 0.009 [0.212, 0.256] 133	0.229 \pm 0.007 [0.215, 0.238] 26	0.242 \pm 0.005 [0.230, 0.252] 12
EYE ₉₀₀	0.220 \pm 0.007 [0.209, 0.242] 37	0.238 \pm 0.007 [0.219, 0.256] 206	0.244 \pm 0.008 [0.225, 0.266] 133	0.236 \pm 0.007 [0.224, 0.247] 26	0.249 \pm 0.003 [0.246, 0.258] 12
dCIAn/CS ₉₀₀ [%]	3.79 \pm 0.42 [3.00, 4.67] 37	3.91 \pm 0.46 [2.81, 5.48] 206	4.28 \pm 0.40 [3.57, 5.16] 133	4.04 \pm 0.41 [3.30, 5.08] 26	4.46 \pm 0.20 [4.11, 4.80] 12
MaDe ₉₀₀	8.20 \pm 0.36 [8.0, 9.0] 13	8.26 \pm 0.44 [7.1, 9.7] 91	8.37 \pm 0.49 [7.0, 9.1] 83	8.18 \pm 0.31 [8.0, 9.0] 13	8.53 \pm 0.45 [8.1, 9.0] 3
sqPDCL ₉₀₀	4.63 \pm 0.44 [3.53, 5.57] 53	4.56 \pm 0.49 [3.39, 6.12] 528	4.35 \pm 0.42 [3.37, 5.56] 167	5.19 \pm 0.49 [4.33, 6.39] 26	4.99 \pm 0.41 [4.24, 5.84] 12
PLF ₉₀₀	31.1 \pm 1.1 [28.7, 32.1] 16	32.9 \pm 2.0 [27.5, 37.0] 32	33.1 \pm 3.0 [28.0, 40.7] 48	33.9 \pm 1.5 [30.7, 37.1] 15	32.1 \pm 1.8 [29.6, 35.3] 12
GuHL/CS ₉₀₀	0.114 \pm 0.011 [0.078, 0.132] 53	0.097 \pm 0.014 [0.039, 0.129] 213	0.091 \pm 0.015 [0.000, 0.143] 167	0.125 \pm 0.013 [0.096, 0.151] 26	0.089 \pm 0.010 [0.077, 0.107] 12
PnHL/CS ₉₀₀	0.150 \pm 0.010 [0.122, 0.174] 53	0.146 \pm 0.012 [0.115, 0.176] 238	0.140 \pm 0.015 [0.089, 0.177] 167	0.144 \pm 0.010 [0.125, 0.164] 26	0.162 \pm 0.009 [0.148, 0.177] 12
nOcc ₉₀₀	10.9 \pm 2.0 [3.5, 15.7] 53	8.7 \pm 2.5 [2.1, 16.7] 528	8.3 \pm 2.5 [1.6, 15.2] 167	10.7 \pm 3.5 [4.3, 15.3] 26	9.0 \pm 3.0 [4.6, 14.8] 12
nGen ₉₀₀	2.0 \pm 1.3 [0.0, 5.4] 53	0.8 \pm 1.0 [0.0, 4.9] 239	1.4 \pm 1.3 [0.0, 6.2] 164	2.6 \pm 1.7 [0.0, 6.3] 26	2.3 \pm 1.3 [0.0, 4.2] 12
nGu ₉₀₀	4.2 \pm 1.2 [0.5, 6.6] 53	2.8 \pm 1.0 [0.0, 7.4] 528	2.7 \pm 1.2 [0.0, 6.9] 167	4.5 \pm 1.5 [1.7, 7.2] 26	2.5 \pm 0.8 [1.5, 3.8] 12
nSc ₉₀₀	0.4 \pm 0.8 [0.0, 4.5] 53	1.0 \pm 2.2 [0.0, 16.7] 215	0.7 \pm 1.3 [0.0, 8.5] 167	0.4 \pm 0.6 [0.0, 2.1] 26	4.6 \pm 3.9 [0.0, 12.3] 12
nHT ₉₀₀	3.2 \pm 1.5 [0.0, 7.2] 53	2.4 \pm 1.6 [0.0, 10.6] 239	2.8 \pm 2.0 [0.0, 9.8] 167	2.6 \pm 2.6 [0.0, 7.4] 26	6.2 \pm 3.8 [0.0, 10.2] 12
nSt ₉₀₀	5.7 \pm 1.3 [2.0, 8.6] 53	3.6 \pm 1.5 [0.0, 7.0] 238	2.6 \pm 1.3 [0.0, 7.1] 164	5.1 \pm 1.0 [3.2, 7.1] 26	2.2 \pm 1.1 [0.5, 3.9] 12

