

## A taxonomic revision of the members of the *Camponotus lateralis* species group (Hymenoptera: Formicidae) from Europe, Asia Minor and Caucasia

Bernhard Seifert

Senckenberg Museum of Natural History Görlitz, Am Museum 1, 02826 Görlitz, Germany  
E-mail: bernhard.seifert@senckenberg.de

Received 11 December 2018 | Accepted 7 March 2019

Published online at [www.soil-organisms.de](http://www.soil-organisms.de) 1 April 2019 | Printed version 15 April 2019

DOI 10.25674/so-91-1-02

### Abstract

A taxonomic revision of the *Camponotus lateralis* group based on methods of Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT) is presented considering the Palaearctic region west of 46°E. One size, nine shape and three setae characters were recorded in a total of 260 samples with 587 worker individuals. Species hypotheses were formed by three exploratory data analyses: the hierarchical methods NC-Ward and NC-part.hclust and the iterative vector-quantization method NC-part.kmeans. Samples with classifications disagreeing among the methods were finally allocated to a particular cluster by wild-card runs in a controlling linear discriminant analysis.

Results: The taxonomy of the *C. lateralis* group is complicated by the superimposition of three types of intraspecific polymorphism: (a) minor vs. major worker size dimorphism, (b) polymorphism of pigmentation pattern and (c), in at least one species, extreme dimorphism of shape and setae characters independent from size. A two-step cluster analysis and principal component analysis considering head and scape length indices and absolute size resulted in fully coincident separations of minors and majors with a general rule applicable for a collective of four long-headed and another rule applicable for a collective of four short-headed species. The identity of 42 taxa was evaluated on the basis of original descriptions and type specimens to exclude a junior synonymy of the taxon introduced here. A key is provided for nine valid species occurring in the area of Europe, Asia Minor and Caucasus: *Camponotus lateralis* (Olivier 1792), *C. piceus* (Leach 1825), *C. atricolor* (Nylander 1849), *C. dalmaticus* (Nylander 1849), *C. candiotes* Emery 1894, *C. rebecca* Forel 1913, *C. anatolicus* Karaman & Aktac 2013, *C. honaziensis* Karaman & Aktac 2013 and *C. heidrunvogtae* sp. nov. The latter is restricted to a 120 000 km<sup>2</sup> area of the Balkans. *Camponotus ebneri* Finzi 1930 (stat. nov.) from Lebanon was raised to species level and is considered as sister species of *C. dalmaticus*. Seven taxa from North Africa, the Canaries and Middle East, showing a lot of similarities with species of the *C. lateralis* group, were excluded to represent synonyms of one of the ten aforementioned valid species. Further, seven *Camponotus* taxa from Europe, Asia Minor and the Middle East were clearly excluded from the *C. lateralis* group. *Camponotus melanogastes* (Latreille 1802), *Camponotus axillaris* (Spinola 1808), *C. merula* (Losana 1834) (syn. nov.), *C. armouri* Wheeler 1926, *C. lateralis balearis* Santschi 1929 (syn. nov.), *C. lateralis purius* Santschi 1929 (syn. nov.) and *C. kosswigi* Donisthorpe 1950 are synonymized under *C. lateralis*. *Camponotus foveolata* (Mayr 1853), *C. ebeninus* Emery 1869 (syn. nov.), *C. piceus* st. *spissinodis* var. *dusmeti* Santschi 1932 and *C. figaro* Collingwood & Yarrow 1969 (syn. nov.) were synonymized under *C. piceus*, *C. lateralis* var. *cypriidis* Santschi 1939 (syn. nov.) under *C. rebecca* and *C. lateralis* var. *rectus* Forel 1892 under *C. atricolor*. Due to insufficient original descriptions and missing types, there is no chance to conclude on either the specific, generic or tribal identity of six taxa supposed by previous authors of belonging to the *C. lateralis* group. These taxa – *Formica bicolor* Latreille 1798, *Formica pallidinervis* Brullé 1833, *Camponotus hemipsila* (Förster 1850), *Camponotus sicheli* Mayr 1866, *Camponotus kiesenwetteri angustatus* Forel 1889, and *Camponotus lateralis* var. *rhodia* Santschi 1934 – were listed under Incertae Sedis.

**Keywords** numeric morphology-based alpha-taxonomy | nest centroid clustering | cryptic species | size dimorphism | color polymorphism

## 1. Introduction

The hyperdiverse ant genus *Camponotus* Mayr 1861 contains a minimum of 1000 species world-wide and was subdivided into the incredible number of 45 subgenera a clear delimitation of which is frequently not given (Bolton 2003). Borowiec (2014) listed 118 species of *Camponotus* for Europe, the Mediterranean Basin and adjacent areas. The subgenus *Myrmentoma* Forel 1912 was characterized by Forel (1912) by nothing more than ‘Thorax echanré. Epinotum cubique.’ and among the species he collected under this subgenus were *Camponotus lateralis* (Olivier 1792) and *C. kiesenwetteri* (Roger 1859). *Camponotus lateralis* was later assigned as type species of *Myrmentoma* (Wheeler 1913, Bolton 2003). It is obvious that the characters named by Forel cannot serve to delimit a subgenus because of morphological transitions to other members of the genus *Camponotus*. This dilemma is not easily resolved but Forel’s characterization provides an idea what we may operationally consider here as a *Camponotus lateralis* group. The Westpalaeartic species of the *C. lateralis* group are size dimorphic, rather small-sized in terms of the genus and are mainly found in warm or hot regions with Mediterranean climate – a more thorough definition of this group is given in the results section of this paper.

During a study attempting to find unambiguous and powerful means to separate some black and cryptic European species of the group, I discovered a cluster of samples from the western Balkans with a rather outstanding morphometry which I supposed to represent an undescribed species. Characters of this species were described by Seifert (2007) under the nomenclatorily invalid code name ‘*Camponotus piceus* sp. 2’. In order to justify the description of only a single new species, I checked in the time since then the identity of 42 Westpalaeartic taxa by evaluation of original descriptions and types. The methodology applied in this taxonomic revision revealed that the picture was additionally complicated by (a) extreme allometries, (b) intraspecific color polymorphism, (c) size dimorphism and (d) size-independent dimorphism of shape and setae characters. This shows how challenging taxonomic work in the hyperdiverse genus *Camponotus* is.

Reasonable order in this chaos and strong reduction of taxonomic error can be achieved by (i) numeric description of any form of phenotypical characters according to clearly defined recording protocols, (ii) hypothesis formation by advanced exploratory data analyses, (iii) checking these hypotheses by supervised data analyses and background data, and (iv) using a practicable and unambiguous species concept. Seifert

(2009) has named this methodological approach Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT). Both this naming and its acronym have not been used by other taxonomists so far but I suggest that we must have an indicative name for a stringent working philosophy which contrasts with the idiosyncratic approaches unfortunately predominating in morphology-based alpha-taxonomy up to the present. This paper will show that application of NUMOBAT in the *Camponotus lateralis* group leads to apparently easier species delimitations than similar approaches in such extremely difficult groups as *Tetramorium* or *Chthonolasius*. Maybe that this impression will turn out later as too optimistic pending the discovery of further cryptic species.

## 2. Material

NUMOBAT data were recorded in a total of 260 samples and 587 worker individuals. The material came from Europe, Asia Minor, Caucasia, immediately adjacent parts of the Middle East and North Africa. The material examined is listed in the individual species treatments in the following sequence and format: site, date in the format yyyy.mm.dd, sample number, [latitude in decimal format, longitude in decimal format, altitude above sea level in meters]. The accuracy of coordinates is proportional to the number of decimal points and ‘xx’ in the sampling date sequence means missing data. In some samples without any direct or derived information on date, the collector is given to allow an approximate conclusion on the time period of collection. Sample or field collection numbers are missing in many samples. The abbreviations of depositories are as follows: BMNH London – Natural History Museum, London, Great Britain; FMN Helsinki – Finnish Museum of Natural History Helsinki, Finland; MCSN Genova – Museo Civico die Storia Naturale Genova, Italy; MCZ Cambridge – Museum of Comparative Zoology Cambridge, Massachusetts, USA; MHN Genève – Muséum d’histoire naturelle de Genève, Genève, Switzerland; NHM Basel – Naturhistorisches Museum, Basel, Switzerland; NHM Wien – Naturhistorisches Museum, Wien, Austria; SMN Görlitz – Senckenberg Museum für Naturkunde Görlitz, Görlitz, Germany

### 3. Methods

#### 3.1 Equipment and measurement procedures

All measurements were made on mounted and dried specimens using a pin-holding stage, permitting full rotations around X, Y and Z axes. A Leica high-performance stereomicroscope M165C equipped with a 2.0 planapochromatic objective (resolution 1050 lines/mm) was used at magnifications of 120-360x. A Schott KL 1500 LCD cold-light source equipped with two flexible, focally mounted light-cables, providing 30°-inclined light from variable azimuth 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 optimum 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 the voltage up and down. A Leica cross-scaled ocular micrometer with 120 graduation marks was used. To avoid the parallax error, its measuring line was constantly kept vertical within the visual field. The mean relative measuring error over all magnifications was 0.3%. To avoid rounding errors, all measurements were recorded in  $\mu\text{m}$ , even for characters for which this precision is impossible. The z-stack photos were made with a Leica Z6 APO photomicroscope, equipped with an objective Planapo 2.0x and a Leica microscope camera DFC420.

#### 3.2 The morphometric characters and removal of allometric variance

Fourteen morphometric characters were investigated in worker ants. In bilaterally developed characters, arithmetic means of both sides were calculated. Setae counts are restricted to setae with distinctly larger diameters compared to long standing pubescence hairs. The counts included pits of seta bases in which remains of broken-off setae could be detected during careful scrutiny at highest resolution.

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

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

**CW** – maximum cephalic width - either across, anterior or posterior of eyes, whichever yields the maximum measurement.

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

**ScI** – Index of scape diameter extension near scape base. SCI is the maximum scape diameter near scape base divided by minimum scape diameter distal of the point with the maximum diameter. The adjustment of scape remains the same in both measurements. ScI has the value 1.0 if no extension is visible.

**MW** – maximum width of mesosoma.

**MGr** – depth of metanotal groove relative to the tangent going through the dorsalmost points of promesonotum and propodeum.

**nMn** – number of standing setae on mesonotum as arithmetic mean of both body sides.

**nPn** – number of standing setae on pronotum as arithmetic mean of both body sides.

**nPr** – number of standing setae on propodeum dorsal of the spiracle as arithmetic mean of both body sides.

**nSc** – unilateral number of standing setae on dorsal plane of scape as mean value of both scapes.

**PeW** – maximum width of petiole.

**PrL** – maximum length of upper propodeal surface from the posterior margin of dorsal plane to the center of the metanotal suture (that may be wide in major workers).

**PrW** – maximum width of dorsal plane of propodeum.

**RipD** – mean distance of fine transverse ripples on dorsal surface of 1<sup>st</sup> gaster tergite given in  $\mu\text{m}$ ; a minimum of  $n = 50$  ripples crossing a longitudinal line length  $S$  has to be counted.  $\text{RipD} = S/n$ . Several shorter line segments should to be added when vaulted or polluted surfaces disturb the count.

In order to reveal in comparative tables which shape variables do really differ between the species independent from body size, a removal of allometric variance (RAV) was performed with the procedure described by Seifert (2008). RAV was calculated by overall functions computed as average of specific functions of 8 species/phenotypes with data for >30 workers available: *C. atricolor*, *C. candiotes*, *C. dalmaticus*, *C. lateralis* morph 1, *C. lateralis* morph 2, *C. heidrunvogtae* sp. nov., *C. piceus* and *C. rebecca*. This overall correction was preferred to enable a direct comparison of data in tables and because pair-specific corrections did not provide significant improvement. RAV was calculated assuming all individuals to have a cephalic size of  $\text{CS} = 1.25$  mm. Due to an expressed minor vs. major dimorphism in all species of the *C. lateralis* group, it was performed in a number of characters as a diphasic function:

For workers with  $\text{CS} \leq 1.25$  mm

$$\text{CL}/\text{CW}_{1.25} = \text{CL}/\text{CW} / (-0.0278 * \text{CS} + 1.1248) * 1.0901$$

$$\text{SL}/\text{CS}_{1.25} = \text{SL}/\text{CS} / (-0.3344 * \text{CS} + 1.3754) * 0.9574$$

$$\begin{aligned} \text{MW/CS}_{1.25} &= \text{MW/CS} / (-0.0577 * \text{CS} + 0.8205) * 0.7484 \\ \text{ScI}_{1.25} &= \text{ScI} / (-0.1508 * \text{CS} + 1.3252) * 1.1367 \\ \text{PrW/CS}_{1.25} &= \text{PrW/CS} / (-0.0091 * \text{CS} + 0.2931) * 0.2818 \\ \text{PrL/CS}_{1.25} &= \text{PrL/CS} / (-0.0718 * \text{CS} + 0.4875) * 0.3977 \\ \text{PeW/CS}_{1.25} &= \text{PeW/CS} / (+0.0193 * \text{CS} + 0.3589) * 0.3831 \\ \text{MGr/CS}_{1.25} &= \text{MGr/CS} / (-0.0164 * \text{CS} + 0.0903) * 0.0680 \end{aligned}$$

For workers with CS > 1.25 mm

$$\begin{aligned} \text{CL/CW}_{1.25} &= \text{CL/CW} / (-0.2162 * \text{CS} + 1.3603) * 1.0901 \\ \text{SL/CS}_{1.25} &= \text{SL/CS} / (-0.3851 * \text{CS} + 1.4387) * 0.9574 \\ \text{MW/CS}_{1.25} &= \text{MW/CS} / (-0.1348 * \text{CS} + 0.9169) * 0.7484 \\ \text{ScI}_{1.25} &= \text{ScI} / (-0.1443 * \text{CS} + 1.3168) * 1.1367 \\ \text{PrW/CS}_{1.25} &= \text{PrW/CS} / (-0.0271 * \text{CS} + 0.3157) * 0.2818 \\ \text{PrL/CS}_{1.25} &= \text{PrL/CS} / (-0.0970 * \text{CS} + 0.5189) * 0.3977 \\ \text{PeW/CS}_{1.25} &= \text{PeW/CS} / (-0.0506 * \text{CS} + 0.4463) * 0.3831 \\ \text{MGr/CS}_{1.25} &= \text{MGr/CS} / (-0.0237 * \text{CS} + 0.0958) * 0.0680 \end{aligned}$$

In the following characters, a monophasic removal of allometric variance was a good approximation over the full size range:

$$\begin{aligned} \text{RipD}_{1.25} &= \text{RipD} / (+0.828 * \text{CS} + 7.653) * 8.689 \\ \text{nSc}_{1.25} &= \text{nSc} / (+6.389 * \text{CS} - 2.842) * 5.02 \\ \text{nMn}_{1.25} &= \text{nMn} / (+5.094 * \text{CS} - 2.434) * 3.93 \\ \text{nPr}_{1.25} &= \text{nPr} / (+5.12 * \text{CS} - 1.109) * 5.294 \\ \text{nPn}_{1.25} &= \text{nPn} / (+5.601 * \text{CS} - 3.986) * 3.02 \end{aligned}$$

Removal of allometric variance led to a very strong reduction of intraspecific variation in a number of shape and setae characters. The mean within-species or within-phenotype coefficient of variation was reduced in 8 data sets each containing more than 30 workers by 74 % in SL/CS, 55 % in CL/CW, 52 % in MW/CS, 43 % in PrL/CS, 32 % in nMn, 27 % in ScI, 21 % in nPr, 13 % in nSc, 11 % in PeW/CS, 11 % in MGr/CS, 7 % in RipD and 6 % in PrW.

### 3.3. NUMOBAT: Explorative and supervised data analyses, classification and statistical testing

Analyzing the NUMOBAT data, four different forms of exploratory data analyses 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), and, accessorially, nonmetric multidimensional scaling combined with iterative vector-quantization NC-NMDS-k-means (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 Pragmatic Species Concept (Seifert 2014) which requires that the mean error of the applied exploratory data analyses 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 overfeeding 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 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 and PCA was 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  $X^2$  tests were run with the SPSS 16.0 software package.



