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A revision of the Palaearctic species of the ant genus *Cardiocondyla* Emery 1869 (Hymenoptera: Formicidae)

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Abstract

A synopsis of the Palaearctic species of the ant genus *Cardiocondyla* Emery 1869 is provided. The four species groups which are of Palaearctic origin or which are restricted in their distribution to this faunal zone, the *C. elegans*, *C. ulianini*, *C. batesii* and *C. stambuloffii* group—consisting of 25 recognized species—are taxonomically revised. Further nine species belonging to species groups of Ethiopic and Oriental origin which may penetrate into and build up true outdoor populations in the southern Palaearctic are only treated in the determination key. The main working rationale of this revision is Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT) with formation of species hypotheses largely based on exploratory data analyses and checking these hypotheses by discriminant analysis. NUMOBAT data of the species considered comprise 727 worker samples with 1555 individuals and 23,300 primary data. Including high-resolution photos of surface microstructures, all species are depicted by z-stack imaging in four standard visual positions. Numeric data on 19 phenotypical characters are presented in comparative tables and supplementary verbal descriptions are given. In contrast to species groups with Ethiopian, Oriental and Australasian origin, no member of the four Palaearctic species groups has developed a tramp species potential to spread globally. Four cryptic species are described as new: *Cardiocondyla dalmaticoides* **n. sp.**, *C. caspiense* **n. sp.**, *C. verdensis* **n. sp.** and *C. rolandi* **n. sp.** Confirmed were the synonymies of *Cardiocondyla elegans santschii* Forel 1905, *C. provincialis* Bernard 1956 and *Xenometra gallica* Bernard 1957 with *C. elegans* Emery 1869, that of *C. elegans eleonorae* Forel 1911 with *C. bulgarica* Forel 1892, that of *C. elegans torretassoi* Finzi 1936 with *C. nigra* Forel 1905, and that of *C. bogdanovi* Ruzsky 1905, *C. montandoni* Santschi 1912 and *C. stambuloffii taurica* Karavajev 1927 with *C. stambuloffii* Forel 1892. *Cardiocondyla bicoronata* Seifert 2003 was newly synonymized with *C. nigra* Forel 1905.

Key words: cryptic species, numeric morphology-based alpha-taxonomy

Introduction

The members of the ant genus *Cardiocondyla* Emery 1869 have very early attracted the attention of evolutionary biologists in studies of diverse sociobiological questions (Hamilton 1979, Kinomura & Yamauchi 1987, Stuart *et al.* 1987, Heinze & Hölldobler 1993, Heinze 2017). All species show a character extremely rare within ants: they develop ergatoid males with a lifelong spermatogenesis which try to eliminate competing males in order to monopolize all intranidal matings with female sexuals. The species are distributed worldwide across the tropical, subtropical and temperate zones. They are not native in the Americas whereto they have been anthropogenically introduced. *Cardiocondyla* ants seem to play an inferior role within the ecosystem context: their effect on flow of matter and energy is negligible compared to other ant genera and they often occur in marginal habitats or ecotones. There are also no reports that polygynous *Cardiocondyla* tramp species with worldwide spread have ever become an economic or ecological problem in introduction areas.

According to the collection material investigated by the author in the last three decades, the world-wide fauna of the ant genus *Cardiocondyla* Emery 1869 comprises 79 separable species six of which are still undescribed. Three modern revisionary works dealing with several species groups of *Cardiocondyla* ants have been published after the turn of the millennium. Seifert (2003) considered the four species groups which are of fully Palearctic origin and those five species groups of Ethiopic and Oriental origin some members of which may penetrate the southern Palaearctic. The amount of data collected since then prompted Seifert *et al.* (2017) to re-analyze the *C. nuda* group and to separate it into eight species. The last addition to *Cardiocondyla* taxonomy was the long overdue revision of eight species groups with Oriental and Australasian origin in which eleven new species were described (Seifert 2023). The latter publication also proposed a subdivision of the global fauna into 17 species groups.

The revision presented here considers in its taxonomic part only the members of those species groups of the ant genus *Cardiocondyla* Emery 1869 which are of Palaearctic origin or which are restricted in their distribution to this faunal zone. These are 25 species of the *Cardiocondyla elegans*, *C. ulianini*, *C. batesii* and *C. stambuloffii* species groups of which four species are described here as new. In order to comprise all species with outdoor occurrence in the Palaearctic, the key added nine species of species groups with other zoogeographic origin which range reached into the southern Palaearctic. The main working rationale of this revision is Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT, Seifert 2009) with formation of species hypotheses largely based on exploratory data analyses and checking these hypotheses by discriminant analysis.

Material

This revision is almost completely worker-based. Gynes (female sexuals) were only considered when primary types were fixed in this caste. NUMOBAT data of the species groups considered in this paper comprise 727 worker samples with 1555 individuals and 23,300 primary data. With the exception of type specimens and other samples of special relevance, data of this material are not presented in detail in the main text of this paper but listed up in the electronic supplementary information SI1 and SI2. The abbreviations of type depositories are as follows:

MCSN Genova—Museo Civico die Storia Naturale Genova, Italy
MCZ Cambridge—Museum of Comparative Zoology of the Harvard University, Cambridge, USA
MCZ Lausanne—Musée cantonal de zoologie, Lausanne, Switzerland
MHN Genève—Muséum d'histoire naturelle de Genève, Genève, Switzerland
MNHN Paris—Muséum nationale d'histoire naturelle de Paris, Paris, France
NHM Basel—Naturhistorisches Museum, Basel, Switzerland
NHM Wien—Naturhistorisches Museum Wien, Wien, Austria
SIZ Kiev—Schmalhausen Institute of Zoology, Kiev, Ukraine
SMN Görlitz—Senckenberg Museum für Naturkunde, Görlitz, Germany
ZIPAS Warszawa—Zoological Institute of the Polish Academy of Sciences, Warszawa, Poland
ZM Lund—Zoologiska Museet Lund, Lund, Sweden
ZMLU Moskva—Zoological Museum of Moscow Lomonossov University, Moskva, Russia
ZM St. Petersburg—Zoological Museum of the St. Petersburg University, St. Petersburg, Russia

Methods

The applied species concept

The GAGE species concept (Seifert 2020) is used here. It states that species are separable clusters defined alone by nuclear genes and/or their expression products. The morphology investigated here is such an expression product. The concept requires to test taxonomic hypotheses by exploratory and hypothesis-driven data analyses and using the threshold principle to evaluate evolutionary divergence. Yet, this ideal approach was not applicable in 24% of the 25 species considered here. These species were only represented by a single sample and I had to content myself with an assessment if their NUMOBAT data, shape and surface structures were outside the range of variation of the next similar species with sufficient sample size. One reason for this sample size deficiency is the difficulty to collect nest samples because of the very time-consuming locating of the extremely concealed nest sites and easy overlooking due to small forager numbers and very small body size. Unfortunately, there is so far no taxonomically informative investigation of nuclear DNA in *Cardiocondyla* and we are completely uninformed about how frequent interspecific hybridization, known in a single species pair from laboratory crossbreeding experiments (Yamauchi *et al.* 2007), occurs in the natural context. Yet, compared to other ant groups, the genus is expected to show a lower hybridization frequency due to the increased rate of intranidal mating and the rarity of normal swarming flights with outcrossing.

Another repeat of my earlier statements on Ernst Mayr's species concept (Seifert 2014, 2018, 2020) appeared necessary here as result of the peer reviewing process. The GAGE species concept considers allopatric populations as different species if they are clusterable below a small threshold of error. This is a pragmatism avoiding disputes in which no party has convincing arguments. Why ? When a taxonomist performs a revisionary work over a large geographic range as the Palaearctic region, he/she inevitably encounters a lot of clearly allopatric entities isolated by deserts, seas, or high up in mountain areas. Here and in many other practical situations it is undecidable if there is "reproductive isolation," "moderate gene flow," or "unlimited gene flow." The entities are not in contact in the given natural context and crossbreeding experiments with them in captivity are problematic and can often not provide an answer (Seifert 2020). This is due to the fact that reproductive isolation between species is established amazingly late. For instance it occurs about 5 million years after phylogenetic splitting in passerine birds with a shorter generation time and 17 million years in nonpasserine birds with a longer generation time (Price & Bouvier 2002) or after 30 million generations in *Heliconius* butterflies (Edelmann *et al.* 2019). As a consequence, the reproductive isolation criterion (Mayr 1942, 1982) is only applicable in a minority of situations: in the special cases when the taxa to be separated are sympatric, semipatric or at least in direct contact along a front line. Given this, for instance, if you only consider the ants of Madagascar, Mayr's concept is a good tool to strengthen a species hypothesis. Yet, the concept is useless in probably > 80% of all protozoan or metazoan species ever described on a worlwide scale which are allopatric, parthenogenetic or allochronic (the latter in case of differing fossil strata).

Equipment, measurement procedures, character definitions, data analyses and classification

Stereomicroscopic and photographic equipment, measurement procedures, condition of investigated specimens, the running of explorative and supervised data analyses, classification and statistical testing are as reported in Seifert (2023). I repeat here only the description and terminology of morphometric and shape characters.

CL: maximum cephalic length in median line; the head must be carefully tilted to the position yielding the true maximum; excavations of hind vertex and/or clypeus reduce CL.

CW: maximum cephalic width; the maximum is usually found across and including the eyes, exceptionally posterior of the eyes.

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

dFOV: mean inner diameter of foveolae or of meshes of a reticulum on vertex at about half way between the median line of head and the inner eye margin. These structures usually have the base of a pubescence hairs in their center. At least seven measurements at magnifications of 360x are averaged.

EYE: eye-size: the arithmetic mean of the large (EL) and small diameter (EW).

Foveolae types: either simple cup-shaped, simple flat-bottomed, bicoronate or compound depressions of cuticular surface which are usually most strongly developed on dorsal head and have the base of a pubescence hair in the center. Bicoronate foveolae show in perpendicular view additionally to the outer margin ring a second smaller ring just around the hair base. Compound foveolae show in perpendicular view inner cuticular ridges reminiscent of the outlines of a three- or four-leafed clover leaf.

FRS: distance of the frontal carinae immediately caudal of the posterior intersection points between frontal carinae and the lamellae dorsal of the torulus. If these dorsal lamellae do not laterally surpass the frontal carinae, the deepest point of scape corner pits may be taken as reference line. These pits take up the inner corner of scape base when the scape is fully switched caudad and produce a dark triangular shadow in the lateral frontal lobes immediately posterior of the dorsal lamellae of scape joint capsule (Fig. 1).

Longitudinal mesosomal axis : in lateral view is defined as a straight line from the center of propodeal lobe (center of circus in Fig.4) to the border point between anterior pronotal shield and propleuron.

MGr: Depth of metanotal groove or depression, measured from the tangent connecting the dorsalmost points of promesonotum and propodeum.

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

MW: maximum mesosoma width of alates before the tegulae

PeH: maximum petiole height. The straight section of ventral petiolar profile at node level is the reference line perpendicular to which the maximum height of petiole node is measured at node level.

PeW: maximum width of petiole.

PigCap: pigmentation score of dorsal head.

PigCon: pigmentation contrast between dorsal head and mesosoma; PigCon = PigCap / PigMes.

Pigmentation score: variation of pigmentation from light yellowish or reddish (score 4) to blackish brown (score 12) assessed by subjective comparison of a standard color table (Fig. 5) with the stereomicroscopic image seen at a magnification of 150x and reflected-light with a color temperature of 2800 K.

PigMes: pigmentation score of dorsal mesosoma.

PLG: mean length of pubescence hairs on dorsum of first gaster tergite as arithmetic mean of at least seven measurements taken at magnifications of 360x.

PpH: maximum postpetiole height; the lateral suture of dorsal and ventral sclerites is the reference line perpendicular to which the maximum height of postpetiole is measured.

PpW: maximum width of postpetiole.