Tab. 4: The *Lasius paralienus* species complex

	<i>bombycina</i> (n=52)	<i>paralienus</i> (n=182)	<i>paralienus</i> Sardinia (n=6)	<i>kritikos n.sp.</i> (n=11)	<i>casevitzi</i> (n=36)
CS [μm]	894 \pm 67 [744,1076] 52	861 \pm 72 [682,1138] 182	927 \pm 53 [867,1023] 6	866 \pm 41 [793, 919] 11	845 \pm 41 [779, 912] 36
CL/CW ₉₀₀	1.076 \pm 0.013 [1.048,1.118] 50	1.067 \pm 0.016 [1.011,1.110] 124	1.074 \pm 0.008 [1.063,1.082] 6	1.074 \pm 0.011 [1.051,1.084] 11	1.066 \pm 0.015 [1.041,1.106] 36
SL/CS ₉₀₀	0.968 \pm 0.020 [0.920,1.009] 52	0.986 \pm 0.016 [0.933,1.042] 182	0.998 \pm 0.018 [0.968,1.015] 6	1.007 \pm 0.012 [0.984,1.024] 11	0.999 \pm 0.014 [0.973,1.029] 36
MP6/CS ₉₀₀	0.160 \pm 0.008 [0.141,0.180] 50	0.183 \pm 0.007 [0.167,0.201] 106	0.177 \pm 0.005 [0.170,0.184] 6	0.217 \pm 0.010 [0.201,0.234] 11	0.212 \pm 0.008 [0.197,0.232] 36
PoOc/CL ₉₀₀	0.239 \pm 0.008 [0.223,0.260] 50	0.242 \pm 0.007 [0.227,0.263] 106	0.236 \pm 0.008 [0.228,0.250] 6	0.241 \pm 0.004 [0.234,0.250] 11	0.241 \pm 0.007 [0.229,0.254] 36
EYE ₉₀₀	0.237 \pm 0.005 [0.227,0.250] 50	0.241 \pm 0.005 [0.227,0.255] 106	0.238 \pm 0.005 [0.232,0.243] 6	0.242 \pm 0.003 [0.237,0.248] 11	0.243 \pm 0.006 [0.234,0.255] 36
dCIAn/CS ₉₀₀ [%]	4.34 \pm 0.35 [3.73,5.08] 50	4.09 \pm 0.46 [3.16,5.26] 106	4.34 \pm 0.35 [3.73,5.08] 5	4.37 \pm 0.22 [4.00,4.67] 11	4.46 \pm 0.30 [3.93,5.26] 36
MaDe ₉₀₀	8.20 \pm 0.40 [8.0,9.0] 10	8.04 \pm 0.34 [7.2,9.0] 17	8.50 \pm 0.00 [8.5,8.5] 2	no data	8.20 \pm 0.36 [8.0,9.0] 7
sqPDCL ₉₀₀	3.42 \pm 0.22 [3.02,3.93] 52	3.51 \pm 0.21 [3.01,4.06] 182	3.39 \pm 0.09 [3.25,3.47] 6	3.36 \pm 0.24 [2.97,3.63] 11	3.39 \pm 0.18 [2.96,3.69] 36
PLF ₉₀₀	34.1 \pm 1.4 [31.5,36.2] 12	31.8 \pm 1.2 [30.0,34.7] 15	38.9 \pm 1.4 [37.1,40.7] 6	34.1 \pm 2.1 [31.3,37.9] 9	36.7 \pm 1.9 [33.2,40.2] 22
GuHL/CS ₉₀₀	0.115 \pm 0.010 [0.092,0.140] 50	0.103 \pm 0.028 [0.000,0.151] 112	0.118 \pm 0.016 [0.097,0.141] 6	0.095 \pm 0.020 [0.045,0.123] 11	0.109 \pm 0.007 [0.089,0.121] 36
PnHL/CS ₉₀₀	0.161 \pm 0.011 [0.137,0.201] 50	0.135 \pm 0.011 [0.094,0.164] 112	0.157 \pm 0.004 [0.152,0.164] 6	0.155 \pm 0.007 [0.146,0.166] 11	0.159 \pm 0.014 [0.107,0.178] 36
nOcc ₉₀₀	12.3 \pm 2.5 [4.6,17.0] 52	7.9 \pm 2.1 [1.8,15.2] 182	10.2 \pm 0.8 [9.2,11.3] 6	8.0 \pm 1.1 [6.3,9.7] 11	12.4 \pm 1.8 [10.3,15.4] 18
nGen ₉₀₀	1.1 \pm 0.8 [0.0,2.6] 50	0.2 \pm 0.3 [0.0,1.2] 106	0.4 \pm 0.4 [0.0,1.0] 6	1.9 \pm 1.2 [0.3,3.7] 11	4.2 \pm 0.7 [2.7,5.6] 18
nGu ₉₀₀	3.3 \pm 1.1 [1.5,7.1] 52	2.3 \pm 0.8 [0.0,3.9] 182	2.4 \pm 1.0 [1.0,3.9] 6	1.8 \pm 1.2 [0.6,3.1] 11	4.0 \pm 1.0 [2.0,5.9] 18
nSc ₉₀₀	0.6 \pm 0.6 [0.0,2.4] 50	0.3 \pm 0.8 [0.0,4.5] 112	0.2 \pm 0.4 [0.0,0.9] 6	0.9 \pm 0.6 [0.0,1.9] 11	1.3 \pm 1.0 [0.0,3.4] 18
nHT ₉₀₀	3.1 \pm 1.5 [0.6,7.0] 50	1.8 \pm 1.3 [0.0,5.6] 112	2.3 \pm 0.7 [1.6,3.4] 6	2.2 \pm 1.2 [0.0,1.9] 11	8.6 \pm 1.7 [5.7,12.3] 18
nSt ₉₀₀	4.2 \pm 1.1 [1.6,6.5] 50	2.9 \pm 1.1 [0.4,5.5] 106	6.0 \pm 0.6 [5.3,6.7] 6	1.6 \pm 0.9 [0.5,3.5] 11	5.2 \pm 0.8 [3.7,6.9] 18