## 4. Results and discussion

### 4.1 Diagnosis of the *Camponotus lateralis* group and within-group relatedness

Attempts to subdivide species groups within the hyperdiverse genus *Camponotus* will often become unsatisfactory the larger the considered geographical range becomes. Characterizing a *Camponotus lateralis* group is done here for pragmatic reasons – i.e., to collect and consider all species potentially being senior synonyms of the new species introduced here. The *Camponotus lateralis* group, as it is operationally circumscribed here, is distributed in the whole Mediterranean area, the South Temperate Zone of Europe as well as in Asia Minor, the Caucasus and Middle East and can be separated from other sympatrically occurring species groups of *Camponotus* by the following character combination:

Comparably small size, CS ranging between 840 and 2190  $\mu\text{m}$ . Dorsal area of propodeum clearly delimited laterally by strong longitudinal edges and appearing in dorsal view as a rectangle or trapezium. The median part of this area is never much higher than the lateral ones – as result a transverse section of upper propodeum is roughly rectangular with a very weakly concave, straight or weakly convex dorsal part. The overall dorsal profile of mesosoma is discontinuous, always more or less depressed between mesonotum and propodeum. In profile view, the dorsal area of propodeum is straight to convex and forms a distinct angle with the caudal declivity which falls abruptly down. Surface of gaster tergites shining, with fine transverse microripples the mean distance of which is 7–12  $\mu\text{m}$  – the microripples represent the edges of a clinker-like surface structure. Pubescence hairs on gaster tergites short and never dense.

A verifiable subdivision of the *C. lateralis* group is not possible by means of morphology but some groups of related species may be separated. A close relatedness of *C. anatolicus* with the two morphs of *C. lateralis* is indicated by sharing of a large microripple distance on gaster tergites, a deep metanotal groove, a short dorsal plane of propodeum and predominance of reddish brown pigmentation on head and mesosoma. A most probable relatedness between *C. piceus*, *C. candiotes*, *C. atricolor* and *C. heidrunvogtae* n.sp. is indicated by sharing a long dorsal propodeal plane, a small microripple distance on gaster tergites, large propodeal setae numbers and predominance of black pigmentation on head and mesosoma. *Camponotus dalmaticus* appears closely related to *C. ebneri* that is only known in the type specimen. The latter is allocated to the *C. dalmaticus* cluster when run as wild-card in an LDA considering all other entities listed in Tabs 2 and 3. It is not possible,

within the considered geographic range, to name next related species for *C. rebecca* and *C. honaziensis*. Similar to the situation in *Temnothorax*, the average geographic ranges of the species of the *C. lateralis* group appear rather small compared to genera such as *Formica*, *Lasius* or *Myrmica*.

### 4.2 Size dimorphism in all species of the *Camponotus lateralis* group

The species of the *Camponotus lateralis* group show a distinct worker size dimorphism. This minor vs. major dimorphism can be clearly shown for all species in which data of > 30 workers were available. This proves true even when pooling several species with differing mean body size in a single data set. *Camponotus atricolor*, *C. candiotes*, *C. heidrunvogtae* n.sp. and *C. piceus*, having a mean head length index of  $\text{CL}/\text{CW}_{1.25} > 1.090$ , were collected in a long-headed species group and *C. dalmaticus*, *C. lateralis* morph 1, *C. lateralis* morph 2 and *C. rebecca*, having a mean head length index of  $\text{CL}/\text{CW}_{1.25} < 1.086$ , were pooled in a short-headed species group. Using the main characters of head morphometry – i.e., absolute size CS, primary head length index  $\text{CL}/\text{CW}$  and primary scape length index  $\text{SL}/\text{CS}$ , a two-step cluster analysis (TSCA) distinguished two clusters (the minors and majors) within 285 workers of the long-headed group. The first factor of a principal component analysis (PCA), describing 92.5% of total variance, was 100% coincident with this clustering. The grouping proposed by the TSCA and PCA was confirmed by a LDA with an error rate of 0% (Fig. 1). Likewise, the TSCA distinguished two clusters within 250 workers of the short-headed species group which was fully in line with the first factor of PCA that described 93.3% of total variance. This grouping was confirmed by a LDA with an error rate of 0.4% (Fig. 2).

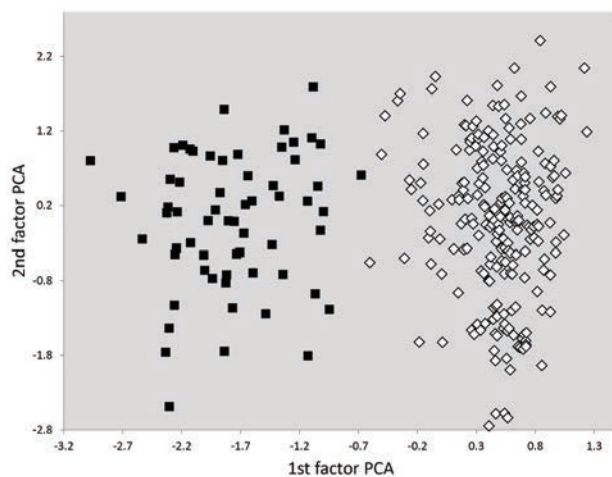
### 4.3 Taxonomic errors due to intraspecific polymorphism of pigmentation, shape and setae characters

The *Camponotus lateralis* group and other members of the subgenus *Myrmentoma* show a number of polymorphic traits which may cause taxonomic confusion. The first issue is the distribution of reddish versus blackish pigmentation on mesosoma. Tab. 1 shows a number of species with a pigmentation pattern that can be assigned to three rather distinct types. There are specimens without significant reddish pigmentation on whole mesosoma (type 1), specimens having only the pronotum distinctly reddish (type 2) and specimens with the whole mesosoma

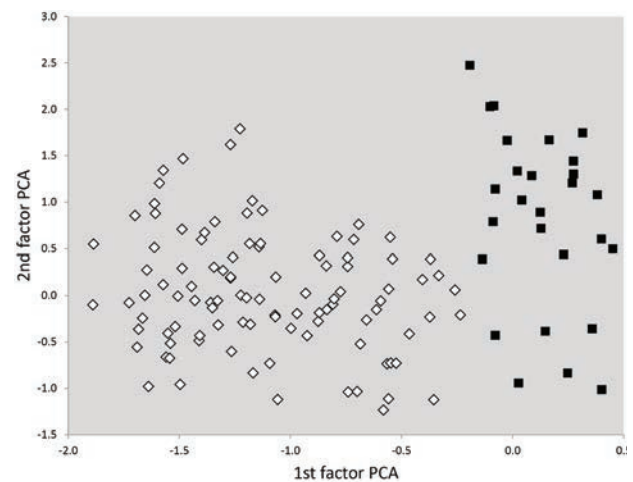
colored reddish (type 3). Color polymorphism may occur in the same nest showing that this is an intraspecific phenomenon. Observed were nests with type 1 and type 2 specimens and such with type 2 and type 3 specimens. The poor data available and unclear queen numbers and mating frequencies exclude speculations on certain pathways of Mendelian inheritance. Yet, in the first instance, it appears reasonable to assume that single mutations may have caused this pattern rather than being modifications by environmental factors. Intraspecific color polymorphism has led to taxonomic errors: specimens of *Camponotus piceus* with type 2 pigmentation, but showing shape characters, surface structure and morphometrics fully within the range of this species have been described from Spain as *Camponotus figaro* Collingwood & Yarrow 1969 (for a more detailed argumentation see section 4.8). Another form of color polymorphism is given in *C. lateralis* that shows a trend to mimic the coloration of the two unpalatable *Crematogaster* species with which it forms parabiocotic associations: in many localities of the western Mediterranean *Camponotus lateralis*

has a reddish head and a dark mesosoma mimicking *Crematogaster scutellaris* (Olivier 1792) whereas in the eastern Mediterranean it usually has both head and mesosoma reddish brown mimicking *Crematogaster schmidti* (Mayr 1853).

A most treacherous, very distinct intraspecific polymorphism of shape, pubescence and setae characters – a true worst case scenario for taxonomists – has been shown by Seifert (2016) for *Camponotus lateralis*. The two morphs are safely separable on the individual level and they represent a syndrome of multiple, seemingly independent characters which may prompt each ant taxonomist with some experience to immediately assume two clearly evolved species. This wrong conclusion was drawn in this case by three different authors: In the determination key of Seifert (2007), the hairy form was separated from *Camponotus lateralis* (Olivier 1792) under the provisional designation ‘*Camponotus lateralis* sp. 2’ and Borowiec & Salata (2014) ascribed the hairy form of *C. lateralis* to the species *C. honaziensis* Karaman & Aktac 2013. An alternative explanation that



**Figure 1.** Principal component analysis (PCA) of worker size dimorphism in 285 worker individuals of the long-headed species *Camponotus atricolor*, *C. candiotes*, *C. heidrunvogtae* n.sp. and *C. piceus*. The PCA is in fully in line with the classification by a two-step cluster analysis separating majors (dark squares) and minors (white rhombs).



**Figure 2.** Principal component analysis (PCA) of worker size dimorphism in 250 worker individuals of the short-headed species *C. dalmaticus*, *C. lateralis morph 1*, *C. lateralis morph 2* and *C. rebecca*. The PCA is fully in line with the classification by a two-step cluster analysis separating majors (dark squares) and minors (white rhombs).

**Table 1.** Species of the *Camponotus lateralis* group the workers of which can be allocated to three types of a rather distinct color polymorphism in mesosoma pigmentation; percentages are given, n = number of inspected specimens. Data of *Camponotus fallax* Nylander 1856 that does not belong to this group are given for comparison.

	whole Mesosoma blackish	only pronotum reddish	whole mesosoma reddish	n
<i>C. fallax</i>	82.0	16.0	2.0	50
<i>C. piceus</i>	94.2	2.9	2.9	139
<i>C. atricolor</i>	100.0	0	0	76
<i>C. heidrunvogtae</i> sp.nov.	94.3	5.7	0	35
<i>C. dalmaticus</i>	1.4	94.4	4.2	71

these phenotypes do represent different species appears unlikely as there is no example known so far worldwide that independent (i.e., non-parasitic) and closely related species form frequent and stable parabioc associations. The fact that in the subgenus *Myrmentoma* three types of polymorphism – namely polymorphism of shape, pubescence and setae characters, color polymorphism and major-minor dimorphism – may superimpose within the same data set shows how cautious taxonomists have to do their work here and how misleading judgement from single specimens may be.

#### 4.4. Synoptic list of the species of the *Camponotus lateralis* group from Europe, Asia Minor and the Caucasus and key to the workers

The analysis could distinguish nine species of the *Camponotus lateralis* group in the area of Europe, Asia Minor and Caucasus which are keyed below:

*Camponotus lateralis* (Olivier 1792)  
*Camponotus piceus* (Leach 1825)  
*Camponotus atricolor* (Nylander 1849)  
*Camponotus dalmaticus* (Nylander 1849)  
*Camponotus candiotes* Emery 1894  
*Camponotus rebecca* Forel 1913  
*Camponotus anatolicus* Karaman & Aktac 2013  
*Camponotus honaziensis* Karaman & Aktac 2013  
*Camponotus heidrunvogtae* sp. nov.

For the status and identification of *Camponotus ebneri* Finzi 1930 from the Middle East, which is close to *C. dalmaticus*, see section 4.8.

#### Key to the workers of the *Camponotus lateralis* species group in Europe, Asia Minor and Caucasus

It should be clear that a very simple key cannot achieve determinations as safe as the application of complex multivariate analyses of complete character sets. The very strong, often biphasic allometries, color polymorphism, size dimorphism as well as shape and setae polymorphism complicate the situation and do not allow simple answers to difficult questions. In order to achieve some simplicity, the key uses absolute measurements. All inputs to discriminant functions have to be in millimeters with exception of RipD where input in micrometers is required.

**1a** Vertex in the majority of specimens in a nest sample not completely blackish; reddish pigmentation at least in patches appearing, whole head often completely reddish brown. Microripples on dorsum of 1<sup>st</sup> gaster tergite more widely set: RipD 8.8 – 14.1 µm. If microripples are more densely set (*C. rebecca*), then whole vertex reddish brown ..... **2**

**1b** Vertex completely blackish. If some small parts of anterior vertex have reddish pigmentation (*C. dalmaticus*), then microripples on dorsum of 1<sup>st</sup> gaster tergite are densely set with RipD  $7.59 \pm 0.55$ ..... **6**

**2a** Dorsal propodeal plane wide; scape base extension very strong, scape long; mesosoma wide  
 Discriminant  $21.98 * PrW + 6.897 * ScI + 4.015 * MW - 9.25 * CL + 0.249 * SL - 6.684 > 2$  [error 0% in 6 specimens]. Asia Minor ..... **honaziensis**

**2b** Dorsal propodeal plane less wide; scape base extension less strong (except *C. lateralis* morph 1); scape shorter; mesosoma narrower. Discriminant  $< 2$  [error 1.6% in 191 specimens] ..... **3**

**3a** Discriminant  $0.712 * nPr + 21.46 * CL - 14.462 * CW - 17.898 * PeW + 297.0 * RipD - 6.225 > 2.3$  [error 0% in 9 specimens]. Dorsal propodeal plane in dorsal view trapezoid, in posterior part much wider than anterior; bilateral sum of setae on mesonotum and propodeum dorsal of spiracle  $19.2 \pm 5.7$  (count also basal pits of detached setae!). Asia Minor..... **anatolicus**

**3b** Discriminant  $< 2.3$  [error 1.7% in 182 specimens]. Dorsal propodeal plane in dorsal view posteriorly not clearly wider than anteriorly; bilateral sum of setae on mesonotum and propodeum dorsal of spiracle  $8.3 \pm 3.7$  (count also basal pits of detached setae!)..... **4**

**4a** Distance of microripples on dorsum of 1<sup>st</sup> gaster tergite small, RipD 7.1–9.5 µm. Discriminant  $6.107 * CL - 24.624 * PrL + 954.7 * RipD - 6.81 < 2.35$  [error 0% in 32 specimens]. Crete, Cyprus, Asia Minor, Syria..... **rebecca**

**4b** Distance of microripples on dorsum of 1<sup>st</sup> gaster tergite larger, RipD 9.1–13.7 µm. Discriminant  $> 2.35$  [error 0% in 149 specimens]. Morphs of *C. lateralis*, co-occurring in 16% of nests. North Mediterranean from Iberia to Turkey..... **5**

**5a** Less hairy and pubescence shorter; unilateral number of setae on dorsal plane of scape low: nSC 1.7 [0–5]; scape base extension large: ScI 1.22 [1.04–1.40];

scape and dorsal propodeal area more elongated. Discriminant  $7.837*ScI-0.525*nSc+7.407*SI+7.275*PrL-17.675 > 0$  [error 0% in 86 workers]. Major workers with sinusoidally curved frontal carinae and the dorsum of propodeum only weakly convex in lateral view.....  
..... *lateralis* morph 1

**5b** Very hairy and with longer pubescence. Unilateral number of setae on dorsal plane of scape larger: nSC 4.29 [0–11.5]; scape base extension small: ScI 1.04 [1.00–1.10]; scape and dorsal propodeal area less elongated. Discriminant  $< 0$  [error 0% in 64 workers]. Majors with less sinusoidally curved frontal carinae and the dorsum of propodeum strongly convex in lateral view..... *lateralis* morph 2

**6a** Scape very long relative to width of mesosoma and dorsal propodeal plane. Discriminant  $28.141*SL-12.125*MW-16.724*PrW-15.683 > 2.1$  [error 0% in 32 specimens]. Balkans ..... *heidrunvogtae* n.sp.