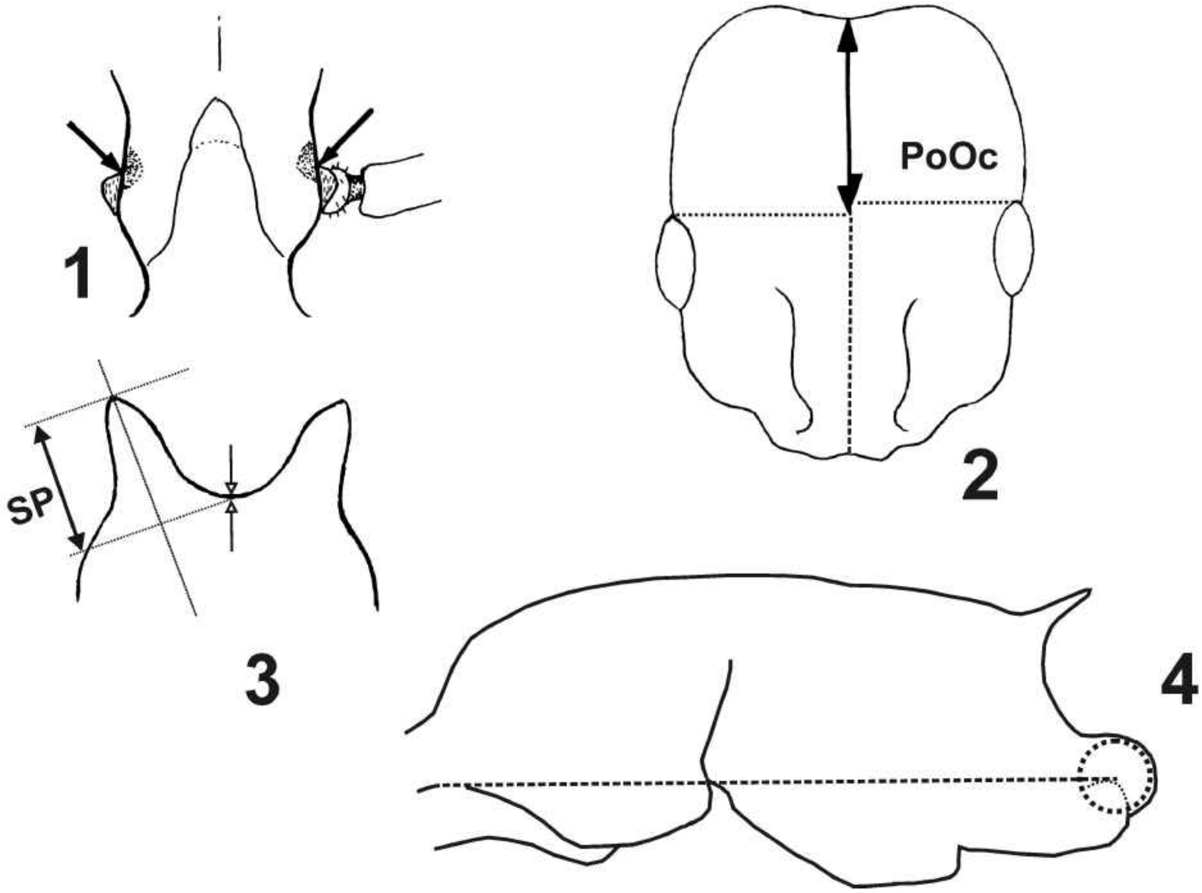
PoOc: postocular distance. Use a cross-scaled ocular micrometer and adjust the head to the measuring position of CL. Caudal measuring point: median occipital margin; frontal measuring point: median head at level of posterior eye margin. Note that many heads are asymmetric; therefore average the left and right postocular distance (Fig. 2).

SL: maximum straight line length of scape excluding the articular condyle given as the arithmetic mean of both scapes.

SP: maximum length of propodeal spines; measured in dorsofrontal view along the long axis of the spine, from spine tip to a line, orthogonal to the long axis that touches the bottom of the interspinal meniscus (Fig. 3). Left and right SP are averaged. This measuring mode is less ambiguous than other methods but yields higher spine length values in species with reduced spines. This is the case in the dentiform spines found in the *C. nuda* group where it is difficult to correctly define the long axis. In such cases, the deviation of the assumed spine axes from longitudinal mesosomal axis should not exceed 30°.

SPBA: the smallest distance of the lateral margins of the spines at their base. This should be measured in dorsofrontal view, since the wider parts of the ventral propodeum do not disturb the measurement in this position. If the lateral margins of spines diverge continuously from the tip to the base, a smallest distance at base is not defined. In this case SPBA is measured at the level of the bottom of the interspinal meniscus.

sqPDG: square root of pubescence distance on dorsum of first gaster tergite. The number of pubescence hairs n crossing a transverse measuring line of length L is counted; hairs just touching the line are counted as 0.5. The pubescence distance PDG is then given by L/n. In order to normalize the positively skewed distributions, the square root of PDG is calculated. Exact counts are promoted by clean surfaces and flat, reflection-reduced illumination directed slightly skew to the axis of the pubescence hairs. Counting is performed at a magnification of 360x. Tergite pubescence is easily torn-off in *Cardiocondyla*. An effort should be made to evaluate undamaged surface spots. In specimens with mostly removed pubescence, PDG can be calculated from the mean distance of hair base pits (BD) and PLG using the formula PDG = BD^2 /PLG.



FIGURES 1–4. 1. Measuring FRS, the arrows mark the endpoints of the measure. **2.** Bilateral measuring of postocular distance PoOc to correct for head asymmetries**. 3.** Measuring spine length in dorsofrontal view. **4.** The dotted line marks the longitudinal axis of mesosoma in lateral view.

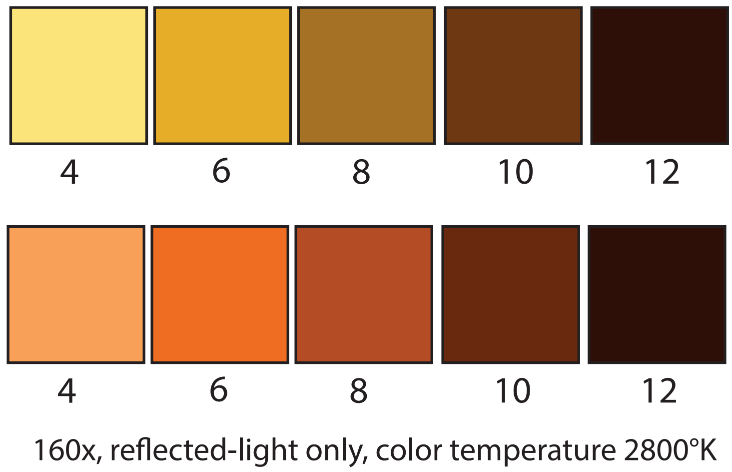


FIGURE 5. Color reference for subjective assessment of pigmentation scores with yellowish and reddish color components.

Results

Delimitation of species groups

A diagnosis of the genus *Cardiocondyla* and the delimitation of 17 species groups of the worldwide fauna was already given by Seifert (2023). Here, I repeat only the characteristics of the four species groups with Palaearctic origin. The members of the *C. batesii*, *C. elegans* and *C. ulianini* groups are morphologically similar. However, this grouping is confirmed by an LDA considering all morphometric characters with positive checks in wild-card runs for rare species with very few samples available.

Cardiocondyla elegans group

Eye large, EYE/CS 0.250 ±0.006 [0.235, 0.266]; postocular distance small, PoOc/CL 0.395 ± 0.009 [0.367, 0.422]; head rather short, CL/CW 1.156 ± 0.017 [1.093, 1.224]; metanotal depression always present, MGr/CS 4.50 ±0.76 [0.5, 6.6]%; propodeal spines short, SP/CS 0.116 ± 0.013 [0.074, 0.153]; pubescence on first gaster tergite very long, PLG/CS 7.84 ± 0.51 [6.11, 9.08]%; postpetiolar sternite without any protrusions. Four species from the southern zone of the West Palaearctic, tramp species unknown: *C. elegans* Emery 1869; *C. dalmatica* Soudek 1925, *C. brachyceps* Seifert 2003 and *Cardiocondyla dalmaticoides* **n. sp.**

Cardiocondyla ulianini group

Eye large, EYE/CS 0.248 ±0.012 [0.215, 0.262]; postocular distance larger, PoOc/CL 0.407 ± 0.031 [0.397, 0.469]; head longer, CL/CW 1.178 ± 0.028 [1.098, 1.272]; metanotal depression always present, MGr/CS 3.85 ±0.84 [1.5, 6.6]%; propodeal spines short, SP/CS 0.114 ± 0.015 [0.066, 0.157]; pubescence on first gaster tergite rather long, PLG/CS 6.55 ± 1.06 [4.96, 8.06]%; postpetiolar sternite without any protrusions. Eight species from the southern zone of the West and Central Palaearctic, tramp species unknown: *C. ulianini* Emery 1889; *C. bulgarica* Forel 1892, *C. sahlbergi* Forel 1913, *C. gallilaeica* Seifert 2003, *C. israelica* Seifert 2003, *C. littoralis* Seifert 2003 and *Cardiocondyla caspiense* **n. sp.**

Cardiocondyla batesii group

Eye very large, EYE/CS 0.263 ±0.08 [0.246, 0.283]; postocular distance very small, PoOc/CL 0.368 ± 0.016 [0.311, 0.397]; head rather long, CL/CW 1.176 ± 0.023 [1.125, 1.256]; metanotal depression always present, MGr/CS 3.51 ±0.82 [0.9, 5.6]%; propodeal spines short, SP/CS 0.100 ± 0.013 [0.069, 0.130]; pubescence on first gaster tergite rather short, PLG/CS 5.50 ± 0.43 [4.48, 6.94]%; postpetiolar sternite without any protrusions. Nine species from the southern zone of the West Palaearctic, tramp species unknown: *Cardiocondyla batesii* Forel 1894, *C. nigra* Forel 1905, *C. kushanica* Pisarski 1967, *C. brachyceps* Seifert 2003, *C. opistopsis* Seifert 2003, *C. rugulosa* Seifert 2003, *C. semirubra* Seifert 2003, *C. tenuifrons* Seifert 2003 and *C. verdensis* **n. sp.**

***Cardiocondyla stambuloffii* group**

True foveolae on vertex completely absent. Instead the bases of pubescence hairs are placed in the center of flat tubercles or flat pits of small diameter, giving a finely punctate surface appearance at lower magnifications, dFOV 8.13 ± 0.78 [5.0, 10.0]. Frons very wide, FRS/CS 0.320 ± 0.015 [0.269, 0.353]. Propodeal spines reduced to blunt dents, SP/CS 0.070 ± 0.013 [0.027, 0.096]. Metanotal depression deep, MGr/CS 3.57 ± 0.83 [1.63, 6.16] %; all numeric data from 153 worker individuals of five species. SE Europe across Asia Minor eastwards to Tibet and Mongolia with four described and one undescribed species, tramp species unknown: *C. stambuloffii* Forel 1892, *C. koshewnikovi* Ruzsky 1902, *C. gibbosa* Kuznetzov-Ugamsky 1927, *C. tibetana* Seifert 2003 and *Cardiocondyla rolandi* **n. sp.**

Key to the species with outdoor occurrence in the Palaearctic

In order to comprise all 34 species with outdoor occurrence in the Palaearctic, the key and the supplementary information SI1 and SI2 additionally included nine species of species groups with other zoogeographic origin. These species either extend their range into the southern Palaearctic or are globally dispersing tramp species potentially occurring in each locality with sufficiently warm climate. The complete taxonomic names of these added species are *Cardiocondyla minutior* Forel 1899, *C. tjibodana* Karavajev 1935 and *C. goa* Seifert 2003 (all three belonging to the *C. minutior* species group), *C. emeryi* Forel 1881 (belonging to the *C. emeryi* species group), *C. fajumensis* Forel 1913 and *C. unicalis* Seifert 2003 (both belonging to the *C. shuckardi* species group), *C. wroughtonii* (Forel 1890) and *C. obscurior* Wheeler 1929 (both belonging to the *C. wroughtonii* species group) and *C. mauritanica* Forel 1890 (belonging to the *C. nuda* species group).