Tab. 5: West and Central Palaearctic species with unclear systematic position

	<i>alienus</i> (n=706)	<i>karpinisi</i> (n=4)	<i>schulzi</i> (n=32)	<i>uzbeki</i> (n=56)	<i>flavescens</i> (n=45)	<i>flavoniger</i> (n=6)
CS [μ m]	823 \pm 55 [665,1006] 706	912 \pm 48 [874,982] 4	854 \pm 29 [800,939] 32	861 \pm 46 [774,967] 56	844 \pm 48 [730,955] 45	872 \pm 15 [858,898] 6
CL/CW ₉₀₀	1.069 \pm 0.016 [0.984,1.109] 391	1.037 \pm 0.012 [1.025,1.052] 4	1.086 \pm 0.013 [1.057,1.106] 32	1.071 \pm 0.013 [1.043,1.095] 56	1.068 \pm 0.014 [1.043,1.097] 45	1.082 \pm 0.011 [1.064,1.093] 6
SL/CS ₉₀₀	0.946 \pm 0.020 [0.880,0.997] 706	1.024 \pm 0.004 [1.021,1.029] 4	1.010 \pm 0.019 [0.973,1.049] 32	0.994 \pm 0.016 [0.954,1.027] 56	0.932 \pm 0.025 [0.881,0.984] 45	1.002 \pm 0.016 [0.985,1.022] 6
MP6/CS ₉₀₀	0.181 \pm 0.010 [0.158,0.206] 109	0.177 \pm 0.010 [0.168,0.191] 4	0.202 \pm 0.010 [0.184,0.217] 19	0.172 \pm 0.009 [0.147,0.189] 54	0.161 \pm 0.009 [0.143,0.183] 42	0.196 \pm 0.019 [0.177,0.217] 6
PoOc/CL ₉₀₀	0.243 \pm 0.007 [0.228,0.258] 111	0.234 \pm 0.002 [0.231,0.236] 4	0.224 \pm 0.006 [0.213,0.233] 21	0.219 \pm 0.007 [0.206,0.236] 54	0.238 \pm 0.008 [0.220,0.254] 42	0.228 \pm 0.002 [0.224,0.230] 6
EYE ₉₀₀	0.239 \pm 0.006 [0.231,0.253] 111	0.244 \pm 0.002 [0.243,0.247] 4	0.238 \pm 0.005 [0.227,0.246] 21	0.264 \pm 0.008 [0.244,0.280] 54	0.242 \pm 0.005 [0.233,0.250] 42	0.229 \pm 0.003 [0.225,0.233] 6
dClAn/CS ₉₀₀ [%]	4.05 \pm 0.36 [3.19,5.13] 111	4.25 \pm 0.23 [3.91,4.43] 4	4.69 \pm 0.38 [3.92,5.28] 20	3.86 \pm 0.36 [3.08,4.53] 54	3.50 \pm 0.40 [2.69,4.39] 42	4.71 \pm 0.14 [4.57,4.88] 6
MaDe ₉₀₀	8.18 \pm 0.42 [7.0,9.6] 117	8.30 \pm 0.48 [8.0,9.0] 4	8.26 \pm 0.54 [7.5,9.0] 8	8.14 \pm 0.54 [7.0,9.0] 23	8.23 \pm 0.43 [7.5,9.0] 21	8.00 \pm 0.00 [8.0,8.0] 3
sqPDCL ₉₀₀	4.11 \pm 0.38 [3.08,6.24] 706	4.18 \pm 0.28 [3.87,4.51] 4	6.43 \pm 0.72 [5.27,8.20] 29	5.01 \pm 0.45 [4.26,6.23] 56	5.18 \pm 0.58 [4.12,6.80] 45	5.52 \pm 0.45 [4.98,6.14] 6
PLF ₉₀₀	31.0 \pm 2.4 [26.5,40.6] 72	33.8 \pm 1.4 [32.6,35.6] 4	33.3 \pm 2.4 [28.8,36.6] 11	35.7 \pm 2.0 [29.9,39.4] 44	36.4 \pm 2.0 [31.2,41.0] 41	35.2 \pm 2.6 [31.9,39.2] 6
GuHL/CS ₉₀₀	0.058 \pm 0.043 [0.000,0.129] 272	0.095 \pm 0.008 [0.087,0.103] 4	0.121 \pm 0.008 [0.106,0.143] 31	0.132 \pm 0.011 [0.110,0.164] 56	0.115 \pm 0.013 [0.079,0.143] 43	0.128 \pm 0.012 [0.107,0.139] 6
PnHL/CS ₉₀₀	0.152 \pm 0.007 [0.134,0.163] 272	0.108 \pm 0.017 [0.089,0.123] 4	0.157 \pm 0.010 [0.137,0.173] 31	0.163 \pm 0.008 [0.144,0.181] 56	0.139 \pm 0.010 [0.119,0.166] 44	0.160 \pm 0.006 [0.148,0.166] 6
nOcc ₉₀₀	4.9 \pm 1.7 [0.0,10.2] 706	8.0 \pm 1.5 [6.4,9.5] 4	15.0 \pm 3.5 [8.8,23.3] 31	9.8 \pm 1.9 [5.6,14.3] 56	18.9 \pm 3.3 [13.0,26.8] 42	19.1 \pm 4.6 [12.9,23.5] 6
nGen ₉₀₀	0.2 \pm 0.4 [0.0,2.6] 320	0.4 \pm 0.6 [0.0,1.2] 4	2.9 \pm 1.1 [1.1,4.7] 20	5.8 \pm 1.8 [2.6,12.3] 54	11.9 \pm 2.7 [6.3,17.9] 25	10.2 \pm 2.0 [8.0,13.3] 6
nGu ₉₀₀	0.8 \pm 0.8 [0.0,4.0] 706	2.6 \pm 0.4 [2.0,3.0] 4	4.5 \pm 1.8 [1.6,10.6] 31	6.7 \pm 2.0 [3.3,10.8] 56	14.1 \pm 3.1 [7.3,20.4] 43	10.5 \pm 2.4 [6.3,12.8] 6
nSc ₉₀₀	0.1 \pm 0.4 [0.0,3.3] 275	0.0 \pm 0.0 [0.0,3.3] 4	0.2 \pm 0.4 [0.0,1.1] 31	3.4 \pm 4.5 [0.0,19.1] 56	23.9 \pm 5.1 [11.2,33.2] 45	10.4 \pm 6.7 [4.0,17.0] 6
nHT ₉₀₀	0.9 \pm 0.9 [0.0,4.0] 272	4.2 \pm 1.3 [3.5,6.1] 4	1.5 \pm 1.0 [0.0,3.5] 31	4.5 \pm 4.6 [0.0,16.7] 56	27.9 \pm 4.2 [18.9,37.8] 44	24.7 \pm 3.4 [20.6,29.1] 6
nSt ₉₀₀	0.3 \pm 0.5 [0.0,3.3] 282	3.5 \pm 0.6 [3.0,4.3] 4	4.1 \pm 0.9 [2.2,5.2] 12	5.5 \pm 1.2 [2.6,7.6] 54	7.3 \pm 1.7 [4.3,11.4] 42	6.6 \pm 0.7 [6.0,8.0] 6