**6b** Scape clearly shorter relative to width of mesosoma and dorsal propodeal plane. Discriminant  $< 2.1$  [error 0% in 321 specimens]..... 7

**7a** Mesonotum and propodeum with very few setae: nMn 2.0 [1–5.5], nPr 2.15 [1–4.5]; width of dorsal propodeal plane and petiole relative to CL smaller. Discriminant  $0.238*nMn+0.192*nPr-13.124*CL+28.124*PrW+5.228*PeW+2.731 < 0$  [error 0% in 67 specimens]. Balkans northwest to S Switzerland..... *dalmaticus*

**7b** Mesonotum and propodeum more hairy: nMn  $4.8 \pm 2.4$ , nPr  $7.40 \pm 3.4$ ; width of dorsal propodeal plane and petiole relative to CL larger. Discriminant  $> 0$  [error 0.8% in 253 specimens]..... 8

**8a** Extension at scape base absent or very weak; metanotal depression very shallow. Discriminant  $16.35*ScI+33.25*MGr+5.962*CW-0.146*nPr-10.773*PeW-20.913 < 0$  [error 1.3% in 76 workers and 0% in 30 nest sample means with at least 2 workers]. Pannonian Plane, Balkans, Ukraine east to Caucasus ..... *atricolor*

**8b** Extension at scape base more developed; metanotal depression deeper. Discriminant  $> 0$  [error 4.0% in 177 workers and 0% in 68 nest sample means of at least 2 workers]..... 9

**9a** Crete, Asia Minor, Caucasus. Discriminant  $13.74*ScI+8.383*CL+8.565*SL-43.51*MGr-26.46*PrL-19.751 < 0$  [error 2.5% in 40 workers]..... *candiotus*

**9b** South Temperate and Mediterranean Europe. Discriminant  $> 0$  [error 2.2% in 137 workers] ..... *piceus*

#### 4.5. Comments on taxa from North Africa, the Canaries and Middle East related to species of the *Camponotus lateralis* group

All taxa considered in this section differ very clearly from *C. heidrunvogtae* sp. nov. and the other 8 focal species listed up in section 4.4.

##### *Camponotus guanchus* Santschi 1908

Investigated was 1 type worker labeled 'Type', 'Tenerife Valle Gimenes 10. IX. 1899.', '*C. lateralis* Ol guancha Sant' and 1 type gyne labeled 'Type', 'Tenerife Bajan.do 23: III : 1902', '*C. lateralis* guancha Sant'; both stored in NHM Basel. This species from the Canaries differs from all Eurocaucasian species shown in Tab. 2 and Tab. 3 by propodeal and petiolar shape. The dorsal surface of propodeum is clearly convex in transverse section. In lateral aspect, dorsum and caudal slope of propodeum form an angle of about 130° and the transition is rounded – i.e., there is no indication of a dorsocaudal protrusion or of an abrupt transition from dorsal plane to slope. The petiolar node is narrow ( $PeW/CS_{1.25} 0.322$ ) but thick in lateral view – corresponding to the situation in *Lasius fuliginosus* (Latreille 1798). These characters may possibly indicate a close relatedness to the North African taxa *C. sicheli rubra* Karavajev 1912 and *C. sicheli nigra* Karavajev 1912.

##### *Camponotus spissinodis* Forel 1909

This taxon has been described by Forel as *Camponotus lateralis* r. *spissinodis* from Lambessa / Tunisia. Two minor worker syntypes from MHN Genève labeled '*C. lateralis* Ol. ♀ r. *spissinodis* Forel type Lambessa', 'ANTWEB CASENT09110434 bottom w.' and 3 major worker syntypes on another pin equally labeled 'ANTWEB CASENT09110433 bottom w.' were examined. The investigation showed that *C. spissinodis* is an African species related to those Eurocaucasian species of the *C. lateralis* group having a completely blackish dorsum of head. Among other characters, the *C. spissinodis* types differ from *C. piceus*, *C. heidrunvogtae* sp. nov. by the absent or very weak scape base extension (mean  $SCI_{1.25}$  of four syntypes 1.062) and the clearest differences to *C. atricolor* is the much larger  $MGr/CS_{1.25}$  (mean 0.077), the larger  $SL/CS_{1.25}$  (mean 1.007) and smaller  $PrL/CS_{1.25}$  (mean 0.397). The relation to *C. candiotus* appears controversial. There is no single NUMOBAT character which is clearly outside the range of *C. candiotus* (Tab. 3). Running a PCA of *C. atricolor*, *C. candiotus* and



the syntypes of *C. spissinodis*, considering 12 RAV-corrected characters and cephalic size, the *C. spissinodis* types are placed by the first five principal components within the *C. candiotes* cluster. NC-part.kmeans and NC-part.hclust allocates the *C. spissinodis* types to the *C. candiotes* cluster but they appear with the latter algorithm as single-sample outlier of the *C. candiotes* cluster. NC-NMDS clustering places the centroid of the type series as outlier in 5 out of 15 bivariate plots of the first six stress vectors. *C. spissinodis* is not proposed here to be synonymous with *C. candiotes* because of outlier placements in two exploratory data analyses and differences in two characters clearly confirmed by ANOVA tests: SL/CS<sub>1,25</sub> ( $F_{1,42}=14.23$ ,  $p<0.001$ ) and PrL/CS<sub>1,25</sub> ( $F_{1,42}=17.94$ ,  $p<0.0005$ ). Furthermore, the types of *C. spissinodis* show a stronger sculpture and more convex profile of dorsal propodeum and absolute size of the largest major worker exceeds the range known for *C. candiotes*.

#### ***Camponotus sicheli rubra* Karavajev 1912**

This taxon was described on the basis of workers and a gyne from Laverdure /Algeria.

The original description indicates a relatedness to the *C. lateralis* group but the mesosomal profile is reported to form a strongly rounded dorsocaudal corner of propodeum which should place the taxon near to *C. guanchus*.

#### ***Camponotus sicheli nigra* Karavajev 1912**

The type specimens of this taxon have been collected near El Kantara which is either in Tunisia or Algeria. The original description indicates similarities in color and propodeal shape to *C. lateralis* but Karavajev noted that the petiole scale is very thick in profile view, being thicker in the upper third than at base, and shows a very rounded crest. This character and the zoogeographic distance suggest that this taxon is not conspecific with *C. lateralis* or *C. rebecca* and is probably close to *C. guanchus*.

#### ***Camponotus piceus spissinodis africanus* Santschi 1929**

The name of this taxon is unavailable according to the provisions of the ICZN. A major and minor type worker, collected at Tanger / Morocco, are depicted in antweb.org under CASENTO911700 and CASENTO911701. They are clearly heterospecific from *C. spissinodis* and show a mesosomal shape and overall pigmentation similar to an average situation in *C. lateralis*. Yet, their head length and scape length indices are clearly higher than the upper extremes in any other species related to *C. lateralis*: CL/CW<sub>1,25</sub> = 1.15 and SL/CS<sub>1,25</sub> = 1.051.

#### ***Camponotus ebneri* Finzi 1930 stat. nov.**

This taxon has been described as *Camponotus lateralis* var. *ebneri* Finzi 1930 from the region of Beskinta to Dsebel Sanin in Lebanon. I examined the single type worker hosted in NHM Wien. It is labeled 'Beskinta – Sannin, Liban. 16.VIII.'28. R. Ebner Mus. Caes. Vind.', 'Type ! *Camponotus lateralis* var. *ebneri* n.v. det. Finzi 1929', 'ANTWEB CASENTO915596'. The specimen is not 'ganz schwarz' as Finzi stated: the lateral pronotum is reddish and meso- and metapleuron reddish black. The taxon appears closely related to *C. dalmaticus* (Nylander 1849). The type specimen of *C. ebneri* is allocated to the *C. dalmaticus* cluster when run as wild-card in an LDA considering the complete character set and all other entities listed in Tab. 2 and Tab. 3. Yet, a synonymization with *C. dalmaticus* appears premature due to the apparently disjunct distribution and because the data of PrW/CS<sub>1,25</sub> and nPr<sub>1,25</sub> are outside the range known for *C. dalmaticus* (Tab. 3). It is hypothesized here to represent an allopatric sister species.

#### ***Camponotus staryi* Pisarski 1971**

This taxon has been described from Northern Iraq. The holotype, a minor worker, is depicted in AntWeb.org under CASENTO917233 and is labeled 'Iraq Sari Rash nr Salahuddin Kurdistan 10.7.1968 leg. Stary 322', 'Holotyp', '*Camponotus staryi* sp. n. det B. Pisarski' and 'ANTWEB CASENTO917223'. The type locality is situated at 36.409°N, 44.317°E, 980 m and thus 1250 km east of the type locality of *Camponotus anatolicus* Karaman & Aktac 2013 in W Anatolia. The holotype of *C. staryi* shows a high similarity to minor workers from the holotype nest of *Camponotus anatolicus* which I could examine. Considering the images in AntWeb.org as well as Pisarski's drawing of the holotype in the original description, the interspecific differences verbally described by Karaman & Aktac (2013) appear most doubtful. The only morphological argument for a possible heterospecificity is the wider petiole in the *C. staryi* holotype: PeW/CS<sub>1,25</sub> was calculated from the AntWeb.org images as 0.418 whereas it is 0.304–0.381 in 9 specimens of *C. anatolicus* (Tab. 2). I refrain here from a synonymization of the two taxa because of the very poor data basis and the rather high geographic distance of the type localities.

### **4.6 Taxa excluded from the *Camponotus lateralis* group**

The taxa listed up in this section show similarities to the members of the *Camponotus lateralis* group in a number of characters but deviate in others. I present a

brief argumentation why they cannot be senior synonyms both of the new species introduced here and of other members of the *C. lateralis* group. The species status of these excluded taxa is not assessed here and they are listed up in the rank as they were introduced in the original description.

***Camponotus kiesenwetteri*** (Roger 1859)

This taxon has been described from Greece. The type specimen depicted in antweb.org under FOCOL2486 shows a much stronger, more reticulate-foveolate sculpture and much denser pubescence on all body surfaces than observed in any member of the *C. lateralis* group. This results in a matt surface appearance at smaller magnifications. Yet, *C. kiesenwetteri* is certainly related to this group considering several body shape characters.

***Camponotus gestroi*** Emery 1878

This taxon has been described from Sardinia. The type specimen depicted in antweb.org under CASENT0905794 shows a very weak or absent metanotal depression, a convex overall dorsal profile line of mesosoma, and the angle between the dorsal plane and declivity of propodeum is about 120°.

***Camponotus libanicus*** André 1881

This taxon has been described from Lebanon. The type specimens depicted in antweb.org under CASENT0913700 shows an absent metanotal depression, a very convex overall dorsal profile line of mesosoma as well as a much stronger sculpture and much denser pubescence on all body surfaces than observed in any member of the *C. lateralis* group.

***Camponotus gestroi creticus*** Forel 1886

This taxon has been described from Crete. The type specimen depicted in antweb.org under CASENT0910430 shows a very weak or absent metanotal depression, a convex overall dorsal profile line of mesosoma, and the angle between the dorsal plane and declivity of propodeum is about 120°. A synonymy with *C. gestroi* appears reasonable at the first impression.

***Camponotus kiesenwetteri nitidescens*** Forel 1889

This taxon has been described from Kephallonia / Greece. Investigation of types of all castes from MHN Genève, all labeled ‘...Kephallonia...nitidescens...type’, showed a much stronger sculpture and much denser pubescence on all body surfaces than observed in any member of the *C. lateralis* group. This results in a matt surface appearance at smaller magnifications. This difference to the *C. lateralis* group is most obvious on gaster tergites. These characters are perhaps a little less

expressed than in the *C. kiesenwetteri* type. Borowiec and Salata (2014) have raised *C. k. nitidescens* to species level and considered it closely related to *C. boghossiani* Forel 1911 without comparing type specimens or discussing photos of type specimens of *C. kiesenwetteri*, *C. k. nitidescens* and *C. boghossiani*.

***Camponotus libanicus abrahami*** Forel 1913

This taxon has been described from Lebanon. Two investigated syntypes from MHN Genève, labeled *Camponotus* (*Orthonotomyrmex*) *libanicus* André v. *abrahami* For type ‘...Libanon...J. Sahlberg...No 141.’ differ from any member of the *C. lateralis* group by the dorsal mesosomal profile being in overall aspect evenly convex with a very shallow metanotal groove.

***Camponotus libanicus sahlbergi*** Forel 1913

This taxon has been described from Asia Minor. Type specimens depicted in antweb.org under CASENT0910440 and CASENT0910441 show an absent or weak metanotal depression, a very convex overall dorsal profile line of mesosoma as well as a much stronger sculpture and much denser pubescence on all body surfaces than observed in any member of the *C. lateralis* group.

#### 4.7 Incertae Sedis

This account considers taxa which have been allocated in the past to the *Camponotus lateralis* group – apparently based only on the original descriptions.

***Formica bicolor*** Latreille 1798

The full text of the original description states ‘Rouge, luisante, rase. Yeux et abdomen noirs. Écaille épaisse, entière.’ Considering that the terra typica is France, this allows only to conclude on an ant of the subfamily Formicinae.

***Formica pallidinervis*** Brullé 1833

This taxon has been described based on a male from Peloponnesus in Greece. The whereabouts of the type are unknown and the original description is insufficient – the more as males are generally poorly studied. The only possible conclusions seems to be that it is an ant of the subfamily Formicinae.

***Camponotus hemipsila*** (Förster 1850)

This taxon was described on the basis of a gyne from Alger /Algeria. Types most certainly do not exist. The description ‘Kopf...Mittelleib roth...nur Mittelbrust und Schildchen ganz schwarz’ may suggest a *Camponotus* related to the *C. lateralis* group.

***Camponotus sicheli*** Mayr 1866

This taxon was collected in the city of Alger. There are no types in the Gustav Mayr collection in NHM Wien. The original description suggests a relatedness to *C. guanchus*, *C. sicheli rubra* and *C. sicheli nigra* but it does not allow conclusions on synonymies with these taxa.

***Camponotus kiesenwetteri angustatus*** Forel 1889

The taxon has been described from Samos. There are no types in the Forel collection in MHN Genève and the original description does not allow an identification to the species level.

***Camponotus lateralis* var. *rhodia*** Santschi 1934

This taxon that was collected on the island of Rhodes has been described under the unavailable name *Camponotus lateralis dalmaticus* v. *rhodia* Emery 1925. The original description is insufficient. According to a message of Maria Tavano of 16 October 2013 there are no type specimens in the Emery collection of MCSN Genova.

#### 4.8 Treatment by species

***Camponotus lateralis*** (Olivier 1792)***Formica lateralis*** Olivier 1792

It was described from woodland in the Provence / France. The original description seems to allow little more than to conclude on an ant of the subfamily Formicinae. However, Olivier reported a strong overall similarity with *Crematogaster scutellaris* in size and pigmentation pattern. This gives a reasonable suggestion that the described ant belongs to that color morph of *Camponotus lateralis* which occurs in the West and Central Mediterranean and mimics the pigmentation pattern of the aggressive and unpalatable *Crematogaster scutellaris* in order to achieve protective Batesian mimicry in a parabiocotic association with this dominant species.

***Camponotus melanogastes*** (Latreille 1802)***Formica melanogastes*** Latreille 1802

It was described from France. The shape and pigmentation characters reported suggest that it may belong to the color morph of *C. lateralis* mimicking *Crematogaster scutellaris*.

***Camponotus axillaris*** (Spinola 1808)***Formica axillaris*** Spinola 1808

It was described in a worker from Liguria / Italy.

According to the shape characters reported, it belongs to the *C. lateralis* group. Furthermore, Spinola's statements on color ('Caput rubrum...Thorax niger...Abdomen nigrum' allow the conclusion that it may belong to the color morph of *C. lateralis* mimicking *Crematogaster scutellaris*.

***Camponotus merula*** (Losana 1834) [New Synonym]***Formica merula*** Losana 1834

This taxon was described from Piedmont / Italy. It appears unlikely that a type specimen of *Camponotus merula* could ever be identified in a collection as the original description gives no type locality and its text and figure do not allow a reasonably safe allocation to a certain species. A total body length of 6 mm with a slender overall body shape and the 'bilobe' mesosoma ('... bilobo, col lobo anteriore piu grande subrotonde...') suggests a member of the *Camponotus lateralis* group. The chestnut-brown color ('colore castagno intenso') and occurrence on poplar trees plagued by aphids ('...d'onde percorre specialmente i pioppi dagli afidi travagliati.') point to *C. lateralis* and make a synonymization with *C. piceus* unlikely. As nobody is currently able to present counter-evidence, I synonymize *C. merula* with *C. lateralis*.

***Camponotus armouri*** Wheeler 1926

Examined was one worker syntype from MCZ Cambridge, labeled 'Barranco de San Juan, Minorca 8-24 - 25 W.M. Wheeler', 'M.C.Z. CoType 1-3 21538'. It is a typical *Camponotus lateralis* morph 1 and is allocated to this cluster with  $p = 1.000$  if run as wild-card in a discriminant analysis considering all investigated characters and all entities given in Tab. 2.