The key presented below almost thoroughly used dichotomous decision schedules for cases requiring combinations of multiple characters and in the same time it aspired to achieve a low error rate inevitably resulting in tedious procedures. Lamenting does not help here and those who think that simple answers can be given for difficult problems bark up the wrong tree. The finally best approach is here using a software providing linear discriminant functions (LDA), measuring the full set of morphometric characters and running the investigated samples as wild-cards within the data space of the hypothesis-providing supplementary file SI2. It is convenient to run the analysis with primary (raw) measurements instead with ratios. A good check of the result is then comparing with the images that are given for any species in four aspects and to consider geographic distribution. The low error rates reported in the key cannot be achieved for such tiny ants without high-resolution optical systems, a good measuring stage and a careful realization of character definitions.

1a Anterior postpetiolar sternite laterally more prominent than in median part—as result an imagined cross section shows a deeply concave ventral margin of the sternite. The lateral protrusions appear in frontolateral view as dents (Fig. 113). *C. wroughtonii* group **2**

1b Anterior postpetiolar sternite in median part more prominent or at equal level as the lateral surface—as result an imagined cross section shows a convex or straight ventral margin of the sternite **3**

2a With all measurements in mm, discriminant 34.21*CW-59.33*PoOc-177.83*EYE+72.15*SL-113.56*FRS-106.46*SP+140.69*PpW-14.15 < 0 [error 0% in 37 nest sample means of two workers measured]. 1st gaster segment in a majority of samples with absent or weakly developed blackish pigmentation. Worldwide tramp species. Outdoor occurrence confirmed for the Middle East**.** Figs. 105–108. . . . . ***wroughtonii***

2b Discriminant > 0 [0% error in 65 nest sample means of two workers]. 1st gaster segment in a majority of samples with strongly developed blackish pigmentation. Worldwide tramp species. Outdoor occurrence confirmed for southern Spain and the Middle East. Figs.109–113 . . . . ***obscurior***

3a True foveolae on vertex dorsal of the eyes completely absent. Instead the bases of pubescence hairs are placed in the center of flat tubercles or flat pits of only 4–10 µm diameter, giving a finely punctate surface appearance at lower magnifications (Figs. 89, 97). Postocular distance large, PoOc/CL 0.416–0.467. Frons usually very wide, FRS/CS > 0.288 (except *C. tibetana,* here 0.280 ± 0.006). Propodeal spines reduced to blunt dents. Metanotal depression deep. *C. stambuloffii* group **4**

3b Bases of pubescence hairs on vertex dorsal of the eyes placed in the center of foveolae or cuticular meshes of > 10 µm diameter (Figs. 9, 25, 117)—if foveolae reduced (*verdensis* **n. sp.**), than PoOc/CL < 0.394. Frons narrower, FRS/CS < 0.288. Metanotal depression varying from nearly absent to deep. Propodeal spines variable. **8**

4a Eye larger, EYE/CS >0.235. Frons narrower, FRS/CS <0.295. Waist segments lower, PeH/CS <0.343, PpH/CS < 0.283. Southern and northern margin of Tarim Basin. Figs. 101–104 . . . . ***tibetana***

4b EYE/CS <0.235, FRS/CS > 0.295, PeH/CS >0.343, PpH/CS < 0.283 . . . . **5**

5a Posterior 40% of vertex surface completely smooth except for tiny pits of 4–5 µm around the bases of pubescence hairs just visible with high-resolution stereomicroscopy. Pubescence longer. With all measurements in mm, discriminant 334.68*PLG-45.456*CW+88.43*PoOc-66.63*EYE -3.60 > 2.3. South Kazakhstan. Figs**.** 98–100. . . . . ***gibbosa***

5b Posterior part of vertex not completely smooth, at least with weak rugulae and small tubercles around the bases of pubescence hairs. Discriminant < 2.3 . . . . **6**

6a Westpalaearctic, known range extending east to the western shores of Caspian Sea. With all measurements in mm, discriminant 44.95*CW+54.68*PoOc+31.14*SL-130.25*SPBA-79.81*PpW +40.84*PeH+90.89*PpH -28.33 < 0.4 [0% error in 82 individuals]. Figs. 86–89. . . . . ***stambuloffii***

6b Central Palaearctic, known range extending from western coast of Caspian Sea east to Mongolia. Discriminant > 0.4 [0% error in 59 individuals]. **7**

7a With all measurements in mm, discriminant 120.6*PoOc-29.53*SL+109.54*PeW-109.42*PeH-157.97*PLG-7.70 < 0.7 [0% error in 37 individuals]. Figs. 94–97. . . . . ***rolandi* n. sp.**

7b Discriminant > 0.7 [0% error in 22 individuals]. Figs. 90–93. . . . . ***koshewnikovi***

8a Propodeal spines reduced to obtusely angled corners (Fig. 115). Postpetiole rather narrow, PpW/CS < 0.46, in dorsal view never suggestively hexagonal. With all measurements in mm, discriminant 48.06*PoOc+27.66*SL-56.96*PpW+119.07*MGr-13.79 > 0 [error 0% in 17 individuals]. **9**

8b Propodeal spines not reduced to obtusely angled corners. If spines occasionally reduced to blunt corners, then EYE/CS > 0.221 and PpW/CS >0.450. Discriminant < 0 [error 0% in 1140 individuals] **10**

9a Head elongated CL/CW > 1.16 (Fig. 114). Dorsum of promesonotum and lateral pronotum with more developed microsculpture (Figs. 115, 116). Head sculpture stronger, foveolae with regular margin (Fig. 117). Egypt and Saudi Arabia. . . . . ***fajumensis***

9b Head very short CL/CW < 1.16 (Fig. 114). Dorsum of promesonotum and lateral pronotum nearly glabrous (Figs. 119, 120). Head sculpture weaker, foveolae sometimes with irregular margin (Fig. 121). Iran. . . . . ***unicalis***

10a Frons very narrow, FRS/CS 0.196—0.228 (Fig. 122), postpetiole with a bulging sternite and high (Fig.123.), PpH/CS 0.306–0.358. With all measurements in mm, discriminant 128.52*FRS+42.56*PeW-143.94*PpH+1.616 < 0 [error 0% in 145 specimens]. Confirmed outdoor occurrence in S Iberia, N Africa and Middle East. Figs. 122–125. . . . . ***emeryi***

10b Frons wider and postpetiole without a strongly bulging sternite. Discriminant > 0 [error 0% in 863 specimens]. **11**

11a Small, CW < 420 mm. Metanotal depression very weak or absent, spines well developed, postpetiole much lower than petiole and with a completely flat sternite (Fig. 127). Vertex with deeply impressed foveolae (Fig.126). All surfaces of head, mesosoma

and waist matt (Fig. 128). Outdoor occurrence confirmed for Egypt and Saudi Arabia . . . . ***minutior, tjibodana & goa***
These species are inseparable by single or few characters. It is recommeded to measure CL, CW, SL, EYE, FRS, SP, PpW, PeH, PpH and PLG and then running the test specimens as wild-cards in a LDA against the data given in supplementary information SI2. The total classification error in 210 worker individuals in SI2 is 2.4%. Users who refrain from doing this time consuming and challenging separation are recommended to name this collective cluster . . . . ***minutior* aggr**.

11b Larger, CW > 420 mm. Minute specimens of *C. mauritanica* may match the character combination of 11a but differ by shorter spines and a thinner petiolar peduncle (compare Figs. 127 and 130). **12**

12a Outlines of postpetiole in dorsal view approximately hexagonal (Fig. 131). Metanotal depression shallow (MGr/CS 2.14±0.52). Propodeal spines developed as short dents (Fig. 130). Gastral pubescence dense (sqPDG 3.72 ± 0.28). Postocular distance large (PoOc/CL 0.447 ± 0.008, Fig. 129). Microsculpture on vertex strongly reticulate (Fig. 132). With MGr, PoOc and SP in mm and sqPDG in µm, discriminant 136.0*MGr-25.0*PoOc*73.99*SP+1.81*sqPDG-7.2322 < 0 [error 0% in 151 specimens]. Mediterranean and South Temperate zone of the Palaearctic. . . . . ***mauritanica***.

12b Outlines of postpetiole in dorsal view not approximately hexagonal. Metanotal depression usually deeper, propodeal spines more developed, gastral pubescence often more dilute, postocular distance usually smaller. Microsculpture on vertex different. Discriminant > 0 [error 0.3% in 619 specimens]. **13**

13a Postocular distance extremely small (PoOc/CL <0.340). Petiole height and postpetiole width very low. With all measurements in mm, discriminant 30.96*PoOc-38.98*CL+17.12*PeH+26.77*PpW+ 7.196 <0 [error in 4 specimens 0%]. Kuweit. Figs. 62–65. . . . . ***opistopsis***

13b Postocular distance larger (PoOc/CL 0.342–0.469]. Petiole height and postpetiole width higher. Discriminant >0 [error 0% in 612 specimens]. **14**

14a Head surface between inner eye margin and paramedian vertex strongly microrugulose (Fig. 69). Dorsal promesonotum longitudinally microrugulose (Fig. 68). All surfaces of head, mesosoma and petiole matt due to more developed microsculpture. Dorsal profile of mesonotum straight, contrasting the clearly convex dorsal profile of propodeum, metanotal depression feebly suggested (Fig. 67). With all measurements in mm, discriminant 95.88*EYE-164.99*MGr-12.035 > 0. Yemen. Figs. 66–69. . . . . ***rugulosa***

14b Body surfaces less microrugulose, often shiny. Dorsal profile of mesosoma different. Discriminant < 0. . . . . **15**

15a Microsculpture of head with irregular foveolar margins (Fig. 73). Additionally differing from members of the *elegans* and *ulianini* group by larger eye (EYE/CS 0.265–0.274] and from members of the *batesii* group by longer tergite pubescence (PLG/CS 6.84–6.94). Afghanistan. Figs. 70–73. . . . . ***kushanica***

15b Foveolae on vertex not with irregular margins. Character combination different **16**

16a Foveolae on vertex extremely small (dFOV 7.0–9.1 µm). Tergite pubescence very dilute (sqPDG 5.88–5.92). Scape and head much elongated (SL/CS 0.854–0.867, CL/CW 1.238–1.256). All body surfaces very shiny. Island endemic of Cape Verde, Figs.82–85. . . . . ***verdense* n. sp.**

16b Foveolae much larger (dFOV 12–21 µm). Tergite pubescence often more dense. Scape and head usually shorter. **17**

17a With sqPDG in µm and all other measurements in mm, discriminant 201.57*PLG-0.32*sqPDG-40.86*CL-10.32*PoOc+70.74*SL+23.72*SPBA-24.27*SP+26.48*PeW+12.96*PpW-73.42*PeH-8.61 > 0 [error 0% in 177 individuals].*C. elegans* group **18**

17b Discriminant < 0 [error 0% in 322 individuals]. *C. batesii* & *C. ulianini* group **21**

18a Occurring from Iberia accross S France to Italy. Contact zone with *dalmatica* in the border region of NE Italy and Slovenia. With all measurements in mm, discriminant 56.7*SP+156*PeW-61.9*PoOc-126.2*PeH-48.2*PpW+126.6*MGr+17.86 >0 [error 0% in 81 two-specimen nest samples]. Figs. 6–9. . . . . ***elegans***

18b Occurring farther east. If found in NE Italy or Slovenia, discriminant < 0. . . . . **19**

19a Combination of larger foveloar diameter on vertex, lower postpetiolar height, longer propodeal spines and higher pubescence distance on gaster tergites. With dFOV, sqPDG in µm and SP, PpH in mm, discriminant 1.623*sqPDG+0.718*dFOV+96.14*SP-62.63*PpH-15.233 > 2 [error 0% in 13 specimens]. S Georgia, NE Turkey, Iran, Afghanistan. Figs. 18–21. . . . . . ***brachyceps***