Tab. 6: Species related to *Lasius niger* and *L. platythorax*

	vostochni (n=7)	niger (n=281)	japonicus (n=104)	chinensis n.sp. (n=41)	platythorax (n=222)	cyperus n.sp. (n=5)
CS [μ m]	826 \pm 49 [770,900] 7	976 \pm 72 [768,1140] 281	950 \pm 79 [732,1119] 104	965 \pm 57 [819,1076] 41	970 \pm 82 [682,1154] 222	894 \pm 45 [852,958] 5
CL/CW ₉₀₀	1.064 \pm 0.019 [1.035,1.083] 7	1.074 \pm 0.016 [1.037,1.137] 278	1.076 \pm 0.016 [1.038,1.117] 104	1.070 \pm 0.016 [1.030,1.094] 41	1.051 \pm 0.015 [1.005,1.094] 222	1.058 \pm 0.014 [1.042,1.072] 5
SL/CS ₉₀₀	0.961 \pm 0.008 [0.948,0.974] 7	0.979 \pm 0.019 [0.909,1.038] 239	1.012 \pm 0.023 [0.962,1.059] 104	1.017 \pm 0.019 [0.966,1.048] 41	0.981 \pm 0.018 [0.938,1.035] 183	0.954 \pm 0.013 [0.938,0.974] 5
MP6/CS ₉₀₀	0.192 \pm 0.003 [0.188,0.199] 7	0.180 \pm 0.009 [0.150,0.201] 144	0.205 \pm 0.010 [0.188,0.236] 59	0.199 \pm 0.009 [0.177,0.220] 41	0.176 \pm 0.007 [0.155,0.190] 111	0.188 \pm 0.008 [0.179,0.199] 5
PoOc/CL ₉₀₀	0.232 \pm 0.002 [0.230,0.235] 7	0.235 \pm 0.009 [0.206,0.258] 144	0.240 \pm 0.007 [0.225,0.255] 59	0.237 \pm 0.009 [0.219,0.255] 41	0.248 \pm 0.008 [0.231,0.269] 111	0.234 \pm 0.007 [0.226,0.244] 5
EYE ₉₀₀	0.252 \pm 0.005 [0.244,0.258] 7	0.245 \pm 0.006 [0.233,0.261] 144	0.244 \pm 0.006 [0.234,0.257] 59	0.240 \pm 0.007 [0.228,0.262] 41	0.236 \pm 0.005 [0.224,0.250] 111	0.229 \pm 0.005 [0.223,0.234] 5
dCIAn/CS ₉₀₀ [%]	4.36 \pm 0.27 [4.12,4.86] 7	4.65 \pm 0.38 [3.69,5.90] 144	5.50 \pm 0.47 [4.42,6.40] 59	5.63 \pm 0.36 [4.63,6.30] 41	4.60 \pm 0.44 [3.60,5.95] 111	4.27 \pm 0.22 [4.06,4.58] 5
MaDe ₉₀₀	no data	8.26 \pm 0.44 [7.9,9.0] 30	8.10 \pm 0.45 [6.9,9.0] 22	8.33 \pm 0.42 [7.9,9.0] 28	8.18 \pm 0.59 [6.9,9.0] 21	8.24 \pm 0.25 [8.0,8.5] 5
sqPDCL ₉₀₀	3.91 \pm 0.41 [3.54,4.58] 7	3.58 \pm 0.32 [2.98,4.90] 276	4.33 \pm 0.37 [3.56,5.58] 104	4.14 \pm 0.35 [3.54,4.82] 41	5.02 \pm 0.56 [3.68,6.72] 222	5.90 \pm 0.56 [5.22,6.74] 5
PLF ₉₀₀	30.4 \pm 3.0 [27.9,36.4] 7	33.6 \pm 2.6 [26.7,36.8] 35	33.5 \pm 2.4 [25.9,36.4] 14	29.9 \pm 2.2 [24.7,33.8] 18	32.7 \pm 2.8 [27.4,36.8] 23	33.4 \pm 1.0 [32.1,34.5] 5
GuHL/CS ₉₀₀	0.098 \pm 0.003 [0.095,0.102] 7	0.094 \pm 0.011 [0.068,0.128] 222	0.116 \pm 0.012 [0.086,0.148] 102	0.121 \pm 0.009 [0.101,0.143] 41	0.135 \pm 0.012 [0.107,0.168] 184	0.138 \pm 0.005 [0.133,0.146] 5
PnHL/CS ₉₀₀	0.128 \pm 0.005 [0.121,0.138] 7	0.123 \pm 0.009 [0.096,0.151] 278	0.150 \pm 0.011 [0.119,0.179] 104	0.159 \pm 0.011 [0.128,0.174] 41	0.162 \pm 0.010 [0.133,0.187] 221	0.172 \pm 0.013 [0.162,0.195] 5
nOcc ₉₀₀	11.7 \pm 3.0 [7.3,14.3] 7	14.5 \pm 2.8 [8.5,23.0] 152	16.3 \pm 3.5 [6.6,26.0] 102	21.6 \pm 3.2 [12.9,31.3] 41	15.8 \pm 3.1 [9.3,23.5] 116	19.4 \pm 3.0 [14.6,22.3] 5
nGen ₉₀₀	4.7 \pm 3.2 [1.7,9.2] 7	6.4 \pm 1.6 [1.3,11.9] 147	7.8 \pm 3.1 [2.5,14.7] 34	11.9 \pm 2.9 [6.7,18.0] 41	8.2 \pm 3.2 [1.5,16.6] 112	13.2 \pm 5.2 [7.0,19.2] 5
nGu ₉₀₀	6.5 \pm 3.6 [3.8,13.7] 7	8.2 \pm 2.3 [3.1,15.0] 154	8.5 \pm 2.7 [4.0,16.7] 92	17.0 \pm 3.5 [8.9,24.0] 41	11.6 \pm 3.9 [1.5,24.3] 116	17.3 \pm 2.3 [14.6,19.2] 5
nSc ₉₀₀	6.1 \pm 3.9 [2.1,12.0] 7	14.6 \pm 3.0 [7.0,23.2] 239	15.0 \pm 4.0 [4.3,26.7] 104	26.2 \pm 6.0 [17.8,40.3] 41	20.0 \pm 4.4 [11.5,36.2] 183	12.2 \pm 2.1 [10.0,14.4] 5
nHT ₉₀₀	14.3 \pm 7.1 [6.3,26.0] 7	15.0 \pm 2.9 [6.8,23.0] 239	15.6 \pm 3.6 [7.2,27.7] 104	21.1 \pm 3.2 [13.9,26.9] 41	20.1 \pm 3.5 [10.9,31.3] 182	27.5 \pm 6.6 [21.2,35.9] 5
nSt ₉₀₀	8.0 \pm 2.1 [5.2,10.7] 7	4.6 \pm 1.1 [2.2,7.9] 154	2.9 \pm 1.1 [0.0,5.9] 59	5.5 \pm 1.2 [3.2,7.6] 41	3.7 \pm 1.0 [0.8,6.5] 116	6.1 \pm 0.8 [4.9,6.8] 5

Tab. 7: Westpalaearctic species related to *Lasius grandis*

	<i>balearicus</i> (n=6)	<i>cinereus</i> (n=58)	<i>grandis</i> (n=198)	<i>mauretanicus</i> n.sp. (n=60)	<i>persicus</i> n.sp. (n=25)
CS [μ m]	847 \pm 35 [822,899] 4	860 \pm 68 [683,1024] 58	984 \pm 80 [744,1241] 198	943 \pm 67 [717,1059] 60	908 \pm 102 [703,1075] 25
CL/CW ₉₀₀	1.094 \pm 0.012 [1.049,1.122] 6	1.091 \pm 0.018 [1.049,1.129] 58	1.095 \pm 0.017 [1.051,1.160] 198	1.086 \pm 0.015 [1.052,1.121] 59	1.064 \pm 0.014 [1.041,1.089] 25
SL/CS ₉₀₀	1.011 \pm 0.008 [1.004,1.022] 4	1.012 \pm 0.021 [0.959,1.046] 58	1.037 \pm 0.020 [0.989,1.081] 198	1.035 \pm 0.015 [0.996,1.066] 59	1.030 \pm 0.018 [0.998,1.060] 25
MP6/CS ₉₀₀	0.186 \pm 0.005 [0.181,0.190] 3	0.197 \pm 0.008 [0.177,0.213] 58	0.208 \pm 0.010 [0.184,0.233] 124	0.224 \pm 0.010 [0.196,0.257] 53	0.192 \pm 0.008 [0.173,0.204] 25
PoOc/CL ₉₀₀	0.234 \pm 0.002 [0.233,0.236] 3	0.219 \pm 0.008 [0.198,0.236] 58	0.222 \pm 0.008 [0.200,0.245] 151	0.222 \pm 0.006 [0.209,0.236] 54	0.239 \pm 0.008 [0.229,0.261] 25
EYE ₉₀₀	0.236 \pm 0.003 [0.233,0.238] 3	0.233 \pm 0.006 [0.223,0.246] 58	0.239 \pm 0.006 [0.227,0.254] 151	0.242 \pm 0.005 [0.228,0.252] 54	0.238 \pm 0.005 [0.230,0.254] 25
dCIAn/CS ₉₀₀ [%]	5.43 \pm 0.15 [5.30,5.39] 3	5.01 \pm 0.45 [4.06,6.06] 58	5.01 \pm 0.51 [3.97,6.30] 151	5.41 \pm 0.44 [4.38,6.33] 54	5.33 \pm 0.34 [4.71,5.94] 25
MaDe ₉₀₀	8.60 \pm 0.10 [8.5,8.7] 3	8.69 \pm 0.57 [8.0,9.5] 8	8.62 \pm 0.44 [7.9,9.1] 19	8.55 \pm 0.49 [8.0,9.0] 10	8.70 \pm 0.41 [8.0,9.0] 6
sqPDCL ₉₀₀	5.00 \pm 0.31 [4.58,5.26] 4	4.37 \pm 0.48 [3.55,5.45] 58	4.53 \pm 0.49 [3.51,6.66] 197	3.92 \pm 0.39 [3.24,5.20] 60	5.11 \pm 0.46 [4.47,6.58] 25
PLF ₉₀₀	23.0 \pm 1.4 [21.5,24.2] 3	23.5 \pm 1.8 [19.6,27.4] 58	27.2 \pm 1.8 [22.3,33.2] 94	27.5 \pm 1.9 [23.8,33.1] 56	26.7 \pm 1.9 [22.9,29.8] 25
GuHL/CS ₉₀₀	0.135 \pm 0.010 [0.129,0.146] 3	0.116 \pm 0.015 [0.093,0.159] 58	0.125 \pm 0.014 [0.080,0.157] 198	0.123 \pm 0.013 [0.078,0.165] 60	0.140 \pm 0.009 [0.124,0.159] 25
PnHL/CS ₉₀₀	0.133 \pm 0.008 [0.127,0.142] 3	0.146 \pm 0.012 [0.123,0.177] 58	0.145 \pm 0.013 [0.107,0.183] 194	0.151 \pm 0.012 [0.119,0.184] 60	0.161 \pm 0.015 [0.127,0.184] 25
nOcc ₉₀₀	21.8 \pm 0.8 [21.0,22.5] 3	16.9 \pm 3.2 [9.9,25.2] 58	15.7 \pm 3.8 [6.6,27.2] 151	22.6 \pm 5.7 [13.6,34.0] 55	13.7 \pm 2.7 [8.2,18.2] 25
nGen ₉₀₀	14.5 \pm 2.2 [13.0,17.0] 3	8.0 \pm 2.7 [2.4,13.8] 58	7.3 \pm 2.1 [3.4,13.4] 151	12.8 \pm 2.7 [7.8,19.5] 54	9.8 \pm 3.0 [2.5,14.8] 25
nGu ₉₀₀	17.8 \pm 1.2 [16.5,18.5] 3	13.2 \pm 4.9 [5.4,24.3] 58	9.8 \pm 3.3 [2.3,19.0] 151	16.3 \pm 3.6 [7.4,26.9] 54	11.7 \pm 4.2 [3.4,20.4] 25
nSc ₉₀₀	29.4 \pm 1.9 [27.3,31.0] 3	22.6 \pm 5.5 [2.2,33.6] 58	17.5 \pm 6.3 [5.4,35.7] 198	21.4 \pm 5.6 [7.4,32.4] 60	23.3 \pm 5.9 [9.7,32.6] 25
nHT ₉₀₀	25.3 \pm 2.5 [22.5,27.0] 3	20.1 \pm 4.1 [10.0,30.5] 58	19.4 \pm 4.6 [2.2,33.1] 198	22.5 \pm 4.0 [14.9,33.3] 60	20.6 \pm 4.5 [10.9,31.8] 25
nSt ₉₀₀	7.6 \pm 1.9 [5.5,8.4] 3	4.7 \pm 1.2 [2.4,8.0] 58	4.2 \pm 1.0 [2.3,8.4] 151	7.6 \pm 1.7 [4.3,11.4] 54	3.8 \pm 0.9 [2.4,6.5] 25