***Camponotus lateralis balearis*** Santschi 1929

Investigated were three syntype workers from NHM Basel, labeled 'Type', 'Balears Ekker', and 'Camponotus (Myrmentoma) lateralis Ol v. balearis Sant'. All types are typical *Camponotus lateralis* morph 1 and each is allocated to this cluster with  $p=1.000$  if run as wild-card in discriminant analysis considering all investigated characters and all entities given in Tab. 2.

***Camponotus lateralis purius*** Santschi 1929 [New Synonym]

Investigated were two worker syntypes from Algeria, stored in NHM Basel, mounted on the same pin and labeled 'Camponotus lateralis Ol. / v. purius Sant / SANTSCI det. 1928', 'Alger Bequaert', 'Type',

'CASENT 09111698' [major worker], 'ANTWEB CASENT 0911699' [minor worker]. Considering all characters and running the syntypes as wild-cards in a 4-class LDA considering the four species presented in Tab. 2, they are allocated to the *C. lateralis* cluster with posterior probabilities of 0.9998 and 0.9974. A wild-card run of the syntypes within the *C. lateralis* cluster, allocated the major to morph 1 with  $p=0.998$  but the minor to morph 2 with  $p = 0.986$ .

#### *Camponotus kosswigi* Donisthorpe 1950

The lecto- and paratype, stored in BMNH London, were collected in Erbeyli / W Turkey, 14.V.1947. Pictures of syntypes in antweb.org under CASENT0903594 (major worker) and CASENT0903595 (minor worker) strongly suggest a synonymy with *Camponotus lateralis* morph 1 based on diagnostic setae and shape characters. A synonymy with *Camponotus lateralis* morph 2 and *C. rebecca* is excluded by the large scape base index SCI which is about 1.23 in the specimen with CW = 1.46 mm and 1.37 in the specimen with CW = 0.96 mm.

**Material examined.** A total of 66 nest samples with 152 workers were subject to NUMOBAT investigation.

**BULGARIA:** Arkutino, 1978.08.01, [42.351, 27.707, 8]; Nessebar, 1964.10.xx, [42.66, 27.71, 10]; Nessebar, 1974.07.20, [42.66, 27.71, 10]; Obsor, 1979.08.01, [42.82, 27.88, 30]; Ropotamo, 1982.09.18, [42.302, 27.728, 9]. **GEORGIA:** Tbilissi-2 km S, [41.666, 44.865, 420]. **CROATIA:** Krk: Airport- 1 km N, 1997.05.31, No 444, [45.229, 14.572, 92]; Krk: Punat- 5 km SE, 1997.06.01, No 464, [44.985, 14.650, 170]; Krk: near Markini, 1997.06.01, No 573, [45.120, 14.550, 126]; Mlini, 1958.08.31, [42.622, 18.208, 20]; Mlini, 1958.09.14, [42.622, 18.208, 20]; Pakostane, 2008.09.04, [43.917, 15.500, 5]; Pula, 2013.06.07, No 37, [44.884, 13.883, 65]; Skradin, Krka, 2014.05.31, No 16, 43.817, 15.933, 11]; Slano-0.5 km NW, 2014.06.01, [42.790, 17.883, 35]; Split: Marjan, 2013.08.15, No H = 52, [43.514, 16.416, 23]; Split: Marjan, 2013.08.15, No H = 53, [43.511, 16.406, 53]; Urgini-16 km N, 45.257, 14.795, 1250]. **CYPRUS:** Cedar Valley, 2012.05.05, [34.995, 32.687, 1196]. **FRANCE:** Banyuls-sur-Mere, no date, [42.45, 3.07, 60]; Corsica: Ajaccio, 1956.04.05, [41.926, 8.731, 75]; Marseille, no date, [43.307, 5.460, 120]. **GREECE:** Andros: Gavrio, 1992.06.xx, [37.880, 24.749, 20]; Corfou: Doukades, 2013.06.08, [39.701, 19.751, 174]; Corfou: Klimatia, 2013.06.06, [39.741, 19.790, 311]; Crete: Argiroupolis, 2013.05.13, [39.293, 24.343, 197]; Crete: Georgioupolis-12 km E, 2007.04.30, [35.350, 24.350, 7]; Crete: Georgioupolis-S, 2007.05.03, [35.333, 24.283, 60]; Crete: Karoti, 2007.04.30, [35.330, 24.340, 2]; Crete: Vrises-6 km S, 2007.05.01, [35.317,

**Table 2.** Species with at least small parts of vertex with reddish pigmentation components. Absolute size, and RAV-corrected shape and seta characters referring to CS=1.25 mm; sequence of data: arithmetic mean  $\pm$  standard deviation [minimum, maximum]. The definitions of the characters and their computation are explained in section 3.2.

	<i>lateralis</i> morph 1 (i=87)	<i>lateralis</i> morph 2 (i=65)	<i>anatolicus</i> (i=9)	<i>honaziensis</i> (i=6)	<i>rebecca</i> (i=36)
CS	1369 $\pm$ 287 [904,1830]	1164 $\pm$ 217 [876,1715]	1220 $\pm$ 212 [882,1518]	1053 $\pm$ 129 [ 936,1293 ]	1184 $\pm$ 232 [ 873,1744 ]
CL/CW <sub>1.25</sub>	1.062 $\pm$ 0.023 [1.013,1.107]	1.053 $\pm$ 0.017 [1.013,1.100]	1.107 $\pm$ 0.032 [1.046,1.168]	1.066 $\pm$ 0.015 [1.044,1.079]	1.077 $\pm$ 0.025 [1.014,1.118]
SL/CS <sub>1.25</sub>	0.931 $\pm$ 0.030 [0.842,0.994]	0.884 $\pm$ 0.024 [0.819,0.934]	0.901 $\pm$ 0.037 [0.848,0.951]	0.983 $\pm$ 0.033 [0.917,1.010]	0.974 $\pm$ 0.038 [0.894,1.029]
SCI <sub>1.25</sub>	1.233 $\pm$ 0.080 [1.075,1.475]	1.026 $\pm$ 0.031 [0.966,1.118]	1.096 $\pm$ 0.037 [1.051,1.158]	1.415 $\pm$ 0.115 [1.248,1.592]	1.083 $\pm$ 0.038 [1.029,1.169]
MW/CS <sub>1.25</sub>	0.737 $\pm$ 0.018 [0.702,0.784]	0.723 $\pm$ 0.019 [0.675,0.768]	0.733 $\pm$ 0.015 [0.707,0.750]	0.779 $\pm$ 0.011 [0.767,0.799]	0.761 $\pm$ 0.024 [0.696,0.808]
PrW/CS <sub>1.25</sub>	0.269 $\pm$ 0.017 [0.233,0.309]	0.251 $\pm$ 0.018 [0.215,0.290]	0.273 $\pm$ 0.016 [0.248,0.295]	0.312 $\pm$ 0.010 [0.294,0.320]	0.275 $\pm$ 0.019 [0.236,0.312]
PrL/CS <sub>1.25</sub>	0.359 $\pm$ 0.020 [0.320,0.420]	0.329 $\pm$ 0.017 [0.268,0.361]	0.352 $\pm$ 0.015 [0.332,0.369]	0.400 $\pm$ 0.010 [0.388,0.414]	0.412 $\pm$ 0.018 [0.370,0.444]
PeW/CS <sub>1.25</sub>	0.373 $\pm$ 0.020 [0.329,0.416]	0.374 $\pm$ 0.022 [0.325,0.419]	0.336 $\pm$ 0.029 [0.304,0.381]	0.386 $\pm$ 0.013 [0.365,0.398]	0.366 $\pm$ 0.018 [0.325,0.420]
MGr/CS <sub>1.25</sub>	0.087 $\pm$ 0.013 [0.059,0.125]	0.096 $\pm$ 0.011 [0.070,0.126]	0.115 $\pm$ 0.013 [0.098,0.141]	0.086 $\pm$ 0.018 [0.068,0.104]	0.074 $\pm$ 0.014 [0.038,0.104]
RipD <sub>1.25</sub>	10.79 $\pm$ 0.76 [9.1,12.7]	10.87 $\pm$ 1.02 [8.8,14.1]	11.08 $\pm$ 1.00 [9.8,12.6]	9.90 $\pm$ 1.18 [ 8.4,11.9]	8.03 $\pm$ 0.53 [7.2,9.2]
nSc <sub>1.25</sub>	1.29 $\pm$ 0.99 [0.0,3.7]	8.52 $\pm$ 2.19 [3.5,12.7]	3.80 $\pm$ 1.44 [1.7,5.9]	0.92 $\pm$ 1.19 [0.0,2.8]	1.24 $\pm$ 1.47 [0.0,5.3]
nMn <sub>1.25</sub>	1.25 $\pm$ 0.63 [0.6,3.7]	2.74 $\pm$ 1.07 [0.9,6.8]	4.70 $\pm$ 1.87 [2.7,8.9]	3.58 $\pm$ 1.31 [2.4,5.1]	1.84 $\pm$ 0.60 [0.6,3.4]
nPr <sub>1.25</sub>	1.98 $\pm$ 0.60 [0.0,3.3]	2.81 $\pm$ 0.89 [1.1,5.0]	5.30 $\pm$ 1.45 [3.8, 8.2]	5.93 $\pm$ 2.30 [3.5, 9.6]	2.74 $\pm$ 1.02 [1.3,6.0]



24.200, 2]; Kassandra: Siviri, 2009.07.25, [40.033, 23.350, 7]; Kassandrino-Polichronon, 2009.08.29, [40.400, 23.517, 594]; Metamorfofi, 2009.09.02, [40.233, 23.600, 117]; Olympos Mts.: Petra, 2012.09.07, [40.178, 22.330, 584]; Rhodos: Rhodos City, 2008.07.07, [36.433, 28.217, 30]; Rhodos: Apollakia, 2008.07.05, [36.050, 27.783, 34]; Rhodos: Kiotari, 2008.07.02, [36.033, 27.950, 3]; Rhodos: Prasonisi, 2008.07.11, [35.933, 27.767, 29]; Samos (von Oertzen), pre 1918.xx.xx, [37.75, 26.00, 200]; Samos: Nightingale Valley, 2013.06.09, [37.783, 26.817, 450]; Samos: Pythagoreio, 2013.06.04, [37.693, 26.935, 50]; Sikourio-Spilia, 2012.09.06, [39.777, 22.611, 544]. **ITALY:** Capodimonte, 2011.11.xx, [42.533, 11.900, 315]; Friaul: Gradisca, 1993.05.31, [45.990, 13.120, 45]; Garda-E, 1995.06.13, [45.57, 10.84, 580]; Roma, 1932.xx.xx, [41.90, 12.49, 52]. **MACEDONIA:** Drvos-1.5 km N, 2010.04.20, [41.50, 22.77, 438]. **MONTENEGRO:** Herceg Novi, 2013.05.09, No 1, [42.453, 18.574, 81]; Herceg Novi, 2013.05.10, No 9, [42.454, 18.552, 65]; Herceg Novi, 2013.05.10, No 15, [42.453, 18.550, 70]; Herceg Novi, 2013.05.11, No 17, [42.453, 18.552, 107]. **SPAIN:** Mallorca, without exact site and date, pre 1945.xx.xx, [39.60, 2.90, 400]; Mallorca: Cala Mandia, 1991.11.xx, [39.522, 3.307, 20]; Mallorca: Ermita de Betlem, 2009.05.12, [39.717, 3.317, 378]; Mallorca: Felanitx, 2009.05.10, [39.450, 3.175, 335]; Mallorca: La Palma (Ekker), pre 1925.xx.xx, type *C. balearis*, [39.58, 2.66, 50]; Mallorca: Puig de Randa, 2009.05.16, [39.517, 2.917, 370]; Minorca: Barranco de San Juan, 1925.08.24, type *C. armouri* [39.973, 3.893, 50]. **TURKEY:** Demirtas-22 km NE, 1997.05.04, [37.475, 32.273, 450]; Kemer-Somasekri, 2010.07.01, [36.583, 30.467, 319]; Phaselis, 2010.06.29, [36.517, 30.550, 20]; Tasucu-10 km SW, 1997.05.14, No 354, [36.268, 33.814, 50]; Temessos, 2010.07.03, [36.967, 30.450, 1018]; Yayladagi, 1997.05.13, No 334, No 337, [36.593, 30.447, 500].

**Geographic range.** In addition to the range indicated by the material account given above, specimens determined by subjective inspection originated from the Iberian Peninsula, S France, and S Alps (Ticino and S Tyrol /Alto Adige). The northernmost sites in the Southern Alps are at 47.7°N. According to the information currently available, it is the only Eurocaucasian species of the *C. lateralis* group extending its range to N Africa: occurrence in Algeria is documented by the type series of *Camponotus lateralis purius* Santschi collected in the city of Alger.

**Diagnosis.** For the character combinations to identify this species and its two morphs see key and Tab. 2. Morph 1 is imaged in AntWeb.org under the specimen identification numbers ANTWEB1038014, CASENT0179871, CASENT0249989, CASENT0249990, CASENT0903594, CASENT0903595, CASENT0912190, CASENT0912191, CASENT0914267 and morph 2 under ANTWEB1038013, CASENT0911698, CASENT0911699, CASENT0914262.

**Biology.** see Seifert (2018) and Wagner (2014).

**Comments.** The distribution east of Asia Minor and Caucasus is not studied. The sample from Algeria shows that dimorphism of shape and setae apparently applies to the whole Mediterranean region.

### *Camponotus anatolicus* Karaman & Aktac 2013

#### *Camponotus anatolicus* Karaman & Aktac 2013

Investigated were five paratype workers from the holotype nest, stored in SMN Görlitz and labeled 'TUR: 36.4635°N 30.3339°E Altinyaka-Village, 551 m leg. C.Karaman 2007.06.06 -7/0888b' and 'Paratypes *Camponotus anatolicus* Karaman & Aktac 2013'. Note that the original description gives a wrong geographic latitude and longitude. These data are corrected here according to a personal communication with C. Karaman in 2018.

**All material examined.** A total of 3 nest samples with 9 workers were subject to NUMOBAT investigation.

**TURKEY:** near Altinyaka village, 2007.06.06, No 7/0888b, [36.4635, 30.3339, 551 m]; near Kayadibi village, 2007.06.03, No 07/767a, [36.517°N, 29.426°E, 398]; near Yenikisla village, 2007.06.07, No 07/0916, [36.523, 30.194, 886].

**Geographic range.** Only known so far from a small area in the Antalya and Mugla region of Anatolia.

**Diagnosis** (Tab. 2, Figs 3–8). The character combinations to identify this species can be derived from the key, Tab. 2 and the z-stacks. The dorsal propodeal plane is in dorsal view trapezoid – i.e., in posterior part much wider than anteriorly. The mesosoma is more hairy: the bilateral sum of setae on mesonotum and propodeum dorsal of spiracle is 13–27. The metanotal depression is very deep. Head, scape, mesosoma and petiole reddish to reddish brown; mesosoma, petiole, legs reddish to reddish brown; the first gaster segment often reddish to reddish-brown, the rest of gaster blackish.

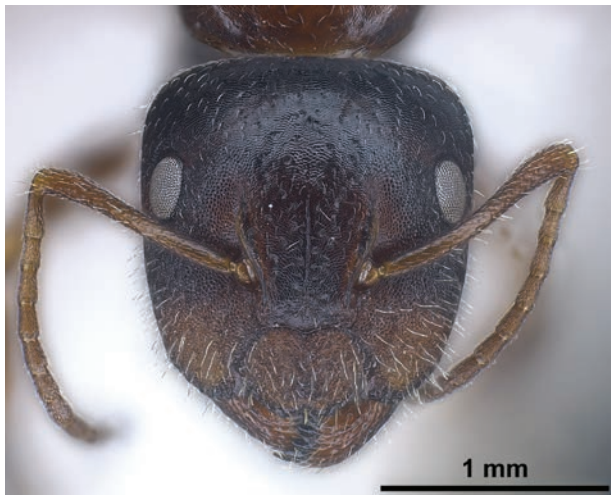
**Biology.** It seems to be connected to woodland. Karaman & Aktac (2013) reported it to occur in *Pinus*- and *Quercus*-dominated forests along brooks in altitudes between 282 m and 886 m.