19b Foveolar diameter smaller, postpetiolar height larger, spines shorter, pubescence distance smaller. Discriminant < 2 [error 1.4% in 72 specimens]. **20**

20a Bases of propodeal spines more approached, petiole narrower and higher, surface of propodeum glabrous, propodeal spines very acute, petiole high with a very steep anterior profile of the node. With all measurements in mm, discriminant 163.8*PeH-29.1*PeW-134.63*SPBA-5.68 >2 [error 0% in 6 specimens]. Asia Minor. Figs. 14–17. . . . . ***dalmaticoides* n. sp.**

20b Bases of propodeal spines more distant, petiole wider and lower, surface of propodeum less glabrous, propodeal spines less acute, petiole lower with a less steep anterior profile of the node. Discriminant <2 [error 0% in 59 specimens]. From N Italy across the whole Balkans, Cyprus and Asia Minor east to the Iran. Northern range border in Austria, Slovakia and Hungary at 48°N. Figs. 10–13. . . . . ***dalmatica***

21a With all measurements in mm, discriminant 32.44*CW-103.36*CL+134.03*PoOc-44.05*EYE+23.08*SL-41.77*SPBA+48.21*PpW-0.135 < 0 [error 0% in 98 individuals]. Species of the *C. batesii* group. **22**

21b Discriminant > 0 [error 0.4% in 241 individuals]. Species of the *C. ulianini* group. **25**

22a Frontal carinae notably diverging frontad, FL/FR >1.109. Postocular distance large, PoOc/CL >0.408. Metanotal depression very shallow, MGr < 2.5 %. Jordan. Figs. 74–77. . . . . ***tenuifrons***

22b Frontal carinae less diverging, FL/FR <1.110. Postocular distance smaller, PoOc/CL <0.409. Metanotal depression deeper, MGr usually > 2.5 %. **23**

23a Petiole massive, ratio PeW /PpW > 0.57. With all measurements in mm, discriminant 152.578*PeW-69.53*PpW+2.092*SL+30.63*PoOc-10.57 > 2.5 [error 0% in 4 individuals]. Only known from two sites in Asia Minor. Figs. 58–61. . . . . . ***semirubra***

23b Petiole less massive, ratio PeW/PpW in 97% of individuals <0.57. Discriminant < 2.5 [error 0% in 132 individuals. Figs.

54–57. . . . . **24**

24a With all measurements in mm, discriminant 63.22*CL-63.18*PoOc+55.89*SL+64.64*PeW-184.93*PeH-93.82*PpH-11.19 < 0 [error 0% in 37 specimens]. Morocco, Tunisia, Algeria, Spain. Figs. 54–57. . . . . ***batesii***

24b Discriminant > 0 [error 0% in 95 specimens]. Portugal, Morocco, Algeria, Tunisia, Egypt, Cyprus, Turkey, Middle East, Iran eastwards to 56°E. Color polymorphic. Figs. 78–81. . . . . ***nigra***

25a Frons very narrow, FRS/CS 0.225; propodeal spines acute but very short, SP/CS 0.071; postocular distance small, PoOc/CL 0.403; postpetiole wide PpW/CS 0.552. With all measurements in mm, discriminant 160.18*FRS+41.17*PoOc-45.99*PpW-15.23 <0. Israel. Figs. 34–37 . . . . ***gallilaeica***

25b Frons wider; propodeal spines longer; postocular distance larger; postpetiole often narrower. Discriminant > 0 [error 0% in 240 specimens]. **26**

26a Combination of large propodeal spine base distance, small eye, large postocular distance, broad and high postpetiole. With all measurements in mm, discriminant 44.74*PoOc-167.14*EYE+161.96*SPBA-56.07*PpW+31.77*PpH+0.543 >0 [error 0% in 179 specimens]. **27**

26b Propodeal spine base distance smaller, eye larger, postocular distance smaller, postpetiole narrower and lower. Discriminant < 0 [error 0% in 61 specimens]. **29**

27a With sqPDG in µm and all other measurements in mm, discriminant 163.54*PoOc+0.755*sqPDG-57.89*CL-58.26*CW+197.78*EYE+47.39*FRS-54.85*SP+55.08*PeW-109.15*PeH+53.45*PpH-178.59*PLG-4.19 > 0.5 [error 0% in 84 specimens]. S Balkans and Asia Minor. Figs. 42–45. . . . . ***bulgarica***

27b Discriminant < 0.5 [error 0% in 95 specimens]. **28**

28a Microsetae on clypeus shorter (Fig. 46), pubescence on all body parts shorter, foveolae on vertex less densely packed (Fig.49), postpetiole wider, petiole node in lateral view more symmetric (Fig.47), dorsum of mesosoma and waist shiny and mesosoma frequently darker. With dFOV in µm and all other measurements in mm, discriminant 0.965*dFOV+164.79*EYE-38.64*PpW+123.49*PLG +77.67*MGr-32.49 < 0 [error 2.9% in 69 specimens]. SE Balkans, Asia Minor, Israel, Caucasus, Caspian region, Iran, Afghanistan, Kyrgistan. Figs, 46–49. . . . . ***sahlbergi***

28b Microsetae on clypeus longer (Fig. 50), pubescence on all body parts longer, foveolae on vertex more densely packed (Fig. 53), postpetiole narrower, petiole node in lateral view more asymmetric (Fig. 51), dorsum of mesosoma and waist less shiny and mesosoma frequently lighter. Discriminant > 0 [error 7.7% in 26 specimens]. Georgia, Iran. Figs 50–53. . . . . ***persiana***

29a Vertex with rather large, well-demarcated, bicoronate and densely-packed foveolae and in anteromedian part with well-developed longitudinal sculpture(Figs. 38, 41). Pubescence on gaster tergites more dense. With dFOV, sqPDG in µm and SPBA in mm, discriminant 2.559*sqPDG-0.472*dFov+15.117*SPBA-4.857 < 0 [error 0% in 10 specimens]. Eqypt, Israel. Figs. 38–41 . . . . ***israelica***

29b Vertex with smaller, less demarcated and more spaced foveolae and with very weak or absent longitudinal microsculpture. Pubescence on gaster tergites less dense. Discriminant > 0 [error 0% in 51 specimens] **30**

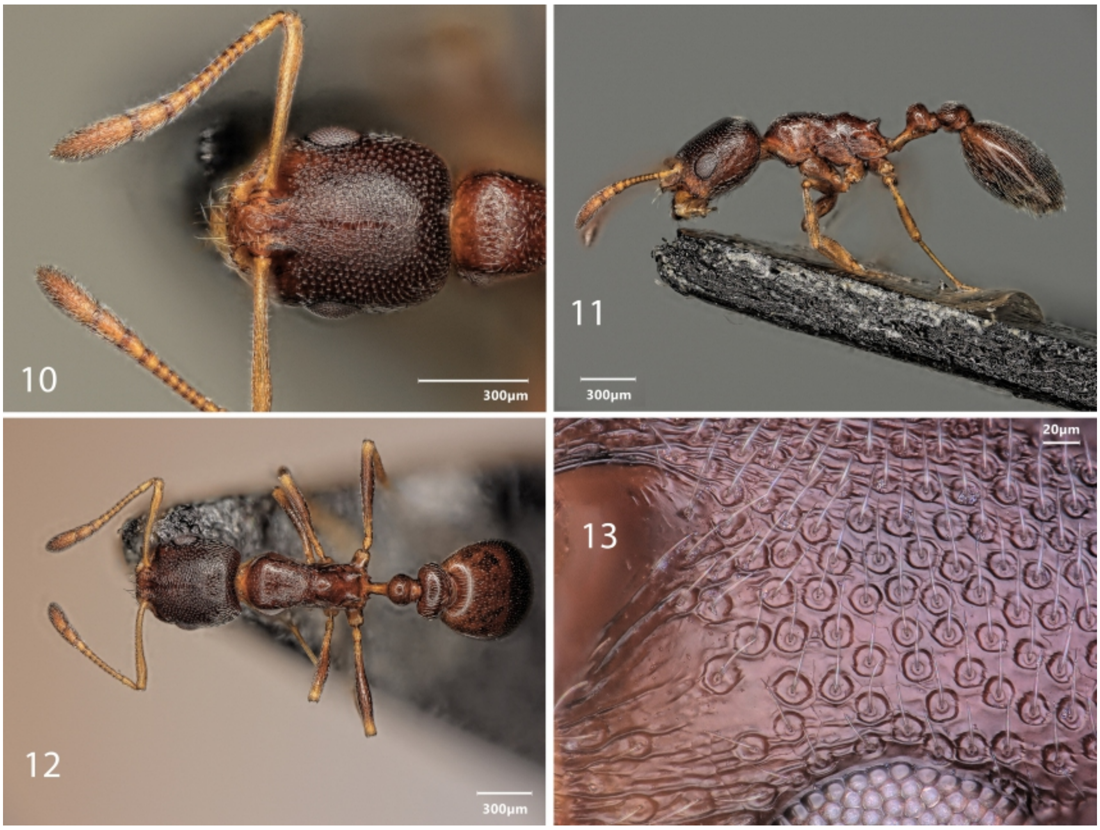
30a Postpetiole and frons wider, pubescence hairs on gaster tergites shorter. With all measurements in mm, discriminant 93.21*FRS+27.62*PpW-406.34*PLG-6.246 > 0 [error 0% in 44 specimens]. Continuously distributed from the S Ukraine (32°E) eastwards to N Xinjang (88°E). Figs. 22–25. . . . . ***ulianini***

30b Postpetiole and frons narrower, pubescence hairs on gaster tergites longer. Discriminant 93.21*FRS+27.62*PpW-406.34*PLG-6.246 < 0 [error 0% in 7 specimens]. **31**

31a Postocular distance and postpetiole height much larger (PoOc/CL > 0.423, PpH/CS > 0.260). Foveolae on vertex mediad of eye with diffuse margins (Fig. 29). Anterior face of petiole node moderately sloping down (Fig. 27). SE Kazakhstan. Figs. 26–29. . . . . ***littoralis***

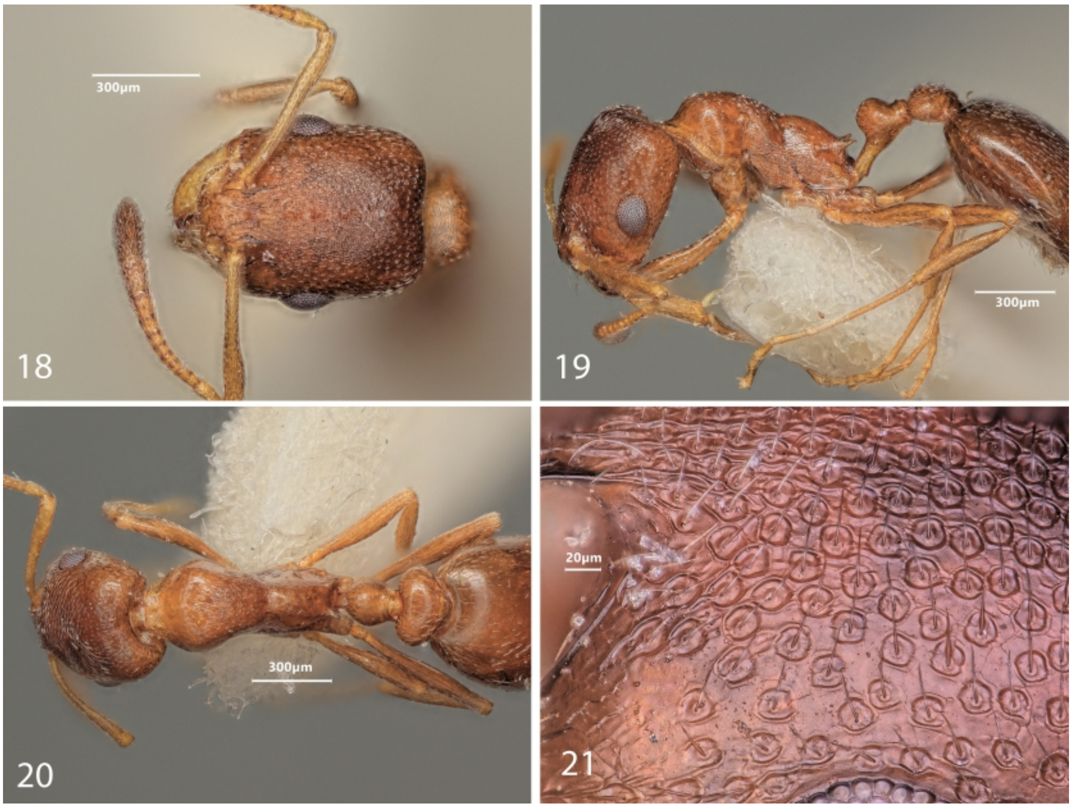
31b Postocular distance and postpetiole height smaller (PoOc/CL < 0.423, PpH/CS < 0.260). Foveolae on vertex mediad of eye more strongly demarcated and bicoronate (Fig. 33). Anterior face of petiole node steeper (Fig. 31). Iranian Caspi region. Figs. 30–33. . . . . ***caspiense* n. sp.**

FIGURES 6–9. *Cardiocondyla elegans;* Fig. 6: head in dorsal view; Fig. 7 lateral view; Fig. 8: dorsal view; Fig. 9: head surface between inner eye margin and paramedian vertex. France: Brehemont-1.1 km E, 2010.07.15.