Tab. 8: Westpalaearctic species related to *Lasius emarginatus*

	<i>emarginatus</i> (n=154)	<i>illyricus</i> (n=94)	<i>maltaeus</i> n.sp. (n=15)	<i>tebessae</i> (n=21)	<i>tunisius</i> n.sp. (n=6)
CS [μm]	962 \pm 85 [740,1138] 154	991 \pm 72 [824,1144] 94	948 \pm 77 [828,1060] 15	966 \pm 43 [892,1030] 21	994 \pm 39 [946,1044] 6
CL/CW ₉₀₀	1.085 \pm 0.015 [1.040,1.119] 154	1.082 \pm 0.016 [1.044,1.124] 94	1.106 \pm 0.011 [1.087,1.122] 15	1.090 \pm 0.009 [1.074,1.104] 21	1.076 \pm 0.017 [1.047,1.090] 6
SL/CS ₉₀₀	1.067 \pm 0.023 [0.998,1.129] 154	1.073 \pm 0.024 [0.996,1.118] 94	1.067 \pm 0.007 [1.058,1.082] 15	1.037 \pm 0.022 [1.003,1.081] 21	1.018 \pm 0.016 [0.989,1.036] 6
MP6/CS ₉₀₀	0.221 \pm 0.009 [0.200,0.246] 94	0.217 \pm 0.014 [0.190,0.235] 14	0.241 \pm 0.007 [0.227,0.257] 15	0.232 \pm 0.008 [0.215,0.249] 21	0.230 \pm 0.004 [0.223,0.234] 6
PoOc/CL ₉₀₀	0.217 \pm 0.007 [0.194,0.240] 150	0.223 \pm 0.007 [0.207,0.238] 94	0.228 \pm 0.008 [0.216,0.244] 15	0.218 \pm 0.006 [0.203,0.229] 21	0.238 \pm 0.005 [0.229,0.242] 6
EYE ₉₀₀	0.253 \pm 0.005 [0.242,0.266] 150	0.250 \pm 0.005 [0.238,0.263] 94	0.247 \pm 0.004 [0.238,0.253] 15	0.249 \pm 0.006 [0.237,0.258] 21	0.253 \pm 0.004 [0.247,0.258] 6
dCIAn/CS ₉₀₀ [%]	5.38 \pm 0.48 [3.79,6.93] 150	5.45 \pm 0.45 [4.24,6.56] 94	5.20 \pm 0.33 [4.81,5.85] 15	5.201 \pm 0.64 [4.01,6.45] 21	4.41 \pm 0.15 [4.22,4.65] 6
MaDe ₉₀₀	8.76 \pm 0.45 [7.5,10.0] 65	8.58 \pm 0.58 [7.7,9.9] 38	8.44 \pm 0.48 [7.9,8.9] 5	8.13 \pm 0.23 [7.9,8.5] 7	8.00 \pm 0.00 [8.0,8.0] 2
sqPDCL ₉₀₀	5.14 \pm 0.61 [4.04,6.92] 154	5.71 \pm 0.80 [4.24,8.11] 94	5.11 \pm 0.52 [4.40,6.07] 15	4.07 \pm 0.38 [3.52,4.97] 21	5.01 \pm 0.17 [4.86,5.35] 6
PLF ₉₀₀	24.8 \pm 2.5 [19.6,33.0] 54	23.9 \pm 3.2 [18.9,29.4] 25	24.6 \pm 1.5 [22.0,27.9] 15	27.6 \pm 1.5 [25.2,32.4] 21	19.0 \pm 0.5 [18.1,19.8] 6
GuHL/CS ₉₀₀	0.126 \pm 0.010 [0.098,0.152] 154	0.124 \pm 0.011 [0.100,0.150] 94	0.120 \pm 0.010 [0.104,0.139] 15	0.136 \pm 0.012 [0.114,0.161] 21	0.123 \pm 0.004 [0.118,0.128] 6
PnHL/CS ₉₀₀	0.139 \pm 0.011 [0.099,0.171] 154	0.137 \pm 0.010 [0.106,0.159] 94	0.136 \pm 0.009 [0.119,0.147] 15	0.155 \pm 0.006 [0.143,0.166] 21	0.112 \pm 0.003 [0.108,0.117] 6
nOcc ₉₀₀	12.2 \pm 3.3 [5.2,21.1] 150	7.8 \pm 2.0 [3.2,12.8] 94	18.2 \pm 2.5 [12.4,22.9] 15	11.6 \pm 2.8 [4.8,15.1] 21	6.4 \pm 1.5 [4.7,7.9] 6
nGen ₉₀₀	6.5 \pm 1.9 [2.5,15.0] 150	4.1 \pm 1.2 [1.9,8.4] 94	13.0 \pm 2.1 [9.1,16.0] 15	6.3 \pm 2.1 [2.5,9.7] 21	3.1 \pm 0.7 [2.3,4.1] 6
nGu ₉₀₀	6.8 \pm 2.3 [0.9,13.2] 150	4.1 \pm 1.3 [1.2,7.9] 94	17.4 \pm 4.0 [10.6,25.8] 15	7.0 \pm 2.6 [3.3,11.9] 21	4.0 \pm 0.7 [3.0,5.1] 6
nSc ₉₀₀	10.4 \pm 6.0 [0.0,32.7] 154	2.1 \pm 2.8 [0.0,12.8] 94	30.1 \pm 6.1 [21.5,43.6] 15	8.8 \pm 4.6 [2.3,16.1] 21	0.0 \pm 0.0 [0.0,0.0] 6
nHT ₉₀₀	18.1 \pm 4.5 [6.8,30.3] 154	7.4 \pm 2.5 [2.1,13.0] 94	26.9 \pm 5.6 [19.4,37.9] 15	14.7 \pm 4.3 [9.0,22.6] 21	0.0 \pm 0.0 [0.0,0.0] 6
nSt ₉₀₀	3.8 \pm 0.9 [1.8,6.3] 150	2.3 \pm 1.0 [0.4,5.5] 94	3.2 \pm 0.8 [2.2,4.9] 15	3.6 \pm 0.8 [1.7,5.1] 21	4.1 \pm 0.5 [3.5,4.9] 6