**Comments.** The high similarity with *Camponotus staryi* Pisarski 1971 was already discussed in section 4.5.

### *Camponotus honaziensis* Karaman & Aktac 2013

#### *Camponotus honaziensis* Karaman & Aktac 2013

Investigated were 3 paratype workers from the holotype nest, stored in SMN Görlitz and labeled 'TUR: 37.467°N, 29.217°E Denizli-Merkez-Cankurtaran 1195 m, Honaz Dagi Nat. Park Karaman 2007.07.15-07/2344' and 'Paratypes *Camponotus honaziensis* Karaman & Aktac 2013'. Note that the original description gives a wrong geographic latitude. These data are corrected here after a personal communication with C. Karaman in 2015.



**Figure 3.** Head of major worker of *C. anatolicus*.



**Figure 4.** Major worker of *C. anatolicus* in lateral view.



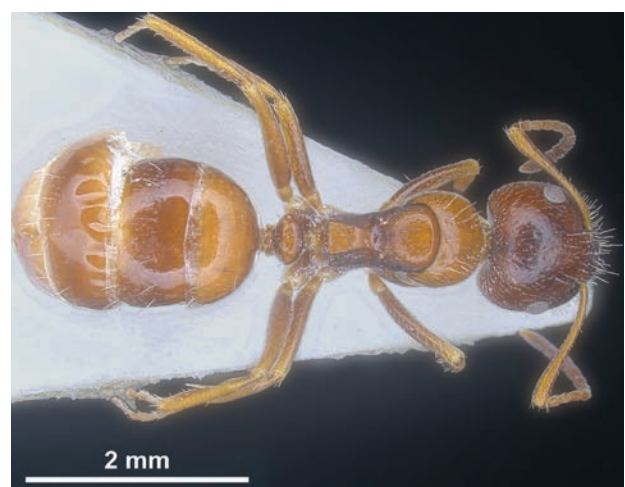
**Figure 5.** Major worker of *C. anatolicus* in dorsal view.



**Figure 6.** Head of paratype minor worker of *C. anatolicus* from the holotype nest.



**Figure 7.** Paratype minor worker of *C. anatolicus* from the holotype nest in lateral view.



**Figure 8.** Paratype minor worker of *C. anatolicus* from the holotype nest in dorsal view.



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

**TURKEY:** Denizli-Merkez-Cankurtaran, 2007.07.15, No 07/2344, paratypes of *C. honaziensis* [37.467, 29.217, 1195]; Dereköy-Village, 2007.05.28, No 07/0412, paratypes of *C. honaziensis* [36.523, 30.194, 886].

**Geographic range.** Only known so far from eight localities in the Denizli and Burdur provinces of Anatolia between 800 and 1850 m altitude.

**Diagnosis** (Tab. 2, Figs 9–11). See key. Within the species having significant reddish pigmentation components on vertex, the species is well separable by a combination of long scape, strong extension of scape base and large width of dorsal propodeal plane. A typical, or frequent, coloration is head, mesosoma and petiole reddish brown and gaster blackish.



**Figure 9.** Head of minor worker of *C. honaziensis* from the holotype nest.



**Figure 10.** Minor worker of *C. honaziensis* from the holotype nest in lateral view.

**Biology.** This species was reported to occur on mountain meadows and *Pinus*, *Juniperus* and *Quercus* stands between 807 and 1831 m altitude.

**Comments.** The minor worker specimen CASENT0914264, depicted in AntWeb.org under *Camponotus honaziensis*, is by no means referable to this species but represents morph 2 of *Camponotus lateralis*.

### *Camponotus rebecca* Forel 1913

#### *Camponotus (Orthonotomyrmex) lateralis* var. *rebecca* Forel 1913

Investigated was a type worker from MHN Genève with missing gaster, labeled ‘Typus’, ‘Damascus’, ‘U.Sahlb.’, ‘*Camponotus (Orthonotomyrmex) lateralis* Ol. v. *Rebecca* type For.’, ‘CASENT0910432’. Running this type specimen as wild-card in a 5-class LDA considering all RAV-corrected characters except RipD (because of missing gaster), it is allocated with  $p = 0.9965$  to the cluster of 36 ants given in Tab. 2. The posterior probabilities of the type specimen of belonging to other species were:  $p = 0.0035$  for *C. lateralis* morph 1 and each  $p = 0.0000$  for *C. lateralis* morph 2, *C. anatolicus* and *C. honaziensis* (for sample size see Tab. 2).

#### *Camponotus (Myrmentoma) lateralis* var. *cypridis* Santschi 1939 [New Synonym]

Investigated were four syntype workers from Cyprus labeled ‘*Camponotus (Myrmentoma) lateralis* Ol. v. *cypridis* Sants’, ‘Chypre 20.7.31 Yermasogia Riv. Movromostakis.’ and ‘Type’, NHM Basel. Considering all NUMOBAT characters and running the syntypes



**Figure 11.** Minor worker of *C. honaziensis* from the holotype nest in dorsal view.

as wild-cards in a LDA considering the five entities presented in Tab. 2, they all were allocated to the *C. rebecca* cluster with  $p = 1.000$ .

**All material examined.** A total of 17 nest samples with 36 workers were subject to NUMOBAT investigation. **CYPRUS:** Aphrodite Bath, 2012.05.04 [34.057, 32.344, 51]; Kidasi-S, Diarizos river, 2012.05.06 [34.798, 32.705, 264]; Yermasogia river, 1931.07.20, types *C. cypridis* [34.76, 33.10, 90]. **GREECE:** Crete: Chania-6 km SW, Agia, 2011.05.03 [35.467, 23.917, 22]; Crete: Georgiupoli-S, 2007.05.04 [35.350, 21.250, 1]; Rhodos: Apollakia, 2008.07.05 [36.050, 27.783, 34]; Rhodos: Dimyilia, 2008.07.09 [36.333, 28.033, 91]; Rhodos: Emponas, 2008.07.10 [36.200, 27.817, 35]; Rhodos: Epta Piges, 2008.07.04 [36.25, 28.10, 92]; Rhodos: Petaloudes, 2008.07.09 [36.333, 28.050, 192]. **SYRIA:** Damascus (Sahlberg), pre 1913.xx.xx, type *C. rebecca* [33.51, 36.31, 696]. **TURKEY:** Antalya: Belek, 2004.02.21 [36.860, 31.059, 8]; Chimaera (Yanatas), 2010.06.30 [36.418, 30.450, 146]; Cirali, 2010.06.30 [36.418, 30.450, 15]; Demirtas-28 km E, 1997.05.04, No 139 [36.52, 32.26, 1000]; Göynük, 2010.06.28 [36.667, 30.533, 49]; ancient Phaselis, 2010.07.05 [36.517, 30.550, 20].

**Geographic range.** The range indicated by the investigated material is rather small but the situation farther east is unknown.

**Diagnosis** (Tab. 2) See key. Within the species having significant reddish pigmentation components on vertex, *C. rebecca* is well characterized by the closely spaced ripples on dorsum of 1st gaster tergite (RipD  $7.99 \pm 0.50 \mu\text{m}$ ) and the rather long dorsal propodeal plane. Minor workers are depicted in AntWeb.org under CASENT0911697 and CASENT0914423 and a major worker under CASENT0911696. The typical coloration is head, mesosoma and petiole medium to dark reddish brown and gaster blackish.

**Biology.** No information.

**Comments.** No comments.

### *Camponotus dalmaticus* (Nylander 1849)

#### *Formica dalmatica* Nylander 1849

Investigated were two syntypes on different pins, a major and minor worker, labeled 'Lagusta \ Zeller \ Coll.Nylldr \ Lagosta [handwritten] \ H:fors Spec. typ. No 50\*\* Formica dalmatica Nyl', FMNH Helsinki. \*\*The syntypes have identical labels except for 'Spec. typ. No' which are '5089' and '5090' respectively. The syntypes represent typical specimens in shape, structure and pigmentation. Running them as wild-cards in a 5-class LDA, they were allocated with a mean posterior probability of  $p = 0.9996$  to the 24 nest samples classified here as *C. dalmaticus*, whereas all other four species with completely blackish vertex

and low RipD presented in Tab. 3 were clearly excluded (for *Camponotus ebneri* see there).

**All material examined.** A total of 25 nest samples with 68 workers were subject to NUMOBAT investigation.

**BOSNIA:** Klek, 2013.05.24, No 27 [42.912, 17.618, 15]; Popove Polje; 20130523, No 26 [42.846, 17.982, 275]. **BULGARIA:** Melnik, 1982.09.02 [41.523, 23.391, 375]; Rozen-2 km SW, 1982.08.27 [41.516, 23.423, 439]. **CROATIA:** Jablanac-0.8 km SE, 2014.08.03, No 96b [44.701, 14.904, 11]; Jurandvor-3 km NW, 1997.05.31 [44.997, 14.708, 100]; Lagosta (= Lastovo), pre 1849.xx.xx, type *C. dalmaticus* [42.767, 16.896, 52]; Pakostane, 2008.09.10 [45.917, 15.500, 38]; Punat-5 km SE, 1997.06.01 [44.985, 14.650, 170]; Sibenj, 1997.06.03, No 500 [44.890, 14.960, 600]; Valalta, 2007.07.21, No 5 [42.128, 13.630, 27]; Valalta, 2007.07.24, No 7 [42.128, 13.630, 27]; Vrgada Island, 2008.09.13 [43.850, 15.500, 60]. **GREECE:** Corfu: Akr. Kefali, 2013.06.05 [39.752, 19.633, 13]; Fotina, 2012.09.01 [40.221, 22.306, 398]; Mazedonien Expedition, 1917 and 1918 [40.0, 21.0, 500; guess]; Metamorfozi-6 km N, 2009.08.27 [40.284, 23.626, 335]; Nestos Delta, 2004.xx.xx [40.850, 24.870, 2]; Pandeimonas-Pori, 2012.09.04 [39.985, 22.585, 545]; Taxiarchis, 2009.08.30 [40.400, 23.517, 594]. **MONTENEGRO:** Herceg Novi, 2013.05.11, No 20 [42.453, 18.552, 107]; Lake Skadar, 2014.06.03 [42.330, 19.071, 129]; Slano-0.5 km N, 2014.06.01, No 13 [42.790, 17.883, 35]; Zagarac, 1911.06.21 [42.620, 18.970, 800]. **SWITZERLAND:** Lugano: Ruvigliana, 1961.xx.xx [46.005, 8.99, 500].

**Geographic range.** The range extends northwest over north Italy to south Switzerland. The northernmost site reported by Kutter (1977) is Ruvigliana near Lugano [46.00°N, 8.99° E, 400 m]. The species is unknown so far from Asia Minor.

**Diagnosis** (Tab. 3) See key. Two major workers are depicted in AntWeb.org under CASENT0179601 (the most frequent color morph) and CASENT0906110 (the rare, entirely black color morph).

**Biology.** See Seifert (2018).

**Comments.** See next species.

### *Camponotus ebneri* Finzi 1930

#### *Camponotus lateralis* var. *ebneri* Finzi 1930

The only specimen available was the type worker from Lebanon, stored in NHM Wien and labeled 'Beskinta – Sannin, Liban. 16.VIII.'28. R. Ebner Mus. Caes. Vind.', 'Type ! *Camponotus lateralis* var. *ebneri* n.v. det. Finzi 1929', 'ANTWEB CASENT0915596'.

**Diagnosis** (Tab. 2). The main difference to *C. dalmaticus* seems to be the much larger width of the dorsal propodeal plane.

**Biology.** unknown.



**Comments.** All forms of exploratory data analyses allocated the *C. ebneri* type specimen to the *C. dalmaticus* cluster and this was confirmed by a wild-card run in a 3-class LDA with posterior probabilities of  $p = 0.969$  for *C. dalmaticus*, 0.006 for *C. candiotes* and 0.025 for *C. piceus*. However, PrW/CS<sub>1,25</sub> and MGr/CS<sub>1,25</sub> of the *C. ebneri* type are above the upper extremes of *C. dalmaticus* (Tab. 3) and there is apparently a big gap between the Balkan range of *C. dalmaticus* and the Lebanon site of *C. ebneri*. For these reasons *C. ebneri* is not synonymized here and assumed to be an allopatric sister species of *C. dalmaticus*.

### *Camponotus atricolor* (Nylander 1849)

#### *Formica atricolor* Nylander 1849

Investigated were three syntypes on three different pins labeled 'Ross.mer. \ Motschulsky 22\ Coll. Nyland \ Motschulsky \ Mus.Zool H:fors Spec. typ. No 5086 Formica atricolor Nyl', FMNH Helsinki. The syntypes have identical labels except for 'Spec. typ. No' which is 5087 and 5088 in the other two specimens. The three syntype workers are allocated to *C. atricolor* with mean  $p = 1.0000$  if run as wild-card in a 5-class LDA considering the five black species of the group given in Tab. 3.

#### *Camponotus lateralis* var. *rectus* Forel 1892 [New Synonym]

[unavailable name, junior primary homonym of *Camponotus lubbocki rectus* Forel 1891] There is no material in the MHN Genève or NHM Basel collection that can be reliably identified as type material. Forel gave as sampling sites the Bulgarian Black Sea towns 'Anchialo' (today named Pomorje) and 'Sozopolis' (today Sozopol) and Forel's description of the mesosomal shape strongly suggests a synonymy with *C. atricolor*. This view is supported by the fact that *C. atricolor* is by far the most abundant of the black species along the western coast of Black Sea. Four investigated workers of topotypical material from Sozopolis in the Forel collection in MHN Genève (possibly types which Forel missed to designate) are allocated to *C. atricolor* with a mean posterior probability of  $p = 0.9975$  if run as wild-card in a 5-class LDA considering the five black species given in Tab. 3.

**All material examined.** A total of 36 nest samples with 77 workers were subject to NUMOBAT investigation. AUSTRIA: Junger Berg, 1999.06.05 [47.960, 16.778, 214];

Zurndorf (leg. Franz), pre 1960.xx.xx [47.961, 16.991, 159]; Gumpoldskirchen-2 km NNE, 1909.06.26 [48.062, 16.292, 350]; Göttlesbrunn, Oberer Haidenberg, 1966.xx.xx [48.080, 16.733, 245]. BULGARIA: Arkutino, 1978.08.01 [42.351, 27.707, 8]; Burgas-7 km S, 2003.09.30, samples No 710, 711, 716, 718 [42.451, 27.469, 1]; Chernomarez, 2006.07.30 [42.450, 27.650, 8]; Melnik, 1982.08.28 [41.524, 23.401, 470]; Melnik, 1982.08.30 [41.529, 23.393, 394]; Melnik, 1982.09.01 [41.524, 23.401, 394]; Nessebar, 1974.06.20 [42.66, 27.71, 10]; Nessebar, 1974.07.20 [42.66, 27.71, 10]; Ropotamo, 1982.09.18 [42.302, 27.728, 9]; Rozen-4 km N, 1982.08.26 [41.567, 23.449, 1180]; Sofia: Lülungebirge, 1909.05.xx [42.66, 23.12, 1000]; Sozopol, 1982.09.20 [42.411, 27.694, 30]; Sozopolis (= Sozopol) (leg. Forel), 1891.08.xx [42.41, 27.69, 30]; Srebarna, 1989.07.14 [44.09, 27.06, 35]; Tirnovo, 1920.xx.xx [43.09, 25.66, 325]. CZECHIA: Kurdejov-1.2 km NW, 2008.05.10 [48.966, 16.751, 322]. GEORGIA: Tbilissi-N, 1985.07.21 [41.78, 44.77, 600]; Tbilissi, 1985.07.25 [41.70, 44.80, 600]. GREECE: Chania: Pilion, 42.41, 27.69, 30]; Holomontas, Stagira, 2009.09.03 [40.517, 23.733, 539]; Mazedonien Expedition, 1917/1918.xx.xx [40.0, 21.0, 500, guess]; Nestos-Delta, 2009.xx.xx [40.85, 24.87, 2]; Paralia Katerini, 2012.08.28/29 [40.264, 22.596, 5]. HUNGARY: Balatonakali, 1987.06.xx [46.893, 17.523, 160]; Budapest-Ujpest, 1909.xx.xx [47.565, 19.092, 110]. ROMANIA: Mehadia, 1909.06.10 [44.90, 22.36, 166]. RUSSIA: Rossia Meridionale, pre 1849.xx.xx [46, 40, 70; guess]. UKRAINE: Crimea: Kamenskoje, 2010.09.xx [45.279, 35.523, 6]; Krim (= Crimea), 1900.xx.xx [45.18, 34.28, 200; guess].