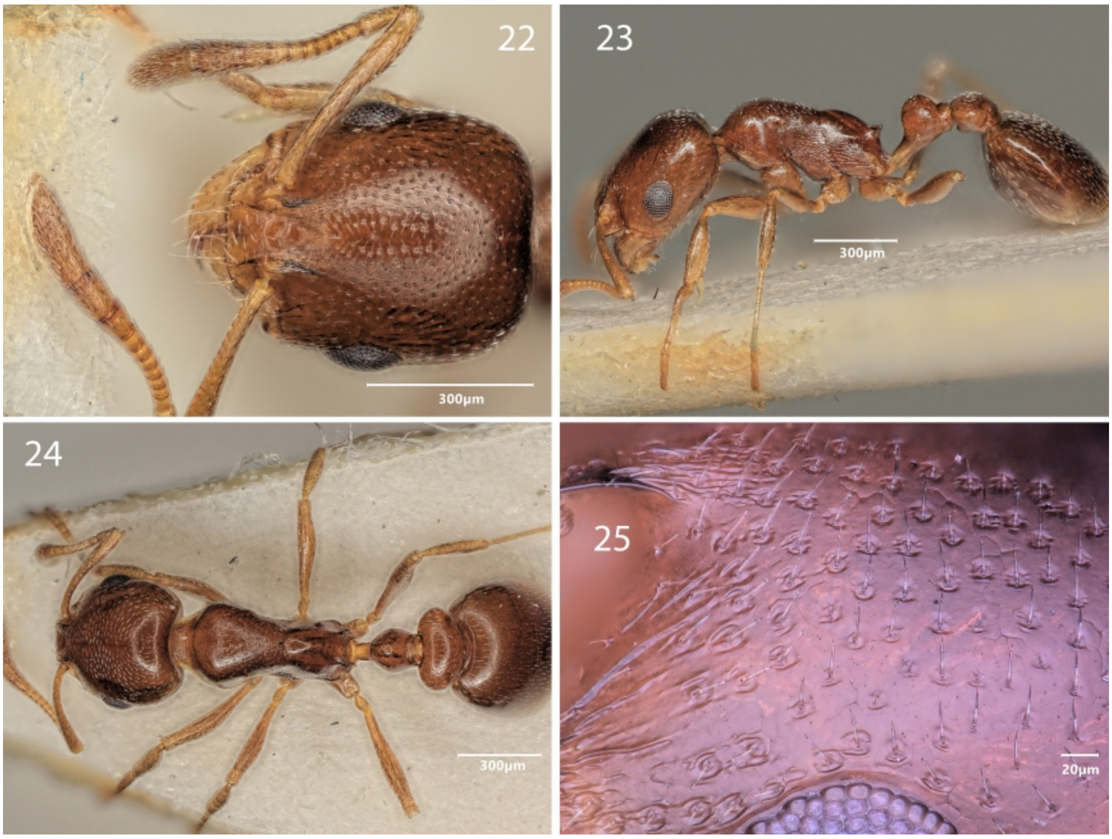


FIGURES 10–13. *Cardiocondyla dalmatica*, Fig. 10: head in dorsal view; Fig. 11: lateral view; Fig. 12: dorsal view; Fig. 13: head surface between inner eye margin and paramedian vertex. Hungary: Balassagyarmat, 2007.06.31

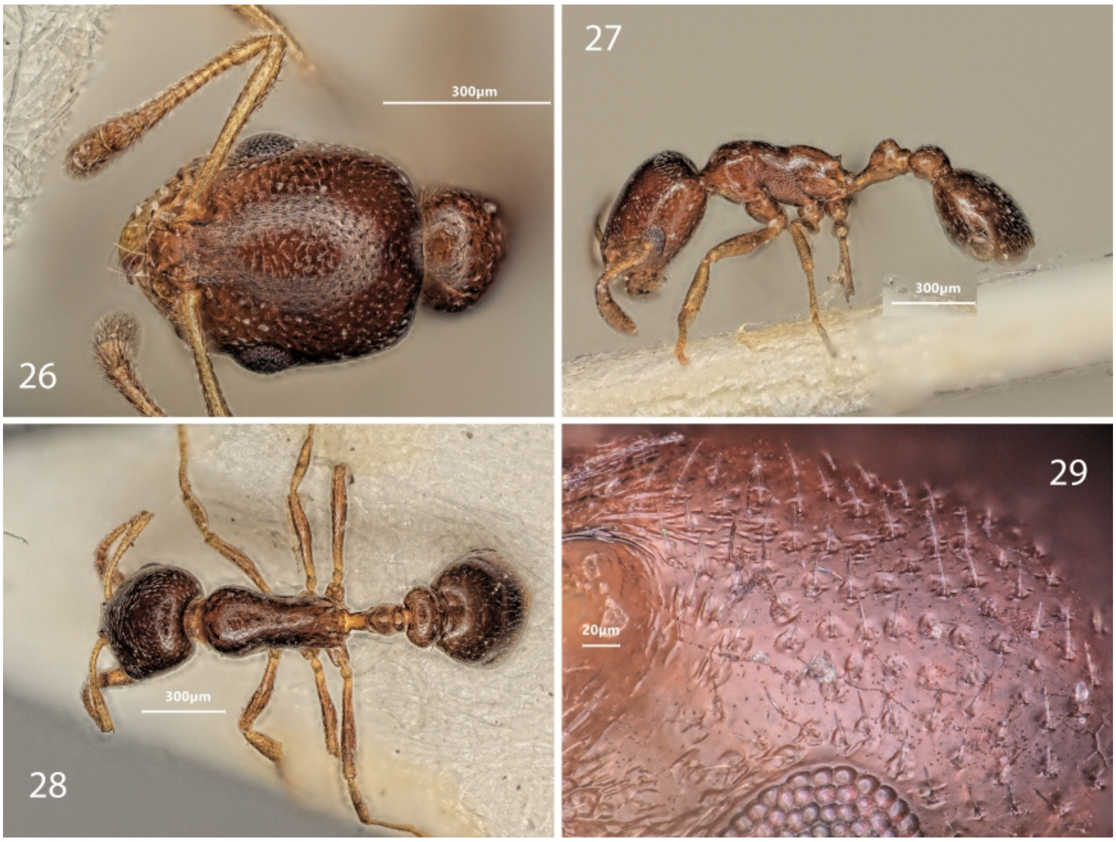
FIGURES 14–17. *Cardiocondyla dalmaticoides* **n. sp.**, holotype; Fig. 14: head in dorsal view; Fig. 15: lateral view, postpetiole and gaster in full lateral view shown upper left; Fig. 16: dorsal view, postpetiole and gaster in full dorsal view shown lower left; Fig. 17: head surface between inner eye margin and paramedian vertex. Turkey: Reyhauli-2 km N, 1993.06.09



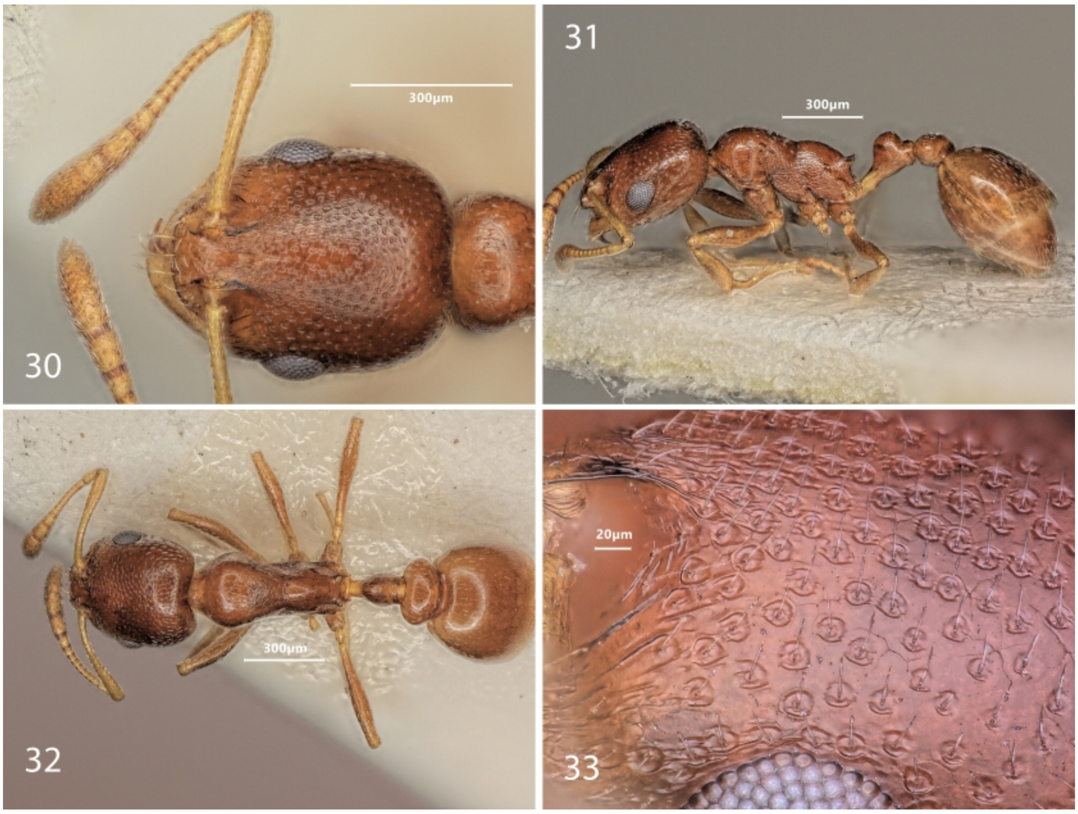
FIGURES 18–21. *Cardiocondyla brachyceps*; Fig. 18: head in dorsal view; Fig. 19: lateral view; Fig. 20: dorsal view; Fig. 21: head surface between inner eye margin and paramedian vertex. Iran: Fars, 1997.09.19