Tab. 9: Himalayan and Tibetan species

	<i>magnus</i> (n=60)	<i>lawarai</i> (n=29)	<i>wittmeri</i> (n=12)	<i>hirsutus</i> (n=6)	<i>schaeferi</i> (n=4)	<i>obscuratus</i> (n=167)
CS [μm]	1153 \pm 108 [908,1416] 60	804 \pm 56 [677, 908] 29	830 \pm 36 [761, 894] 12	919 \pm 71 [833, 992] 6	817 \pm 22 [786, 835] 4	840 \pm 64 [640, 989] 167
CL/CW ₉₀₀	1.138 \pm 0.028 [1.077,1.196] 60	1.086 \pm 0.022 [1.042,1.127] 29	1.071 \pm 0.011 [1.053,1.094] 12	1.082 \pm 0.019 [1.052,1.101] 6	1.092 \pm 0.006 [1.086,1.100] 4	1.065 \pm 0.016 [1.017,1.112] 112
SL/CS ₉₀₀	1.034 \pm 0.022 [0.997,1.089] 60	0.948 \pm 0.028 [0.871,0.998] 29	0.979 \pm 0.014 [0.954,0.998] 12	1.022 \pm 0.009 [1.011,1.034] 6	0.966 \pm 0.010 [0.960,0.981] 4	0.956 \pm 0.019 [0.917,1.012] 167
MP6/CS ₉₀₀	0.191 \pm 0.013 [0.171,0.221] 10	0.173 \pm 0.009 [0.160,0.192] 12	0.182 \pm 0.015 [0.157,0.201] 11	0.175 \pm 0.005 [0.168,0.181] 6	0.176 \pm 0.001 [0.175,0.177] 4	0.173 \pm 0.011 [0.149,0.201] 132
PoOc/CL ₉₀₀	0.253 \pm 0.010 [0.239,0.267] 10	0.261 \pm 0.008 [0.247,0.278] 13	0.241 \pm 0.009 [0.227,0.252] 12	0.236 \pm 0.004 [0.232,0.244] 6	0.240 \pm 0.003 [0.237,0.244] 5	0.234 \pm 0.009 [0.212,0.256] 133
EYE ₉₀₀	0.235 \pm 0.005 [0.229,0.245] 10	0.214 \pm 0.009 [0.202,0.236] 13	0.240 \pm 0.004 [0.232,0.248] 12	0.239 \pm 0.002 [0.235,0.241] 6	0.250 \pm 0.003 [0.247,0.252] 5	0.244 \pm 0.008 [0.225,0.266] 70
dClAn/CS ₉₀₀ [%]	4.90 \pm 0.18 [4.61,5.13] 10	4.12 \pm 0.56 [3.47,5.38] 13	3.60 \pm 0.31 [3.18,4.10] 12	4.52 \pm 0.26 [4.17,4.93] 6	3.65 \pm 0.51 [3.27,4.01] 4	4.28 \pm 0.40 [3.57,5.16] 133
MaDe ₉₀₀	7.11 \pm 0.60 [6.0,7.8] 8	8.72 \pm 0.69 [8.0,10.1] 13	8.50 \pm 0.50 [8.0,9.0] 5	8.75 \pm 0.35 [8.5, 9.0] 2	8.0 \pm 0.00 [8.0,8.0] 2	8.37 \pm 0.49 [7.0,9.1] 83
sqPDCL ₉₀₀	7.24 \pm 0.94 [5.62,9.41] 60	4.36 \pm 0.47 [3.72,5.92] 29	4.47 \pm 0.28 [4.03,4.94] 12	5.27 \pm 0.28 [4.94,5.61] 6	4.62 \pm 0.54 [4.23,5.00] 4	4.35 \pm 0.42 [3.37,5.56] 167
PLF ₉₀₀	27.8 \pm 2.6 [24.2,31.6] 11	36.1 \pm 2.2 [32.1,39.7] 15	38.8 \pm 2.2 [35.2,43.5] 12	39.2 \pm 2.1 [35.3,41.3] 6	29.6 \pm 0.3 [29.3,30.0] 4	33.1 \pm 3.0 [28.0,40.7] 48
GuHL/CS ₉₀₀	0.080 \pm 0.019 [0.032,0.124] 60	0.109 \pm 0.014 [0.082,0.136] 29	0.120 \pm 0.012 [0.102,0.142] 12	0.154 \pm 0.010 [0.145,0.169] 6	0.116 \pm 0.007 [0.112,0.127] 4	0.091 \pm 0.015 [0.000,0.143] 167
PnHL/CS ₉₀₀	0.119 \pm 0.011 [0.089,0.142] 60	0.152 \pm 0.012 [0.133,0.186] 29	0.158 \pm 0.009 [0.134,0.169] 12	0.138 \pm 0.006 [0.126,0.143] 6	0.146 \pm 0.015 [0.126,0.162] 4	0.140 \pm 0.015 [0.089,0.177] 167
nOcc ₉₀₀	10.0 \pm 3.1 [3.4,17.6] 60	8.6 \pm 3.4 [3.3,15.9] 29	11.1 \pm 2.2 [7.8,15.0] 12	21.3 \pm 2.9 [16.5,24.1] 6	8.7 \pm 2.8 [5.5,12.3] 4	8.3 \pm 2.5 [1.6,15.2] 167
nGen ₉₀₀	1.7 \pm 1.4 [0.0,4.1] 10	2.7 \pm 1.7 [0.0,5.5] 13	6.9 \pm 2.9 [2.6,12.1] 12	19.9 \pm 2.8 [16.5,24.1] 6	2.6 \pm 1.2 [1.1,3.9] 4	1.4 \pm 1.3 [0.0,6.2] 164
nGu ₉₀₀	3.4 \pm 2.2 [0.4,10.8] 60	3.6 \pm 1.5 [1.3,7.2] 29	8.7 \pm 3.6 [3.5,14.8] 12	19.2 \pm 4.1 [14.4,25.1] 6	5.1 \pm 0.7 [4.4, 5.9] 4	2.7 \pm 1.2 [0.0, 6.9] 167
nSc ₉₀₀	14.7 \pm 4.3 [7.2,27.0] 60	10.7 \pm 7.1 [0.0,27.7] 29	12.9 \pm 5.0 [4.1,23.4] 12	30.4 \pm 4.8 [23.7,37.1] 6	4.4 \pm 1.8 [1.7,5.8] 4	0.7 \pm 1.3 [0.0,8.5] 167
nHT ₉₀₀	16.7 \pm 3.7 [8.7,23.7] 60	7.8 \pm 3.6 [1.4,15.9] 29	17.2 \pm 3.7 [9.7,22.0] 12	31.2 \pm 3.7 [26.5,35.7] 6	12.7 \pm 0.5 [12.0,13.2] 4	2.8 \pm 2.0 [0.0, 9.8] 167
nSt ₉₀₀	2.4 \pm 0.5 [1.6,3.1] 10	4.9 \pm 1.7 [1.8, 8.5] 14	7.9 \pm 1.6 [5.4,10.8] 12	10.0 \pm 2.0 [7.0,12.4] 6	4.9 \pm 0.7 [4.0, 5.7] 4	2.6 \pm 1.3 [0.0, 7.1] 164