**Geographic range.** Steppe zones of Caucasian lowlands, the south of European Russia and the Ukraine, Balkans, Hungary, E Austria and S Moravia (here the northernmost confirmed site at 49.0°N). There is a strong range overlap with *C. piceus* on the Balkans and some overlap with *C. candiotes* in the Caucasus.

**Diagnosis** (Tab. 3, see key): Differential characters of *C. atricolor* against other blackish species of the group, which are detectable by subjective eye inspection, are the shallow, sometimes nearly absent, metanotal depression, the roughly linear dorsal mesosomal profile and the missing extension of large scape diameter near to its base. However, due the negative allometry of scape base extension, this structure may be missing in large workers of the other four species. A minor worker is depicted in AntWeb.org under CASENT0179869 and a major worker under CASENT0179870.

**Biology.** See Seifert (2018).

**Comments.** *C. atricolor* has been raised to species level by Seifert (1996) and Seifert (2007) but this view did not receive much appreciation by other myrmecologists. It is apparent that *C. atricolor*, *C. piceus* and *C. candiotes* are closely related but only the latter two represent truly cryptic species. The exploratory data analyses NC-part. hclust, NC-part.kmeans and NC-Ward provide a clear separation of *C. atricolor* from the cluster of siblings formed by *C. piceus* and *C. candiotes*. Considering CS and all 12 RAV-corrected shape and seta characters, the error rate on the  $K = 2$  level (*atricolor* vs. *piceus+candiotes*)

in 124 examined samples is 0% in NC-part.hclust, 2.4% in NC-part.kmeans and 0% in NC-Ward (Fig. 12). The three samples misclassified by NC-part.kmeans were rectified by the controlling LDA if run as wild-cards. The mean error rate of the three exploratory data analyses of 0.8% is clearly below the 4% threshold recommended by the Pragmatic Species Concept (Seifert 2014). Thus we have a strong justification for the species status of *C. atricolor* (for the relations between *C. candiotes* and *C. piceus* see there).

This clear result on the nest sample level is confirmed by analyses on individual level. The classification

error by a LDA considering the five blackish species given in Tab. 3 is only 1.3% in 77 worker individuals of *C. atricolor* and 0.8% in 357 individuals of all five species. The corresponding errors in a leave-one-out cross-validation LDA are 1.3% and 1.4% respectively.

### *Camponotus candiotes* Emery 1894

#### *Camponotus lateralis* var. *candiotes* Emery 1894

Investigated were 4 syntype workers labeled 'Creta (Cecconi) Omalo s Cata...' [last word of label illegible], 'SYNTYPUS *Camponotus lateralis*

**Table 3.** Species with completely blackish vertex. Absolute size, and RAV-corrected shape and seta characters referring to CS = 1.25 mm; sequence of data: arithmetic mean  $\pm$  standard deviation [minimum, maximum]

	<i>ebneri</i> (i=1)	<i>dalmaticus</i> (i=68)	<i>atricolor</i> (i=77)	<i>piceus</i> (i=139)	<i>candiotes</i> (i=41)	<i>spissinodis</i> (i=4)	<i>heidrunvogtae</i> (i=32)
	Lebanon	S Central Europe, Balkans	Pannonian Basin, SE Europe, Caucasus	S Temperate to Mediterranean Europe	Crete, Asia Minor, Caucasus	North Africa	Balkans
CS	940	1283 $\pm$ 268 [842,1778]	1140 $\pm$ 243 [858,1830]	1160 $\pm$ 227 [873,1736]	1141 $\pm$ 234 [896,1728]	1414 $\pm$ 461 [1012,1868]	1318 $\pm$ 300 [979,2022]
CL/CW <sub>1.25</sub>	1.113	1.084 $\pm$ 0.037 [1.022,1.143]	1.119 $\pm$ 0.020 [1.071,1.183]	1.110 $\pm$ 0.022 [1.046,1.153]	1.091 $\pm$ 0.023 [1.024,1.124]	1.114 $\pm$ 0.011 [1.094,1.109]	1.140 $\pm$ 0.015 [1.112,1.167]
SL/CS <sub>1.25</sub>	0.957	0.940 $\pm$ 0.035 [0.856,0.997]	0.965 $\pm$ 0.023 [0.899,1.010]	0.976 $\pm$ 0.024 [0.904,1.044]	0.960 $\pm$ 0.024 [0.918,1.026]	1.007 $\pm$ 0.022 [0.986,1.038]	1.069 $\pm$ 0.024 [1.014,1.115]
SCI <sub>1.25</sub>	1.323	1.194 $\pm$ 0.068 [1.094,1.365]	1.061 $\pm$ 0.030 [0.993,1.148]	1.206 $\pm$ 0.046 [1.118,1.322]	1.124 $\pm$ 0.044 [1.039,1.240]	1.062 $\pm$ 0.031 [1.016,1.085]	1.201 $\pm$ 0.042 [1.107,1.302]
MW/CS <sub>1.25</sub>	0.758	0.750 $\pm$ 0.021 [0.695,0.803]	0.786 $\pm$ 0.019 [0.740,0.861]	0.787 $\pm$ 0.018 [0.740,0.855]	0.787 $\pm$ 0.017 [0.740,0.820]	0.774 $\pm$ 0.005 [0.768,0.779]	0.759 $\pm$ 0.015 [0.728,0.789]
PrW/CS <sub>1.25</sub>	0.317	0.263 $\pm$ 0.016 [0.227,0.300]	0.313 $\pm$ 0.019 [0.266,0.371]	0.311 $\pm$ 0.019 [0.264,0.372]	0.314 $\pm$ 0.019 [0.283,0.358]	0.302 $\pm$ 0.018 [0.280,0.325]	0.251 $\pm$ 0.014 [0.229,0.283]
PrL/CS <sub>1.25</sub>	0.399	0.389 $\pm$ 0.021 [0.342,0.441]	0.445 $\pm$ 0.023 [0.401,0.502]	0.396 $\pm$ 0.022 [0.315,0.458]	0.437 $\pm$ 0.019 [0.389,0.470]	0.397 $\pm$ 0.011 [0.383,0.409]	0.429 $\pm$ 0.014 [0.399,0.460]
PeW/CS <sub>1.25</sub>	0.407	0.366 $\pm$ 0.021 [0.329,0.438]	0.427 $\pm$ 0.024 [0.368,0.478]	0.405 $\pm$ 0.026 [0.344,0.480]	0.407 $\pm$ 0.029 [0.362,0.479]	0.409 $\pm$ 0.011 [0.395,0.421]	0.370 $\pm$ 0.022 [0.332,0.417]
MGr/CS <sub>1.25</sub>	0.083	0.058 $\pm$ 0.008 [0.033,0.074]	0.037 $\pm$ 0.012 [0.015,0.080]	0.057 $\pm$ 0.015 [0.024,0.101]	0.076 $\pm$ 0.012 [0.049,0.097]	0.077 $\pm$ 0.012 [0.063,0.089]	0.053 $\pm$ 0.008 [0.040,0.074]
RipD <sub>1.25</sub>	8.35	7.57 $\pm$ 0.49 [6.3, 8.8]	7.61 $\pm$ 0.46 [6.6,9.1]	8.11 $\pm$ 0.60 [6.0, 9.4]	8.27 $\pm$ 0.52 [7.2,9.3]	8.90 $\pm$ 0.66 [8.45, 9.88]	8.44 $\pm$ 0.52 [7.5,9.4]
nSc <sub>1.25</sub>	0.5	0.54 $\pm$ 0.61 [0.0,2.2]	1.90 $\pm$ 1.28 [0.0,5.6]	1.47 $\pm$ 1.09 [0.0,4.8]	0.59 $\pm$ 0.91 [0.0,3.5]	1.50 $\pm$ 1.73 [0.0,3.0]	0.89 $\pm$ 0.82 [0.0,3.1]
nMn <sub>1.25</sub>	3.4	1.95 $\pm$ 0.70 [0.7,3.9]	7.17 $\pm$ 2.20 [1.4,12.8]	5.00 $\pm$ 1.39 [2.1, 9.2]	4.11 $\pm$ 1.18 [1.5,7.2]	4.05 $\pm$ 0.71 [3.6,5.1]	7.60 $\pm$ 1.08 [5.4,9.5]
nPR <sub>1.25</sub>	6.0	2.16 $\pm$ 0.63 [0.9, 3.3]	9.94 $\pm$ 2.85 [3.8,16.4]	7.50 $\pm$ 2.43 [2.5,19.7]	6.69 $\pm$ 1.58 [2.9,10.1]	5.58 $\pm$ 1.69 [3.2, 7.2]	8.05 $\pm$ 2.00 [3.5,12.3]

candiotes Emery, 1894', '*C. lateralis* var. *candiotes* Eme' and 3 syntype workers labeled 'Creta (Ceconi) La C....' [last word of label illegible], 'SYNTYPUS *Camponotus lateralis* candiotes Emery, 1894', 'ANTWEB CASENT0905389'; all material MCSN Genova. Both syntype series are clearly allocated to the cluster of 17 samples given in the next paragraph if run as wild-card in a 5-class LDA considering the five related species shown in Tab. 3 – the series with four syntypes is assigned with  $p = 0.9998$  and that with three syntypes with  $p = 1.0000$ .

**All material examined.** A total of 17 nest samples with 42 workers were subject to NUMOBAT investigation. **GEORGIA:** Tbilissi, 1985.07.16 [41.700, 44.751, 690]; Tbilissi, 1985.07.25 [41.70, 44.80, 600]. **GREECE:** Crete: Chania-6 km SW, Agia, 2011.05.03 [35.467, 23.917, 22]; Crete: Georgiopouli-E, 2007.04.30 [35.333, 24.350, 1]; Crete: Georgiopouli-W, 2007.05.02 [35.367, 24.250, 1]; Crete: Kato Daratso, 2011.05.06 [35.500, 23.983, 12]; Crete: La ... (illegible), pre 1894.xx.xx, syntypes *C. candiotes* [35.0, 25.0, 700; guess]; Crete: Lasithi, pre 1945 [35.08, 25.71, 341]; Crete: Omalos Plateau, 2011.05.03 [35.333, 23.843, 1034]; Crete: Omalos, ), pre 1894.xx.xx, syntypes *C. candiotes* [35.344, 23.905, 1040]; Crete: Rodakino-Sellia, 2013.05.08 [35.205, 24.350, 301]; Crete: vic. Preveli Beach, 2013.05.07 [35.182, 24.465, 58]; Holomontas: Stagira, 2009.09.03, No X [40.517, 23.733, 539]; Rhodos: Apollakkia, 2008.07.05 [36.050, 27.783, 34]; Rhodos: Dimylia, 2008.07.09 [36.333, 28.033, 91]. **TURKEY:** Halkapinar-32 km SE, 1997.05.08, No 224, No 226 [37.348, 34.360, 1700].

**Geographic range.** Crete, Rhodes, Asia Minor, Georgia. Eastern parapatric sibling species of *C. piceus* without safely confirmed range overlap. The single-specimen sample from Holomontas: Stagira, which is outside the known range of *C. candiotes* has a low posterior probability of  $p = 0.820$  when run as wild-card in an LDA against *C. piceus* and may be misidentified. There is sympatric occurrence with *C. atricolor* in Georgia.

**Diagnosis.** The character combinations to identify this species can be derived from the key, Tab. 3 and the following pictures in AntWeb.org: CASENT0281578 (minor worker), CASENT0281579 (minor), CASENT0905389 (minor, syntype of *C. candiotes*).

**Biology.** unknown.

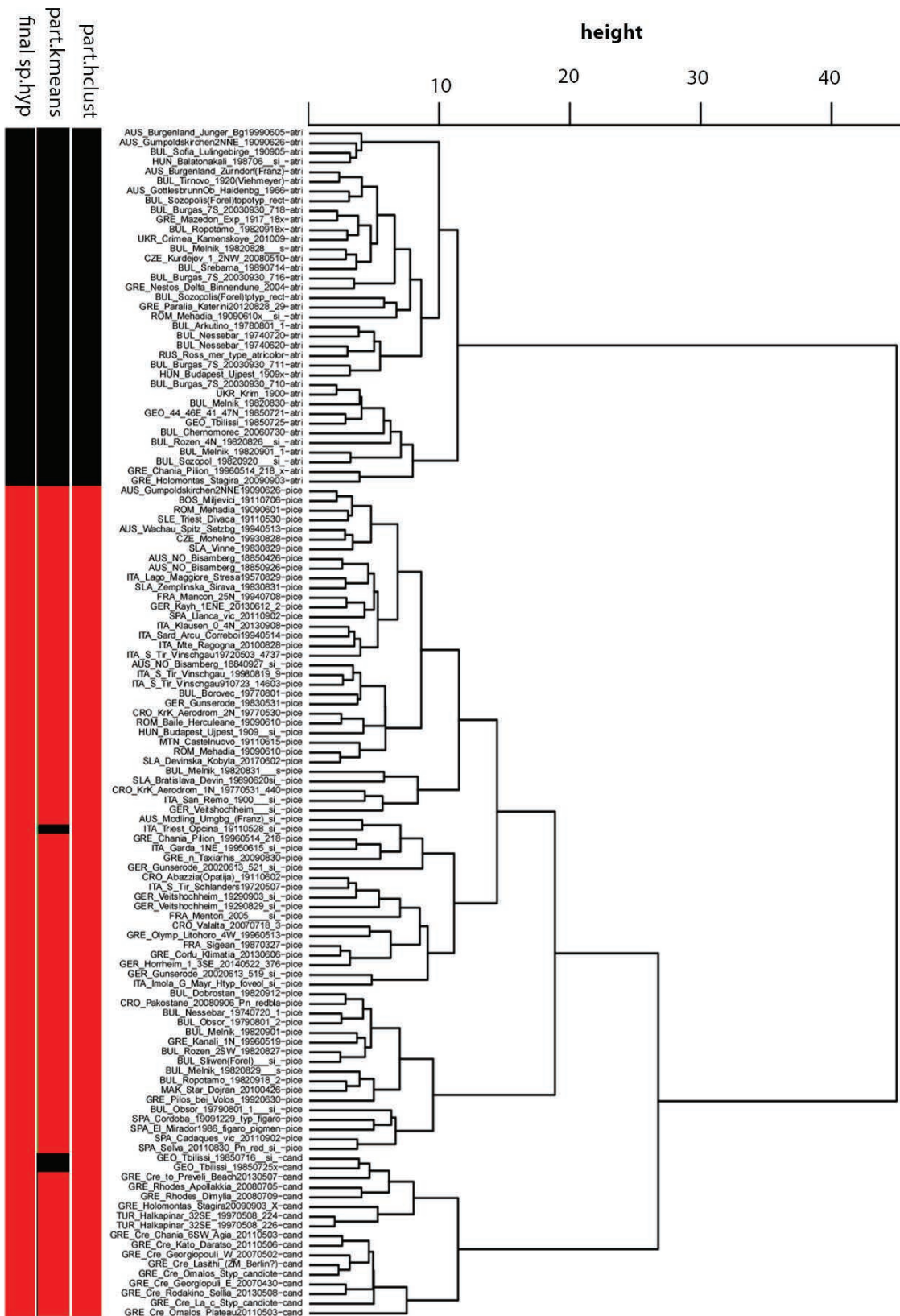
**Comments.** The exploratory data analyses NC-part.hclust, NC-part.kmeans, NC-NMDS-k-means and NC-Ward provided partially contradictory results regarding the heterospecificity of *C. candiotes* and *C. piceus* when CS and all 12 RAV-corrected shape and seta characters are considered. NC-Ward suggested *C. candiotes* to form a separate cluster with only one sample being misplaced (error 1.1% in 87 samples). However, both NC-part.hclust and NC-part.kmeans did not confirm the presence

of more than one cluster. Accepting the hypothesis formed by NC-Ward, a stepwise LDA was run which reduced the considered data set to the characters CL/CW<sub>1.25</sub>, SL/CS<sub>1.25</sub>, ScI<sub>1.25</sub>, MGr/CS<sub>1.25</sub>, nSc<sub>1.25</sub> and PrL/CS<sub>1.25</sub>. Under this setting, NC-part.hclust fully confirmed the hypothesis formed by NC-Ward with three samples of *C. piceus* remaining unclassified – i.e., being placed as outliers. NC-NMDS-k-means clustering fully confirmed the hypothesis of NC-Ward but NC-part.kmeans, however, failed again to confirm the presence of two clusters (Fig. 13). With three exploratory data analyses confirming the final species hypothesis and one failing, I hypothesize *C. candiotes* to represent an eastern parapatric sibling species of *C. piceus*. The classification error in 180 individual workers is 1.1% by an LDA and 1.7% by a leave-one-out cross-validation LDA.