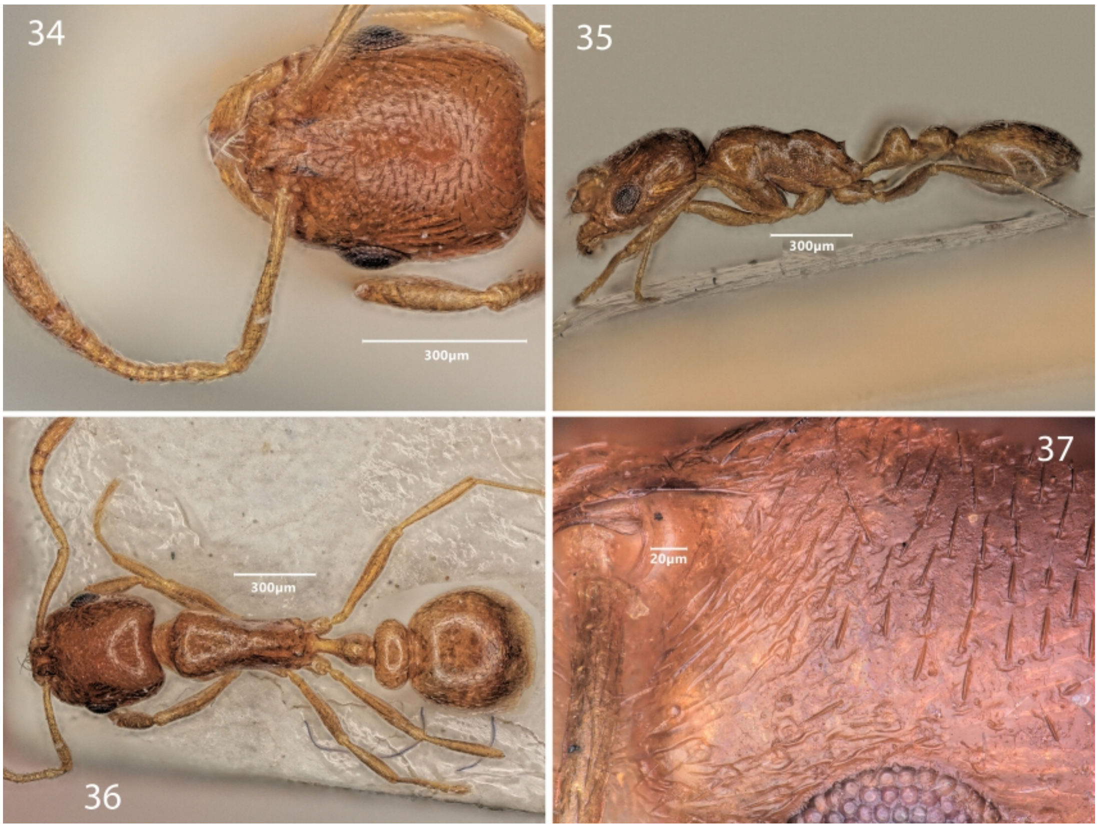
FIGURES 22–25. *Cardiocondyla ulianini*; Fig. 22: head in dorsal view; Fig. 23: lateral view; Fig. 24: dorsal view; Fig. 25: head surface between inner eye margin and paramedian vertex. Kyrgistan: 42.44.41N, 75.49.50E, 2000.07.30-91.



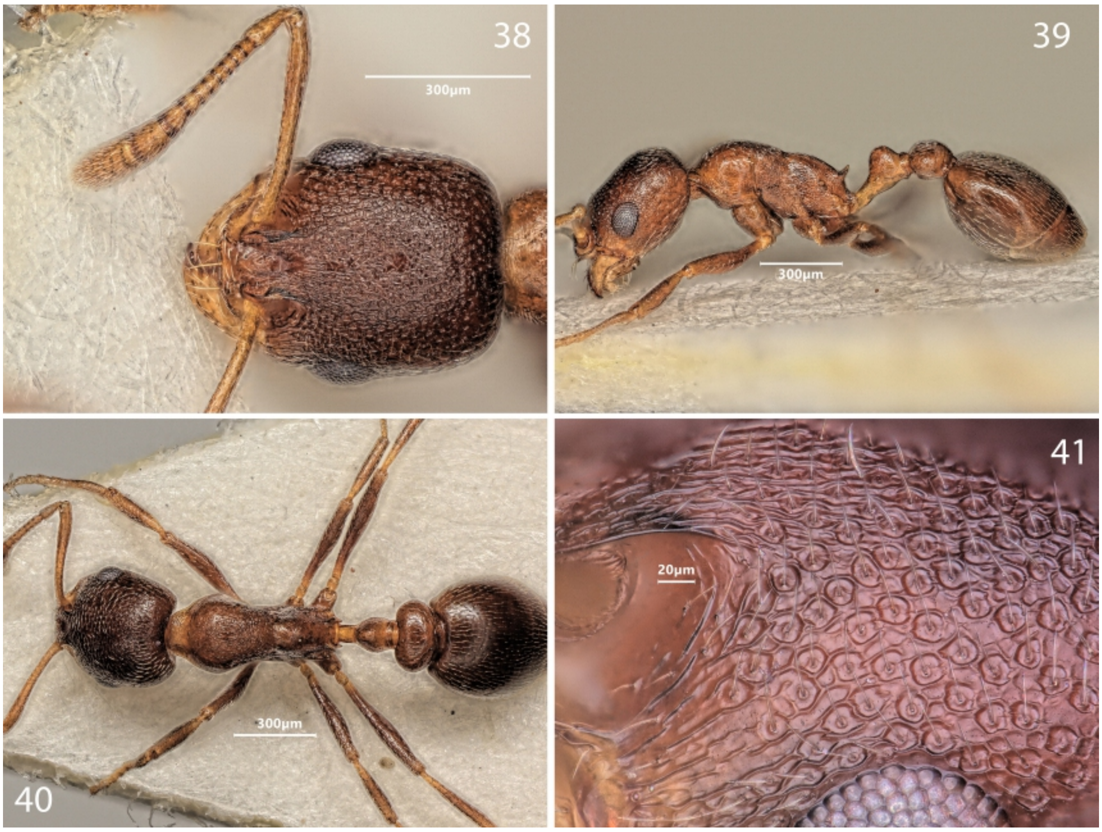
FIGURES 26–29. *Cardiocondyla littoralis*; Fig. 26: head in dorsal view; Fig. 27: lateral view; Fig. 28: dorsal view; Fig. 29: head surface between inner eye margin and paramedian vertex. Kazakhstan: Sassy Kol, 2001.08.07.



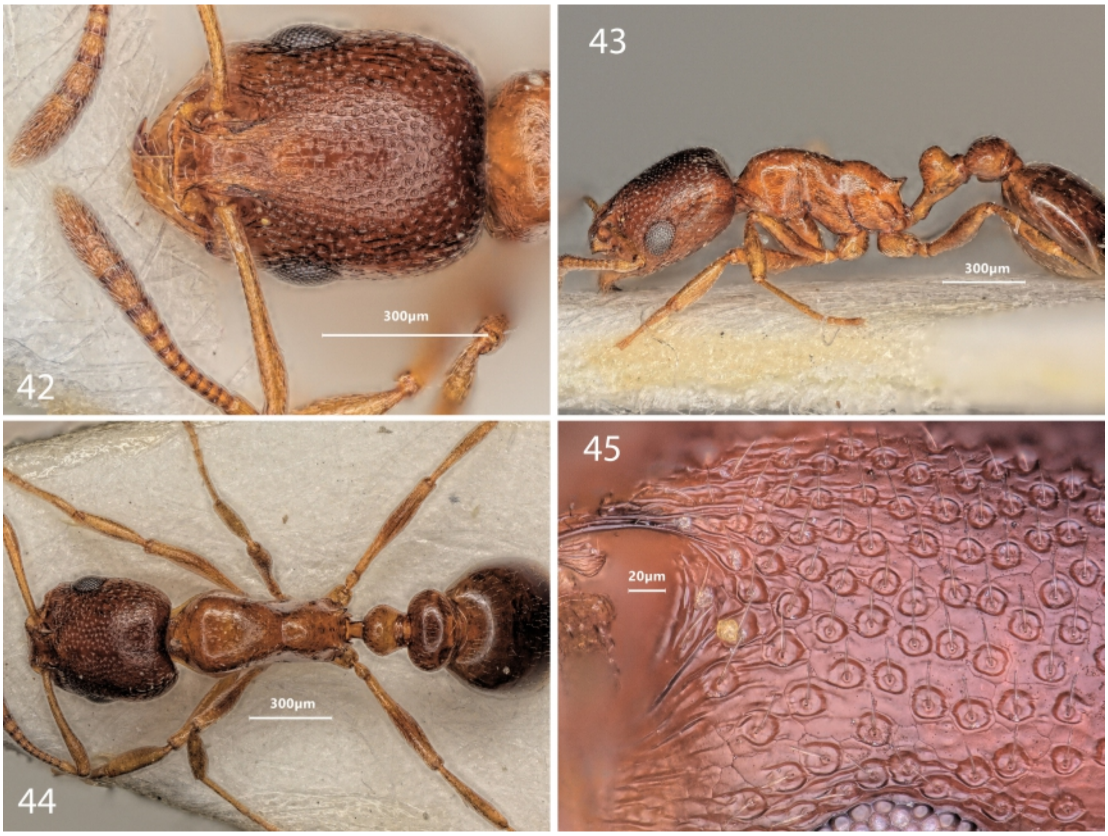
FIGURES 30–33. *Cardiocondyla caspiense* **n. sp.**, holotype; Fig. 30: head in dorsal view; Fig. 31: lateral view; Fig. 32: dorsal view; Fig. 33: head surface between inner eye margin and paramedian vertex. Iran: Miankaleh, 2004.07.23



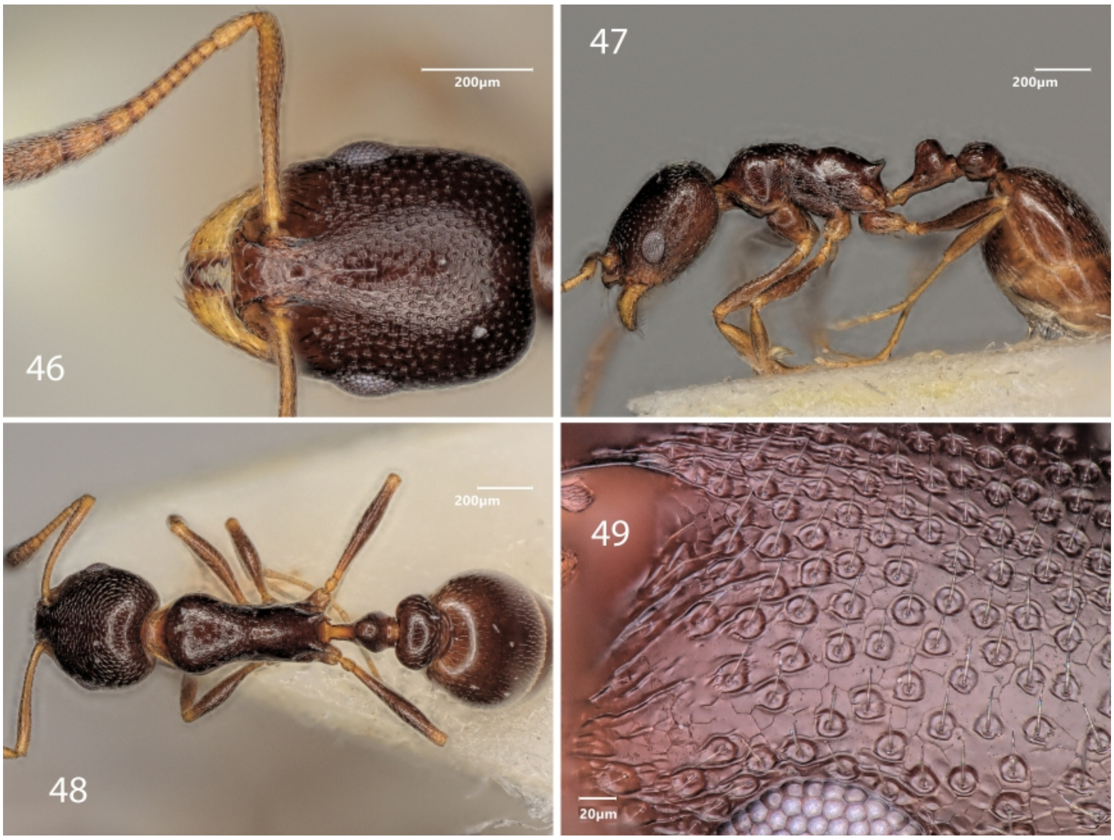
FIGURES 34–37. *Cardiocondyla gallilaeica*, holotype; Fig. 34: head in dorsal view; Fig. 35: lateral view (flipped horizontally); Fig. 36: dorsal view; Fig. 37: head surface between inner eye margin and paramedian vertex. Israel: Sedé Eliyyahu, 1983.09.06