Tab. 10: Chinese-Korean species not related to *L. japonicus*

	<i>coloratus</i> (n=36)	<i>sichuense</i> n.sp. (n=29)	<i>kabaki</i> n.sp. (n=12)	<i>longipalpus</i> n.sp. (n=72)	<i>koreanus</i> (n=9)
CS [μ m]	985 \pm 71 [750,1106] 36	1005 \pm 96 [744,1146] 29	921 \pm 44 [858,1013] 12	888 \pm 54 [746, 975] 72	819 \pm 41 [759, 902] 9
CL/CW ₉₀₀	1.083 \pm 0.014 [1.063,1.126] 36	1.085 \pm 0.024 [1.039,1.126] 29	1.093 \pm 0.010 [1.083,1.110] 12	1.086 \pm 0.014 [1.043,1.113] 72	1.085 \pm 0.014 [1.071,1.109] 9
SL/CS ₉₀₀	1.029 \pm 0.022 [0.980,1.074] 36	0.999 \pm 0.026 [0.938,1.051] 29	0.989 \pm 0.006 [0.963,1.028] 12	1.019 \pm 0.020 [0.964,1.075] 72	0.956 \pm 0.026 [0.921,0.990] 9
MP6/CS ₉₀₀	0.209 \pm 0.013 [0.186,0.248] 34	0.200 \pm 0.015 [0.178,0.228] 29	0.178 \pm 0.006 [0.167,0.187] 12	0.200 \pm 0.014 [0.176,0.239] 68	0.201 \pm 0.008 [0.194,0.211] 6
PoOc/CL ₉₀₀	0.250 \pm 0.007 [0.236,0.263] 34	0.250 \pm 0.007 [0.235,0.261] 29	0.241 \pm 0.007 [0.230,0.253] 12	0.238 \pm 0.007 [0.224,0.257] 68	0.236 \pm 0.011 [0.221,0.253] 7
EYE ₉₀₀	0.230 \pm 0.004 [0.224,0.241] 34	0.232 \pm 0.006 [0.221,0.245] 29	0.245 \pm 0.004 [0.238,0.251] 12	0.250 \pm 0.005 [0.242,0.264] 68	0.252 \pm 0.006 [0.242,0.261] 6
dCIAn/CS ₉₀₀ [%]	5.23 \pm 0.52 [4.12,5.98] 34	4.90 \pm 0.53 [3.79,5.76] 29	5.04 \pm 0.35 [4.18,5.58] 12	4.47 \pm 0.37 [3.79,5.27] 68	4.38 \pm 0.26 [4.02,4.84] 6
MaDe ₉₀₀	8.28 \pm 0.44 [7.0,9.0] 23	7.93 \pm 0.37 [7.0,8.8] 13	8.67 \pm 0.47 [8.0, 9.0] 7	8.08 \pm 0.44 [7.0,9.0] 34	8.12 \pm 0.24 [8.0,8.6] 6
sqPDCL ₉₀₀	4.69 \pm 0.51 [3.53,5.90] 36	4.23 \pm 0.54 [3.31,5.25] 29	5.80 \pm 0.30 [5.32,6.18] 12	5.04 \pm 0.46 [4.17,5.99] 72	4.57 \pm 0.55 [3.90,5.61] 9
PLF ₉₀₀	29.5 \pm 2.5 [26.6,35.8] 16	29.1 \pm 2.0 [24.9,32.9] 12	28.9 \pm 2.2 [25.1,32.2] 8	28.6 \pm 2.5 [23.0,34.2] 42	27.0 \pm 1.6 [25.2,28.9] 6
GuHL/CS ₉₀₀	0.102 \pm 0.014 [0.077,0.148] 36	0.084 \pm 0.018 [0.000,0.105] 29	0.106 \pm 0.014 [0.070,0.121] 12	0.088 \pm 0.017 [0.000,0.124] 72	0.103 \pm 0.012 [0.084,0.121] 9
PnHL/CS ₉₀₀	0.156 \pm 0.019 [0.123,0.193] 36	0.135 \pm 0.010 [0.114,0.153] 29	0.160 \pm 0.008 [0.148,0.172] 12	0.130 \pm 0.016 [0.084,0.177] 72	0.137 \pm 0.008 [0.129,0.151] 8
nOcc ₉₀₀	14.6 \pm 2.9 [9.1,20.9] 36	10.2 \pm 2.9 [5.1,15.7] 29	11.5 \pm 3.3 [6.8,18.4] 12	7.1 \pm 2.8 [1.5,14.5] 72	11.9 \pm 3.5 [9.0,19.3] 9
nGen ₉₀₀	5.5 \pm 2.3 [0.8,10.1] 34	2.6 \pm 0.9 [0.7,4.3] 29	7.6 \pm 2.2 [5.1,12.7] 12	2.1 \pm 2.0 [0.0,7.7] 72	1.1 \pm 1.0 [0.0,2.3] 6
nGu ₉₀₀	6.2 \pm 1.4 [3.6,8.9] 36	2.9 \pm 1.4 [0.0,5.3] 29	5.7 \pm 2.8 [2.4,10.4] 12	2.4 \pm 1.2 [0.0,5.7] 72	4.9 \pm 1.6 [2.3, 7.7] 9
nSc ₉₀₀	24.6 \pm 5.7 [14.0,36.3] 36	9.4 \pm 5.3 [1.3,20.9] 29	9.6 \pm 6.4 [2.5,22.9] 12	2.8 \pm 3.7 [0.0,20.1] 72	2.6 \pm 3.0 [0.0,8.3] 9
nHT ₉₀₀	22.0 \pm 3.7 [15.1,32.1] 35	12.1 \pm 4.5 [4.6,21.4] 29	14.4 \pm 2.2 [10.2,18.2] 12	4.2 \pm 4.0 [0.0,15.6] 72	13.0 \pm 5.1 [3.3,19.4] 9
nSt ₉₀₀	2.6 \pm 1.5 [0.4,5.9] 34	2.9 \pm 1.5 [0.0,5.1] 29	4.9 \pm 0.6 [3.8, 6.3] 12	0.4 \pm 0.6 [0.0,2.3] 72	4.8 \pm 2.6 [0.0, 7.1] 6