### *Camponotus piceus* (Leach 1825)

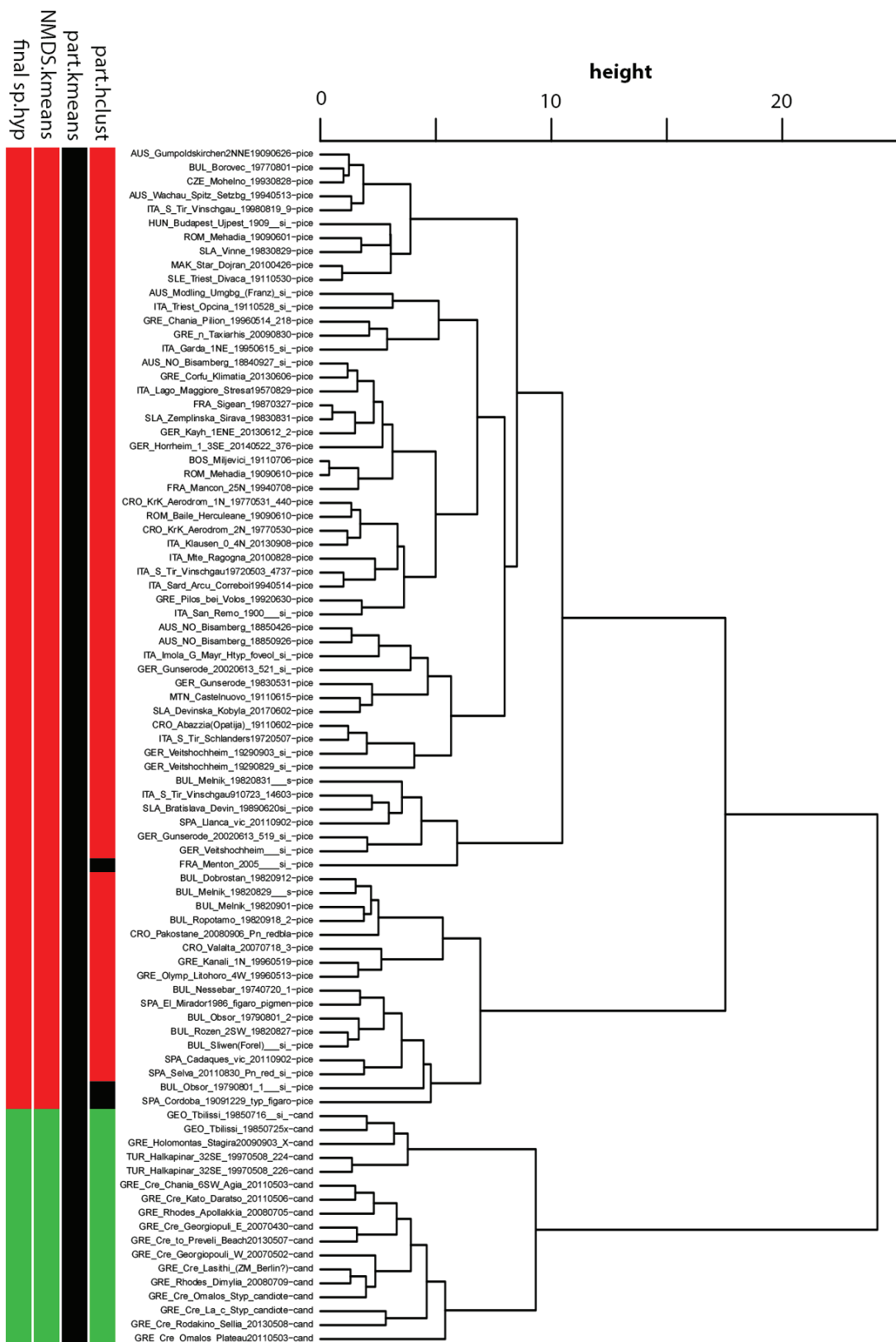
#### *Formica picea* Leach 1825

This taxon has been described from Nice in southern France. The full text of the original description is 'Capite, antennis, thorace, abdomine pedibusque piceis, glaberimis, nitentibus; geniculis tarsisque ferrugineis. Corporis longitudo. M 5 mm, g 10 mm, w 5 mm.' Figures were not given and it seems that no later revising taxonomist has seen original material of Leach and that types do not exist. Hence, it appears difficult to understand how revisers could reasonably allocate such a crude description to a certain species. There are several possible candidates for entirely blackish ants of this size from the environs of Nice with a glabrous shining surface, and apparently having no spines or dents on mesosoma (if so, Leach should have mentioned it as he did in other species descriptions). A *Formica* species, namely *F. gagates* Latreille or *F. fusca* Linnaeus, may be excluded because males of this subgenus do not have a clearly smaller body length than gynes. The jet black *Lasius* (*Dendrolasius*) *fuliginosus* can be excluded too because virgin gynes do not reach 10 mm. Blackish species related to *Lasius niger* might roughly match the size distribution over the three castes, but ferruginous 'knees' (i.e., the femora-tibial joint) contrasting the blackish color of femora and tibiae do not occur here as it is with glabrous, shining and jet black surfaces. It is also not very likely that *Formica picea* Leach could refer to one of the two species of *Proformica* occurring in the vicinity of Nice (Galkowski et al. 2017) as these do not seem to have big differences in total body length between males and gynes and are more medium to dark brown in overall coloration and not glabrous. Hence, this argumentation



**Figure 12.** Classification of *Camponotus atricolor* (black bars) against the cryptic species pair *C. piceus* + *C. candiotes* (red bars) in three different exploratory data analyses using body size and the full (unselected) set of RAV-corrected shape and setae characters. The error relative to the final species hypothesis is 0% in NC-Ward, 0% in NC-part.hclust and 2.4% in NC-part.kmeans.





**Figure 13.** Classification of *Camponotus candiotes* (green bars) and *C. piceus* (red bars) by four exploratory data analyses considering body size and five RAV-corrected shape characters. The error relative to the final species hypothesis is 0% in NC-Ward, 0% in NC-NMDS-k-means and 0% in NC-part.hclust. However, as indicated by black bars, 3.5% of the samples remained unclassified in NC-part.hclust and NC-part.kmeans failed to confirm two separate clusters.

finally points to a black species of the *Camponotus lateralis* group – at least there is no character in Leach's description that is contradictory to this view. As the geographic distribution of the other blackish species of the group, namely *C. atricolor*, *C. candiotes* and *C. heidrunvogtae* n.sp., is much more eastern, there is sufficient reason to maintain the name allocation as it was done by other myrmecologists in the past. To settle this point, I designate herewith a neotype of *C. piceus* in a sample of two workers from near Nice, stored in SMN Görlitz and labeled 'FRA: 43.799°N, 7.488°N, 90 m / Menton – 2.8 km N / leg. C. Galkowski 2011.08.10' and 'Neotype (top) / *Camponotus piceus* (Leach 1825) / des. B. Seifert 2018'. The two workers of the neotype sample are allocated to *C. piceus* with a mean posterior probability of  $p = 0.9998$  if run as wild-card in a 5-class LDA considering the five black species of the group given in Tab. 3.

#### *Camponotus foveolata* (Mayr 1853)

This taxon has been described by Mayr as *Formica foveolata* from Blocksberg near Ofen in Hungary, from Imola in Italy and from Rauhkogel near Mödling in Austria. Herewith, a lectotype is designated in a worker labeled 'Imola G.Mayr', 'z. G.Mayr.Bd.III. p.101-277', 'Form. foveolata det. G.Mayr', 'Type' and 'Lectotype *Formica foveolata* Mayr, 1853 des. B.Seifert 2012'. One paralectotype male is labeled 'Imola G. Mayr', 'z. G. Mayr. Bd.III. p.101-277', 'Form. foveolata det. G. Mayr' and 'Paralectotype *Formica foveolata* Mayr, 1853 des. B.Seifert 2012'. Both specimens are stored in NHM Wien. The lectotype worker is allocated to the *C. piceus* cluster with  $p = 0.9992$  if run as wild-card in a 5-class LDA considering the five black species of the group.

#### *Camponotus ebeninus* Emery 1869

According to a message of Maria Tavano of 16 October 2013 there are no type specimens in the Emery collection of MCSN Genova. Emery's original description of this taxon, that was collected in the vicinity of Naples, indicates a black ant with a mesosomal shape and sculpture similar to *Camponotus piceus*. As other blackish species are not known so far from Italy and because nobody is currently able to present counter-evidence, I synonymize it with *C. piceus*.

#### *Camponotus (Myrmentoma) piceus* st. *spissinodis* var. *dusmeti* Santschi 1932 [unavailable name]

Investigated were three specimens on the same pin from NHM Basel, labeled 'Camponotus spissinodis Fo / v. dusmeti Sants', 'Viladrau (G.) 13.

VIII. 28' 'Type'; 'ANTWEB CASENT 0911703', 'ANTWEB 0911703'. Two of these specimens, a major worker (CASENT0911702) and a minor worker (CASENT0911703), were investigated by NUMOBAT. They were allocated with  $p = 0.9958$  (minor) and  $p = 0.9990$  (major) to the *C. piceus* cluster if run as wild-card in a 5-class LDA considering the five black species of the group shown in Tab. 3 and using all available characters.

#### *Camponotus figaro* Collingwood & Yarrow 1969 [New Synonym]

[first available use of *Camponotus lateralis* subsp. *piceus* var. *figaro* Emery 1924]. Investigated were two syntype workers labeled 'Cordoba 29-XII-922', 'SYNTYPUS *Camponotus lateralis piceus* var. *figaro* Emery, 1924', 'ANTWEB CASENT 0905390' from MCSN Genova. These workers with completely reddish pronotum (see data in section 4.3 on the low taxonomic value of color characters) are allocated to the *C. piceus* cluster with both  $p = 1.0000$  if run as wild-card in a 5-class LDA considering the five black species of the group and they are in any structural character consistent with this species.

**All material examined.** A total of 70 nest samples with 137 workers were subject to NUMOBAT investigation. **AUSTRIA:** Bisamberg, 1884.09.27 [48.319, 16.360, 300]; Bisamberg, 1885.04.26 [48.319, 16.360, 300]; Bisamberg, 1885.09.26 [48.319, 16.360, 300]; Gumpoldskirchen-2 km NE, [48.062, 16.292, 350]; Mödling vicinity (Franz), pre 1960, [48.08, 16.27, 300]; Spitz, Setzberg, 1994.05.13 [48.365, 15.396, 330]. **BOSNIA:** Miljević, 1911.07.06 [43.84, 18.41, 1020]. **BULGARIA:** Borovec, 1977.08.01 [42.26, 23.61, 1300]; Dobrostan, 1982.09.12 [41.92, 24.90, 1470]; Melnik, 1982.08.29 [41.524, 23.401, 460]; Melnik, 1982.08.31 [41.538, 23.406, 465]; Melnik, 1982.09.01 [41.538, 23.406, 465]; Nessebar, 1974.07.20 [42.66, 27.71, 10]; Obsor, 1979.08.01, No1, No 2 [42.82, 27.88, 30]; Ro-potamo, 1982.09.18, No 2 [42.302, 27.728, 9]; Rozen-2km SW, 1982.08.27 [41.516, 23.423, 439]; Sliwen (Forel), pre 1895 [42.69, 26.31, 420]. **CROATIA:** Abazzia (Opatija), 1911.06.02 [45.33, 14.31, 140]; Krk: Aerodrom-1 km N, 1977.05.31 [45.229, 14.572, 92]; Krk: Aerodrom-2 km N, 1977.05.30 [45.237, 14.560, 50]; Pakostane, 2008.09.06 [45.917, 15.500, 0]; Valalta, 2007.07.18 [45.126, 13.627, 25]. **CZECHIA:** Mohelno, 1993.08.28 [49.109, 16.186, 380]. **FRANCE:** Mancon-25 km N, 1994.07.08 [46.581, 4.834, 335]; Menton, 2005.xx.xx [43.777, 7.498, 40]; Menton – 2.8 km N, 2011.08.10, neotype *C. piceus* [43.799, 7.488, 90]; Sigean, 1987.03.27 [43.00, 3.00, 15]. **GERMANY:** Günserode, 1983.05.31 [51.313, 11.049, 170]; Günserode, 2002.06.13, No 519, No 521 [51.313, 11.049, 170]; Hor-rheim, 2014.05.22, No 376 [48.971, 9.003, 226]; Kayh-1 km ENE, 2013.06.12, No 2 [48.581, 8.934, 534]; Veitshöchheim (Goesswald), pre 1930 [49.854, 9.862, 240]; Veitshöchheim, 1929.08.29 [49.854, 9.862, 240]; Veitshöchheim, 1929.09.03 [49.854, 9.862, 240]. **GREECE:** Chania: Pilion, 1996.05.14,

No 218 [39.398, 23.045, 1200]; Corfou: Klimatia, 2013.06.06 [39.741, 19.790, 311]; Kanali- 1 km N, 1996.05.19 [39.076, 20.688, 17]; Lithoro-4 km W, 1996.05.13 [40.112, 22.480, 600]; Volos: Pilos, 1992.06.30 [39.36, 23.08, 600]; Taxiarchis, 2009.08.30 [40.400, 23.517, 594]. **HUNGARY:** Budapest-Ujpest, 1909.xx.xx [47.567, 19.092, 110]. **ITALY:** Garda-1 km NE, 1995.06.15 [45.59, 10.73, 260]; Imola (Mayr), pre 1854, lectotype *C. foveolata* [44.36, 11.71, 44]; Klausen-0.4 km N, 2013.09.08 [46.642, 11.568, 579]; Stresa, 1957.08.29 [45.88, 8.52, 330]; Monte Ragogna, 2010.08.28 [46.187, 12.966, 353]; Schlanders (Silandro), 1972.05.03, No 4737 [46.63, 10.77, 900]; Schlanders (Silandro), 1972.05.07 [46.63, 10.77, 900]; Vinschgau, 1991.07.23, No 14603 [46.690, 11.068, 1000]; Vinschgau, 1998.08.19, No 9 [46.690, 11.068, 1000]; San Remo, 1900.xx.xx [43.82, 7.78, 60]; Sardegna: Arcu Correboi, 1994.05.xx [40.10, 9.35, 1150]; Trieste: Opcina, 1911.05.28 [45.69, 13.79, 323]. **MACEDONIA:** Star Dojran, 2010.04.26 [41.169, 22.717, 240]. **MONTENEGRO:** Castelnuovo, 1911.06.15 [42.46, 18.53, 160]. **ROMANIA:** Baile Herculeane, 1909.06.10 [44.87, 22.41, 135]; Mehadia, 1909.06.01 [44.90, 22.36, 166]; Mehadia, 1909.06.10 [44.90, 22.36, 166]. **SLOVAKIA:** Bratislava-Devin, 1989.06.20 [48.199, 16.975, 193]; Devinska Kobyla, 2017.06.02 [48.199, 16.975, 193]; Vinne, 1983.08.29 [48.819, 21.950, 280]; Zemplinska Sirava, 1983.08.31 [48.621, 21.341, 171]. **SLOVENIA:** Trieste: Divaca, 1911.05.30 [45.68, 13.97, 436]. **SPAIN:** Cadaques, 2011.09.02 [42.300, 3.217, 203]; Cordoba, 1909.12.29, syntypes *C. figaro* [37.888, -4.78, 140]; El Mirador, 1986.xx.xx [37.84, -0.85, 64]; Llanca, 2011.09.02 [42.35, 3.10, 79]; Selva, 2011.08.30 [41.783, -2.850, 230]; Viladrau, 1928.08.13 [41.848, 2.390, 825].