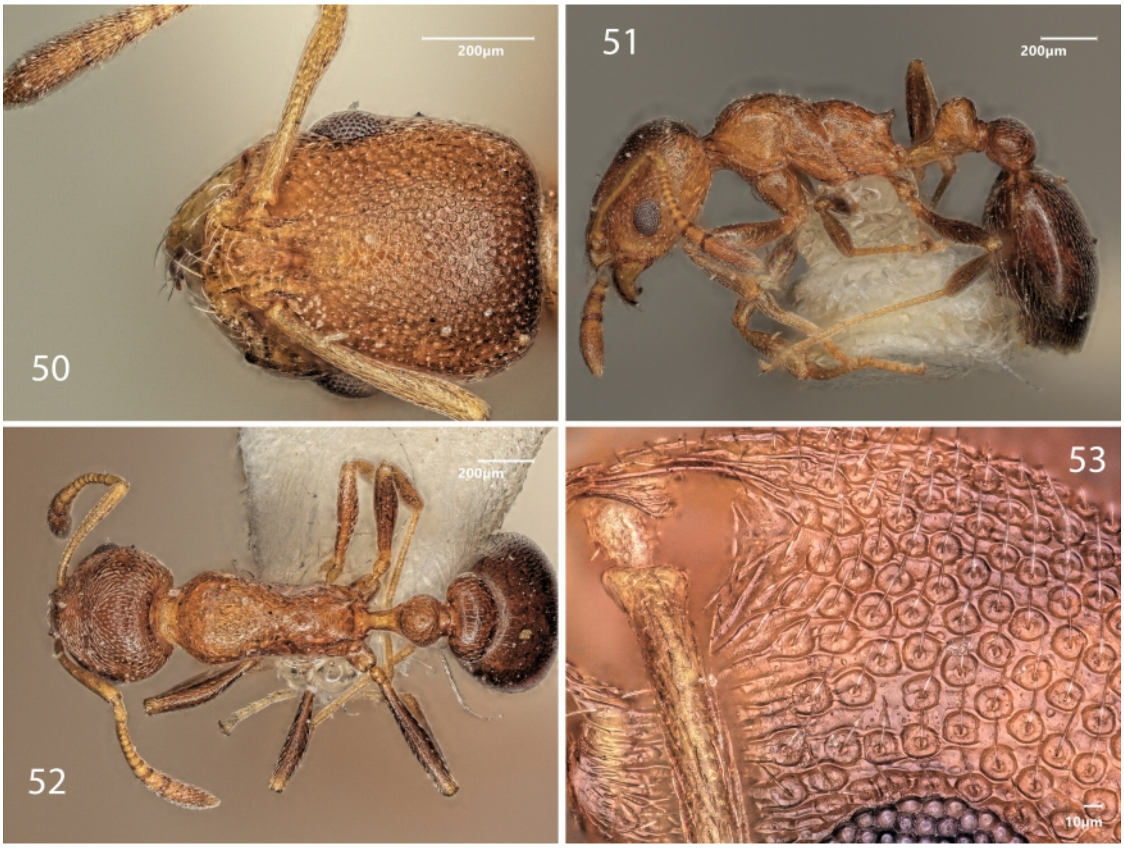
FIGURES 38–41. *Cardiocondyla israelica*; Fig. 38: head in dorsal view; Fig. 39: lateral view (flipped horizontally); Fig. 40: dorsal view; Fig. 41: head surface between inner eye margin and paramedian vertex. Egypt: Ebn Salam Mansora, 2002.11.07



FIGURES 42–45. *Cardiocondyla bulgarica*; Fig. 42: head in dorsal view; Fig. 43: lateral view; Fig. 44: dorsal view; Fig. 45: head surface between inner eye margin and paramedian vertex. Bulgaria: Burgas-7 km S, 2003.09.30

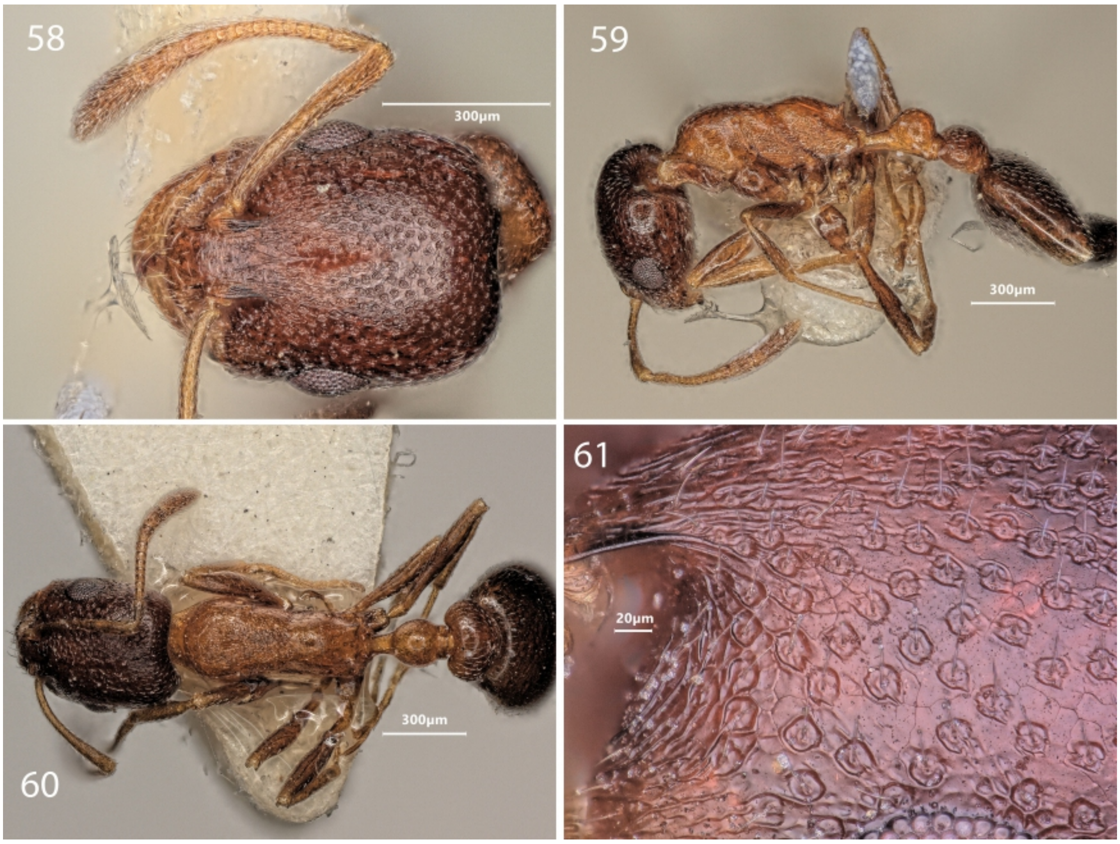


FIGURES 46–49. *Cardiocondyla sahlbergi*; Fig. 46: head in dorsal view; Fig. 47: lateral view; Fig. 48: dorsal view; Fig. 49: head surface between inner eye margin and paramedian vertex. Russia: Barkhan Sarykum, 2017.04.21

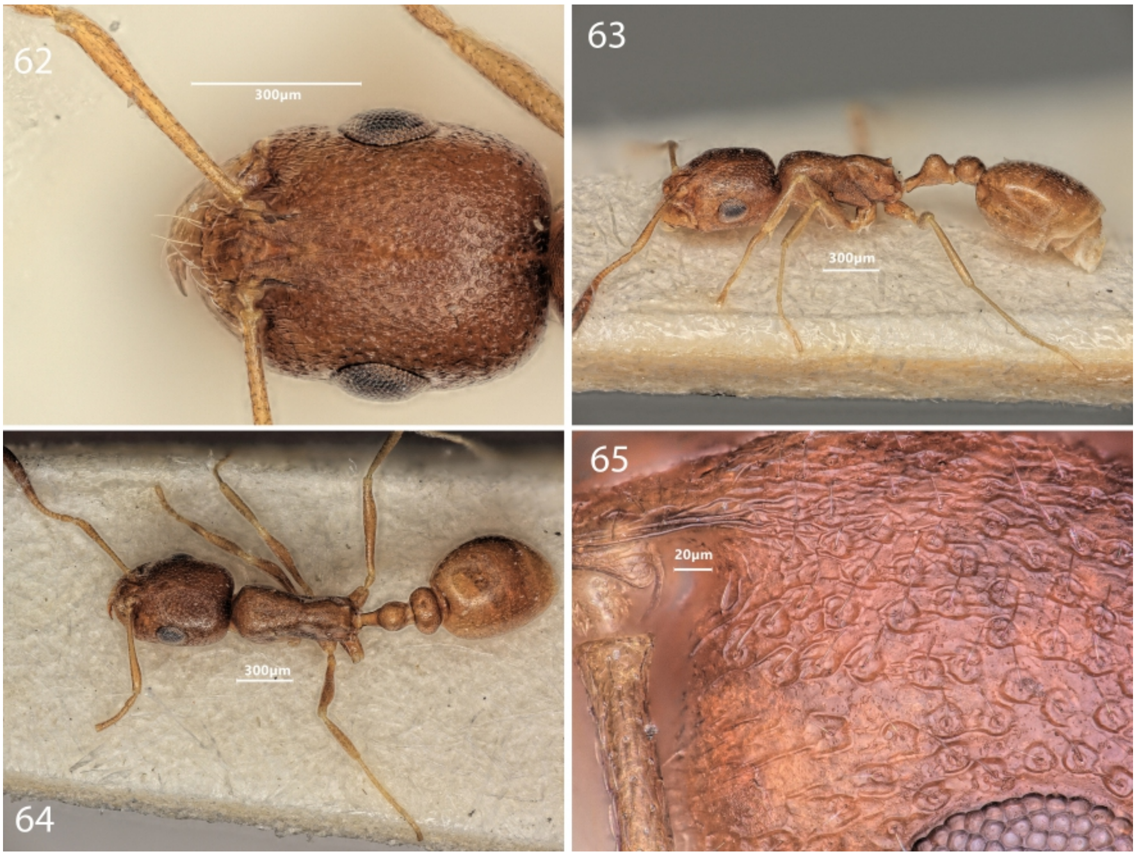


FIGURES 50–53. *Cardiocondyla persiana*, paratype; Fig. 50: head in dorsal view; Fig. 51: lateral view; Fig. 52: dorsal view; Fig. 53: head surface between inner eye margin and paramedian vertex. Iran: Shiraz-7 km NE, 1997.09.18