Tab. 11: Japanese species

	<i>longipalpus</i> n.sp. (n=72)	<i>japonicus</i> (n=104)	<i>productus</i> (n=16)	<i>hayashi</i> (n=29)	<i>sakagamii</i> (n=19)
CS [μ m]	888 \pm 54 [746, 975] 72	950 \pm 79 [732, 1119] 104	1050 \pm 75 [903, 1121] 16	994 \pm 34 [908, 1050] 29	887 \pm 46 [794, 958] 19
CL/CW ₉₀₀	1.086 \pm 0.014 [1.043, 1.113] 72	1.076 \pm 0.016 [1.038, 1.117] 104	1.139 \pm 0.017 [1.117, 1.183] 16	1.049 \pm 0.012 [1.028, 1.071] 29	1.071 \pm 0.016 [1.053, 1.111] 19
SL/CS ₉₀₀	1.019 \pm 0.020 [0.964, 1.075] 72	1.012 \pm 0.023 [0.962, 1.059] 104	1.169 \pm 0.023 [1.125, 1.207] 16	0.978 \pm 0.013 [0.951, 0.999] 29	1.034 \pm 0.025 [0.990, 1.082] 19
MP6/CS ₉₀₀	0.200 \pm 0.014 [0.176, 0.239] 68	0.205 \pm 0.010 [0.188, 0.236] 59	0.293 \pm 0.006 [0.283, 0.300] 6	0.194 \pm 0.007 [0.182, 0.207] 12	0.194 \pm 0.012 [0.173, 0.219] 12
PoOc/CL ₉₀₀	0.238 \pm 0.007 [0.224, 0.257] 68	0.240 \pm 0.007 [0.225, 0.255] 59	0.235 \pm 0.002 [0.232, 0.239] 8	0.241 \pm 0.010 [0.226, 0.257] 13	0.225 \pm 0.007 [0.213, 0.238] 12
EYE ₉₀₀	0.250 \pm 0.005 [0.242, 0.264] 68	0.244 \pm 0.006 [0.234, 0.257] 59	0.248 \pm 0.003 [0.241, 0.251] 8	0.230 \pm 0.005 [0.224, 0.242] 13	0.244 \pm 0.006 [0.236, 0.255] 12
dClAn/CS ₉₀₀ [%]	4.47 \pm 0.37 [3.79, 5.27] 68	5.50 \pm 0.47 [4.42, 6.40] 59	5.65 \pm 0.30 [5.11, 6.06] 8	5.07 \pm 0.57 [4.26, 6.01] 13	5.21 \pm 0.31 [4.76, 5.66] 12
MaDe ₉₀₀	8.08 \pm 0.44 [7.0, 9.0] 34	8.10 \pm 0.45 [6.9, 9.0] 22	7.95 \pm 0.07 [7.9, 8.0] 2	7.95 \pm 0.06 [7.9, 8.0] 4	8.52 \pm 0.48 [8.0, 9.0] 9
sqPDCL ₉₀₀	5.04 \pm 0.46 [4.17, 5.99] 72	4.33 \pm 0.37 [3.56, 5.58] 104	4.35 \pm 0.29 [3.64, 4.74] 16	4.59 \pm 0.43 [3.91, 5.53] 29	3.78 \pm 0.26 [3.23, 4.40] 19
PLF ₉₀₀	28.6 \pm 2.5 [23.0, 34.2] 42	33.5 \pm 2.4 [25.9, 36.4] 14	28.8 \pm 1.7 [27.9, 31.4] 4	28.4 \pm 1.6 [26.3, 31.5] 16	33.0 \pm 2.3 [28.2, 37.6] 15
GuHL/CS ₉₀₀	0.088 \pm 0.017 [0.000, 0.124] 72	0.116 \pm 0.012 [0.086, 0.148] 102	0.117 \pm 0.015 [0.094, 0.148] 15	0.114 \pm 0.012 [0.089, 0.135] 28	0.110 \pm 0.012 [0.085, 0.127] 18
PnHL/CS ₉₀₀	0.130 \pm 0.016 [0.084, 0.177] 72	0.150 \pm 0.011 [0.119, 0.179] 104	0.134 \pm 0.009 [0.116, 0.146] 16	0.154 \pm 0.009 [0.136, 0.172] 29	0.157 \pm 0.009 [0.142, 0.176] 19
nOcc ₉₀₀	7.1 \pm 2.8 [1.5, 14.5] 72	16.3 \pm 3.5 [6.6, 26.0] 102	9.8 \pm 2.3 [6.5, 14.9] 16	13.1 \pm 4.2 [4.1, 22.3] 29	23.4 \pm 3.3 [14.7, 27.6] 19
nGen ₉₀₀	2.1 \pm 2.0 [0.0, 7.7] 72	7.8 \pm 3.1 [2.5, 14.7] 34	3.2 \pm 1.1 [2.4, 5.2] 5	5.1 \pm 2.9 [0.9, 10.1] 13	16.2 \pm 2.4 [10.9, 19.7] 12
nGu ₉₀₀	2.4 \pm 1.2 [0.0, 5.7] 72	8.5 \pm 2.7 [4.0, 16.7] 92	3.1 \pm 1.0 [1.6, 4.8] 15	6.4 \pm 2.4 [3.0, 11.9] 27	18.6 \pm 4.4 [12.1, 30.5] 18
nSc ₉₀₀	2.8 \pm 3.7 [0.0, 20.1] 72	15.0 \pm 4.0 [4.3, 26.7] 104	10.2 \pm 5.7 [4.6, 24.0] 16	18.3 \pm 7.0 [7.1, 31.2] 29	32.0 \pm 5.1 [23.3, 42.2] 19
nHT ₉₀₀	4.2 \pm 4.0 [0.0, 15.6] 72	15.6 \pm 3.6 [7.2, 27.7] 104	6.7 \pm 1.8 [4.3, 11.0] 16	17.4 \pm 4.0 [1.7, 23.3] 29	29.8 \pm 4.9 [21.8, 40.8] 19
nSt ₉₀₀	0.4 \pm 0.6 [0.0, 2.3] 72	2.9 \pm 1.1 [0.0, 5.9] 59	1.9 \pm 0.6 [1.2, 3.0] 8	4.9 \pm 0.9 [3.3, 7.3] 13	12.6 \pm 1.8 [10.0, 15.3] 12