**Geographic range.** From Iberia to Balkans, south Central Europe north to 51.3°N. It is not known so far from Asia Minor and is apparently a western parapatric sibling species of *C. candiotes*. There is broad range overlap with *C. atricolor* in E Central Europe and the Balkans.

**Diagnosis.** The character combinations to identify this species can be derived from the key, Tab. 3, Figs 14 and 15 and the following pictures in AntWeb.org: CASENT0173136 (minor worker), CASENT0249995 (minor), CASENT09115597 (major, lectotype *C. foveolata*).

**Biology.** see Seifert (2018).

**Comments.** For species delimitation from *Camponotus candiotes* and *C. atricolor* by exploratory and hypothesis-driven data analyses see there.

### *Camponotus heidrunvogtae* sp. nov.

= *Camponotus piceus* sp. 2: Seifert (2007)

= *Camponotus* sp. LONG: Seifert (2018)

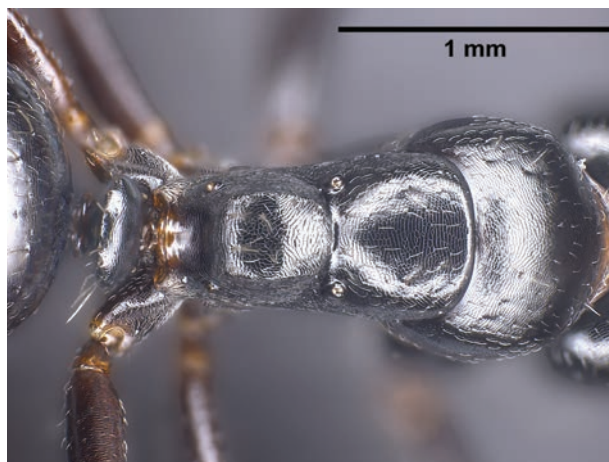
**Etymology.** The species name is dedicated to Heidrun Vogt, the wife of Dieter Vogt who sponsored ant research in Senckenberg Museum of Natural History Görlitz and biodiversity research in general.



**Figure 14.** Head of the neotype minor worker of *Camponotus piceus*.



**Figure 15.** Lateral aspect of the neotype minor worker of *Camponotus piceus*.



**Figure 16.** Dorsal aspect of the neotype minor worker of *Camponotus piceus*.



**Type material.** Holotype worker labeled 'BOS: 43.5978°N, 17.7272°E/ Jablanica, 210 m/ *Carpinus-Fraxinus* wood/ A. Vesnic 2013.08.22-54' and 'Holotype *Camponotus heidrunvogtae* Seifert'; 2 paratype workers from the same nest as holotype, labeled 'BOS: 43.5978°N, 17.7272°E/ Jablanica, 210 m/ *Carpinus-Fraxinus* wood/ A. Vesnic 2013.08.22-54' and 'Paratypes *Camponotus heidrunvogtae* Seifert'; 3 paratype workers from another nest, labeled 'BOS: 43.5978°N, 17.7272°E/ Jablanica, 210 m/ *Carpinus-Fraxinus* wood/ A. Vesnic 2013.08.22-55' and 'Paratypes *Camponotus heidrunvogtae* Seifert'; all material is stored in SMN Görlitz.

**All material examined.** A total of 13 nest samples with 32 workers were subject to NUMOBAT investigation: **BOSNIA** and **HERCEGOVINA:** Jablanica, 2013.08.22, types of *C. heidrunvogtae* n.sp., No 54, No 55 [43.598, 17.727, 210]. **CROATIA:** Jurevo, 1997.06.03, No 516 [44.92, 14.92, 48]; Lukovo, 2005.05.30 [44.856, 14.893, 15]; Pakostane, 2008.09.04 [43.910, 15.510, 18]; Skradin, Krka, 2014.05.31, No 15 [43.817, 15.933, 11]; Ugrini-8 road km N, 1997.06.04, No 560 [45.186, 14.767, 700]. **GREECE:** Corfou: Klimatia, 2013.06.06 [39.741, 19.790, 311]; Corfou: Pandokrator, 2013.06.07 [39.748, 19.864, 736]; Ritini-Elatochori, 2012.09.03 [40.303, 22.266, 748]. **MONTENEGRO:** Podgorica-12 km NE, 2014.06.04, No 21 [42.546, 19.367, 131]; NW of Lake Skadar, 2014.06.03, No 18 [42.304, 19.048, 152].

**Geographic range.** The species seems to be restricted to the W Balkans, with a known geographic range covering only 120 000 km<sup>2</sup>. Most of the known sites are along the Dinaric coast and the western slope of Dinaric mountains and all are situated below 1000 m.

**Diagnosis** (Tab. 3, key). This is the most easily identifiable species of the *C. lateralis* group. Its diagnostic characters are a combination of a very long scape, a narrow dorsal propodeal plane and a blackish head (see key). The major workers achieve a size larger than in any known species of the *C. lateralis* group.

**Description** (in contrast to Tab. 3, all numerics given here are primary, not RAV-corrected data)

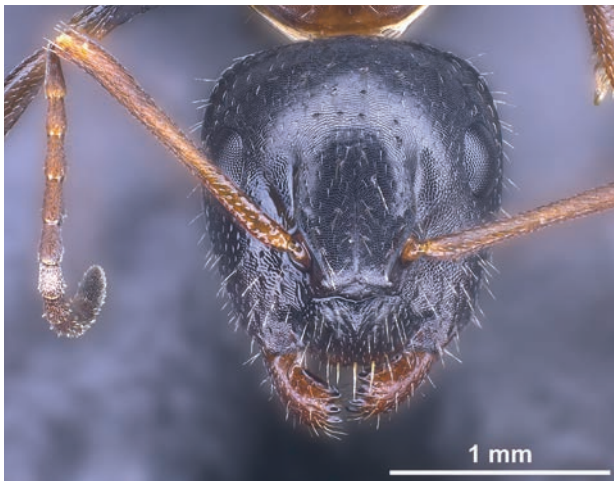
-- Minor worker (Figs 14–16), data of 22 specimens: Larger than related species, CS 1140 ± 122 [979, 1427] µm. Head and scape relatively long, CL/CS 1.144 ± 0.021 [1.084, 1.170], SL/CS 1.113 ± 0.051 [0.999, 1.167]. All surfaces of head, mesosoma and gaster with long erect setae. Extension of large scape diameter near to scape base strong, ScI 1.235 ± 0.041 [1.167, 1.341]. Dorsal plane of scape with occasional semi-erect or erect setae, nSc 0.9 ± 0.6 [0.5, 2.5]. Mesosoma rather narrow, MW/CS 0.759 ± 0.021 [0.707, 0.781]. Mesonotum and propodeum with, in terms of the *C. lateralis* group, many semi-erect to erect setae, nMn 6.5 ± 1.3 [4.0, 8.5], nPr 7.4 ± 1.6 [5.5, 11.5]. Dorsal propodeal plane narrow, PrW/CS 0.252 ± 0.016 [0.229, 0.284], in lateral view moderately convex, its median part a little higher than

at level of its lateral edges (a difference to *C. atricolor*, *piceus* and *dalmaticus*). Metanotal groove moderately deep, MGr/ CS 0.056 ± 0.006 [0.045, 0.076]. Surface of head capsule and mesosoma moderately shining, with clinker-like microsculpture, appearing at smaller magnifications as microripples with reticular component. This microrelief is deeper on dorsal propodeum and flatter on gaster. Distance of micro-ripples on dorsal area of 1st gaster tergite relatively small, RipD 8.35 ± 0.46 [7.44, 9.15] µm. Head, mesosoma, petiole and gaster blackish, pronotum occasionally reddish on its lateral or entire surface. Coxae and femora usually dark brown. Mandibles, antennae, distal part of femora, metatarsae and tarsi usually light reddish brown.

-- Major worker (Figs 17–19) data of 10 specimens: Larger than related species, CS 1710 ± 162 [1494, 2022] µm. Head and scape relatively long, CL/CS 1.025 ± 0.036 [0.967, 1.074], SL/CS 0.864 ± 0.050 [0.769, 0.919]. All surfaces of head, mesosoma and gaster with long erect setae. Extension of large scape diameter near to scape base even in large specimens still visible (at least suggested: ScI 1.096 ± 0.043 [1.058, 1.200]). Dorsal plane of scape with few semi-erect or erect setae, nSc 2.5 ± 1.2 [0.5, 4.5]. Mesosoma rather narrow, MW/CS 0.678 ± 0.023 [0.642, 0.710]. Mesonotum and propodeum with, in terms of the *C. lateralis* group, many semi-erect to erect setae, nMn 11.9 ± 1.6 [8.0, 14.0], nPr 10.6 ± 3.5 [5.0, 17.0]. Dorsal propodeal plane narrow, PrW/CS 0.237 ± 0.013 [0.224, 0.263], in lateral view only very feebly convex, its median part a little higher than at level of its lateral edges. Metanotal groove moderately deep, MGr/ CS 0.049 ± 0.011 [0.039, 0.073]. Vertex with the bases of setae formed as deep foveolae. Surface of head capsule and mesosoma moderately shining, with clinker-like microsculpture, appearing at smaller magnifications as microripples with a reticular component. This microrelief is much flatter on gaster. Distance of micro-ripples on dorsal area of 1st gaster tergite relatively small, RipD 8.82 ± 0.75 [7.80, 9.67] µm. Head, mesosoma, petiole and gaster blackish, entire pronotum occasionally (but its lateral part frequently) reddish. Coxae and femora usually blackish brown. Mandibles dark reddish brown, antennae, distal part of femora, metatarsae and tarsi usually medium reddish brown.

**Biology.** The species was found in open xerothermous habitats which showed much surface coverage by rock or scree. Nests were also found at open, sunny spots within broad-leaved forest (*Quercus*, *Carpinus*, *Fraxinus*). Nests were under stones or in soil. According to Adi Vesnic, the species is more thermophilic than sympatrically occurring *C. piceus*. This assessment on the microclimatic scale is in agreement with macroclimatic data.

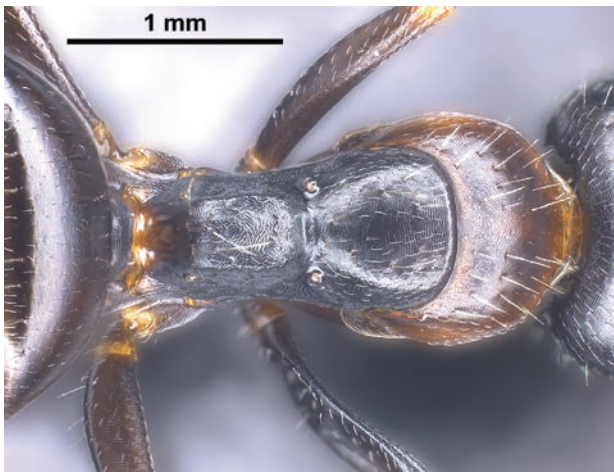




**Figure 17.** Head of a large minor worker of *Camponotus heidrunvogtae* n.sp., holotype.



**Figure 18.** Lateral aspect of large minor worker of *Camponotus heidrunvogtae* n.sp., holotype.



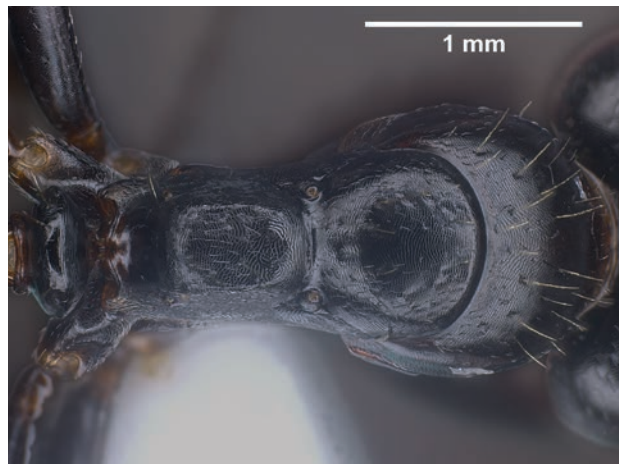
**Figure 19.** Dorsal aspect of large minor worker of *Camponotus heidrunvogtae* n.sp., holotype.



**Figure 20.** Head of major worker of *Camponotus heidrunvogtae* n.sp. from Corfou: Klimatia, 2013.06.06.



**Figure 21.** Lateral aspect of major worker of *Camponotus heidrunvogtae* n.sp. from Corfou: Klimatia, 2013.06.06.



**Figure 22.** Dorsal aspect of major worker of *Camponotus heidrunvogtae* n.sp. from Corfou: Klimatia, 2013.06.06.

## 5. Acknowledgments

With many thanks I acknowledge the arrangement of loans of type specimens by the following curators of ant collections: Anders Albrecht / FMN Helsinki, Stefan Cover / MCZ Cambridge, Celal Karaman / Trakya University of Edirne, Bernard Landry / MHN Genève, Maria Tavano / MCSN Genova, Dominique Zimmermann / NHM Wien and Isabelle Zürcher /NHM Basel. Furthermore I am indebted to Lech Borowiec / Wrocław University, Andreas Schulz / Leverkusen, Adi Vesnic / University of Sarajevo, Herbert Wagner / Graz and Christophe Galkowski / St. Aubin de Medoc for kindly donating ant material they have collected in the field and Roland Schultz /SMN Görlitz for taking and processing the fine z-stack photos of type specimens. I also wish to thank two anonymous referees for useful comments on the manuscript.

## 6. References

- Bolton, B. (2003): Synopsis and classification of Formicidae. – *Memoirs of the American Entomological Institute* **71**: 1–370.
- Borowiec, L. (2014): Catalogue of ants of Europe, the Mediterranean Basin and adjacent regions (Hymenoptera: Formicidae). – *Genus-Monograph* **25** (1-2): 1–340.
- Borowiec, L. & Salata, S. (2014): Redescription of *Camponotus nitidescens* Forel, 1889, new status and notes on ants from Kefalonia, Greece (Hymenoptera: Formicidae). – *Genus* **25**: 499–517.
- Collingwood, C. A. & I. H. H. Yarrow (1969): A survey of Iberian Formicidae (Hymenoptera). – *EOS Revista Española de Entomología* **44**: 53–101.
- Csösz, S. & B. L. Fisher (2015): Diagnostic survey of Malagasy *Nesomyrmex* species-groups and revision of hafahafa group species via morphology based cluster delimitation protocol. *ZooKeys* **526**: 19–59 [<https://doi.org/10.3897/zookeys.526.6037>].
- Forel, A. (1912): Formicides Néotropiques. Part 6. 5me sous-famille Camponotinae Forel. – *Mémoires de la Société Entomologique de Belgique* **20**: 59–92.
- Galkowski, C., C. Lebas, P. Wegnez, A. Lenoir & R. Blatrix (2017): Redescription of *Proformica nasuta* (Nylander, 1856) (Hymenoptera, Formicidae) using an integrative approach. – *European Journal of Taxonomy* **290**: 1–40.
- Seifert, B. (2007): Die Ameisen Mittel- und Nordeuropas. – Lutra, Tauer, Germany: 368 pp.
- Seifert, B. (2008): Removal of allometric variance improves species separation in multi-character discriminant functions when species are strongly allometric and exposes diagnostic characters. – *Myrmecological News* **11**: 91–105.
- Seifert, B. (2014): A pragmatic species concept applicable to all eukaryotic organisms independent from their mode of reproduction or evolutionary history. – *Soil Organisms* **86**: 85–93.
- Seifert, B. (2016): Analyzing large-scale and intranidal phenotype distributions in eusocial Hymenoptera – a taxonomic tool to distinguish intraspecific dimorphism from heterospecificity. – *Myrmecological News* **23**: 41–59.
- Seifert, B. (2018): The Ants of Central and North Europe. – Lutra, Tauer, Germany: 408 pp.
- Wagner, H. C. (2014): Die Ameisen Kärntens. Verbreitung, Biologie, Ökologie und Gefährdung. – *Naturwissenschaftlicher Verein für Kärnten, Klagenfurt*: 464 pp.
- Wheeler, W. M. (1913): Corrections and additions to „List of type species of the genera and - subgenera of Formicidae“. – *Annals of the New York Academy of Sciences* **23**: 77–83.