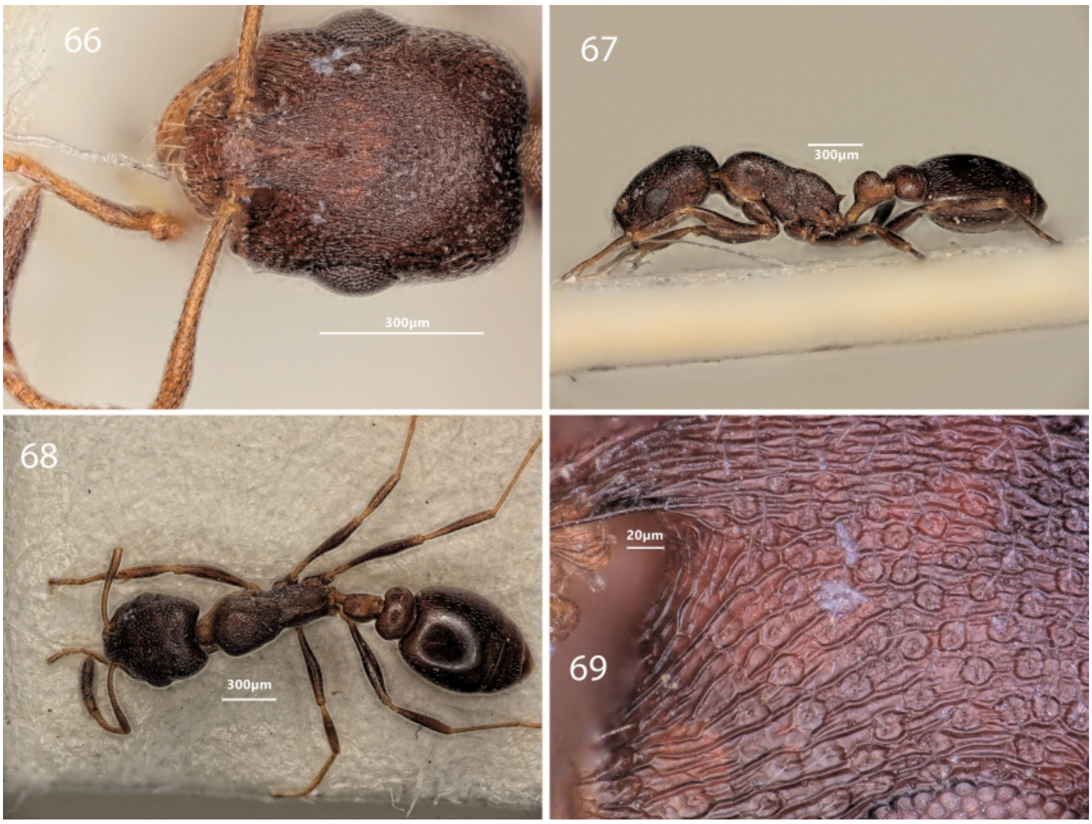
FIGURES 54–57. *Cardiocondyla batesii*; Fig. 54: head in dorsal view; Fig. 55: lateral view; Fig. 56: dorsal view; Fig. 57: head surface between inner eye margin and paramedian vertex. Spain: Padul-4.5 km WNW, 2001.04.18



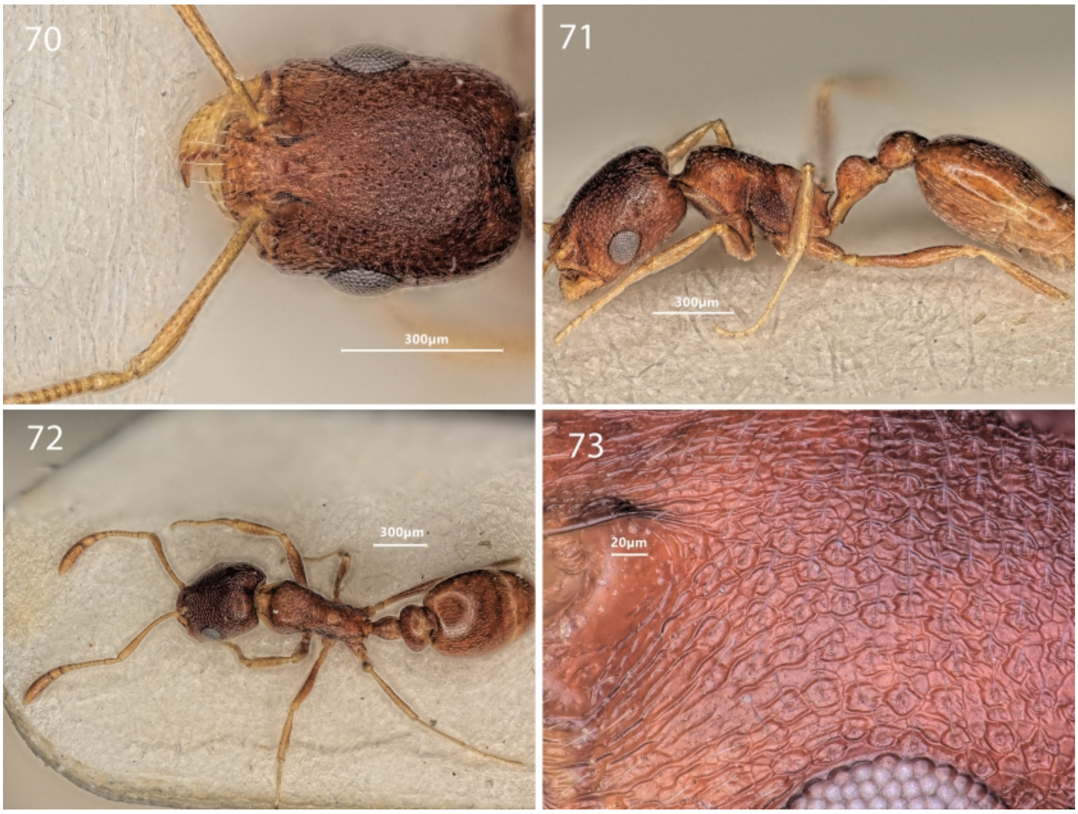
FIGURES 58–61. *Cardiocondyla semirubra*, paratype; Fig. 58: head in dorsal view; Fig. 59: lateral view; Fig. 60: dorsal view; Fig. 61: head surface between inner eye margin and paramedian vertex. Turkey: Sanliurfa-20 km S, 1993.06.12



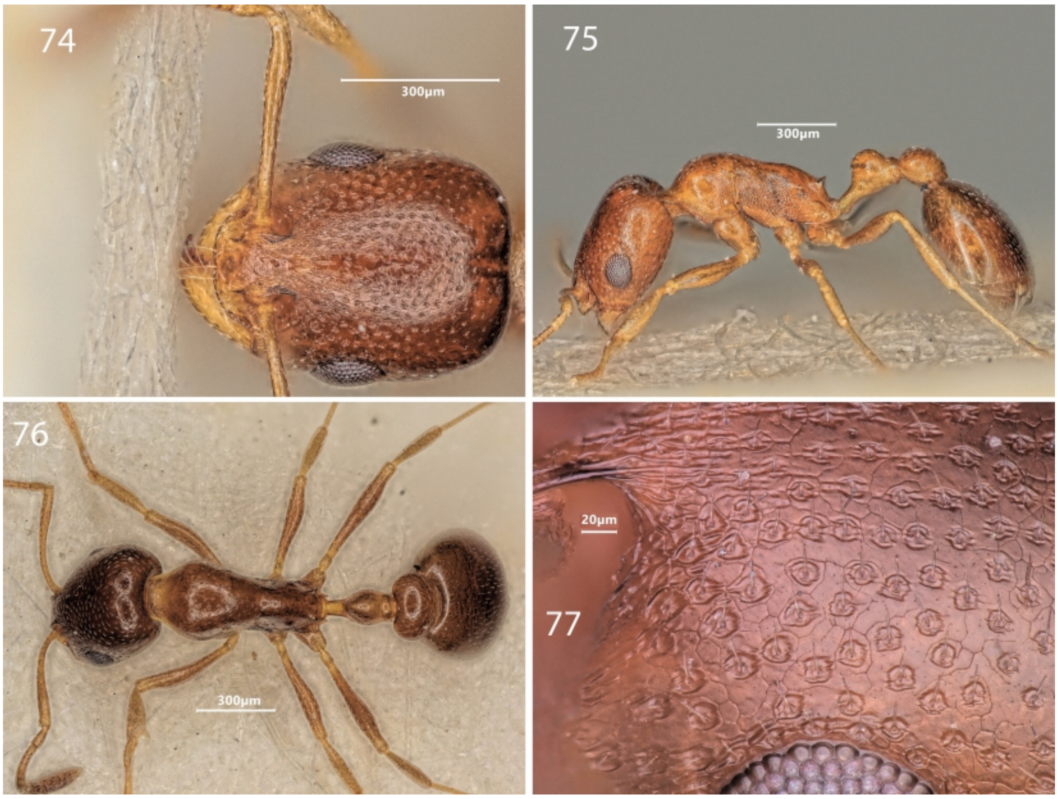
FIGURES 62–65. *Cardiocondyla opistopsis*, holotype; Fig. 62: head in dorsal view; Fig. 63: lateral view (flipped horizontally); Fig. 64: dorsal view; Fig. 65: head surface between inner eye margin and paramedian vertex. Kuweit: Burgan, 1988



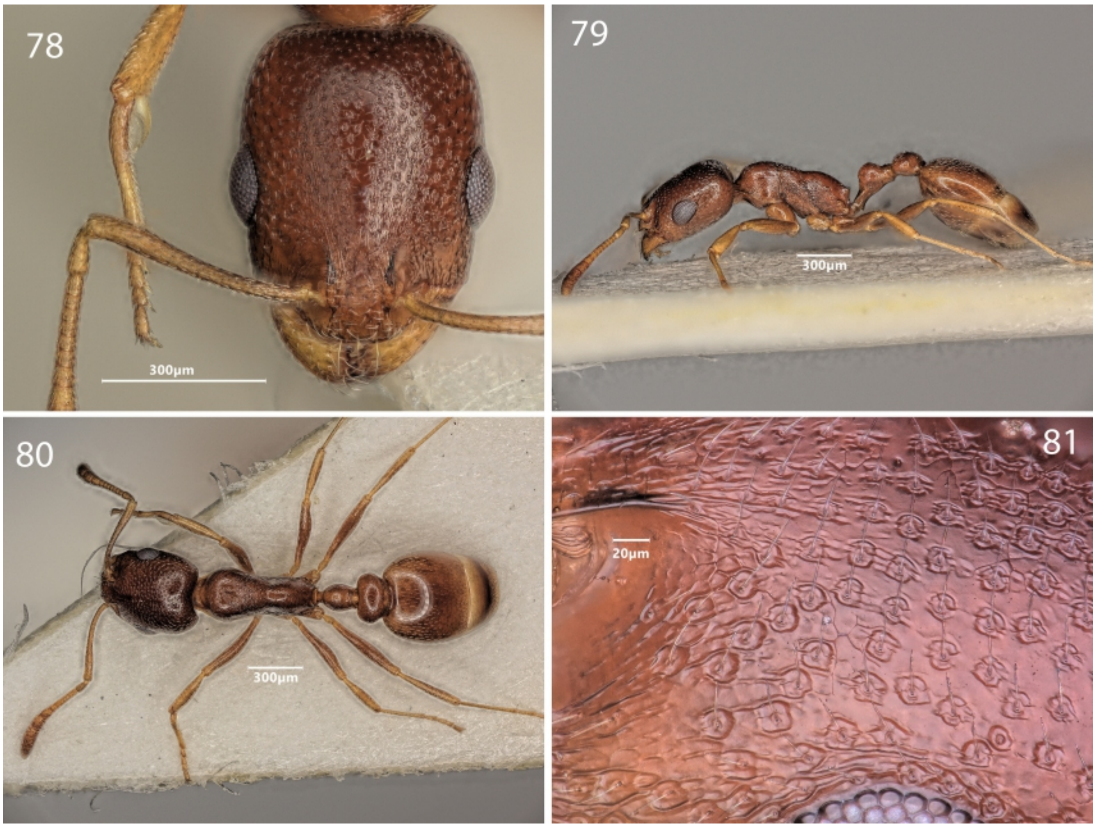
FIGURES 66–69. *Cardiocondyla rugulosa*, holotype; Fig. 66: head in dorsal view; Fig. 67: lateral view (flipped horizontally); Fig. 68: dorsal view; Fig. 69: head surface between inner eye margin and paramedian vertex. Yemen: Sanaa, 1991.05



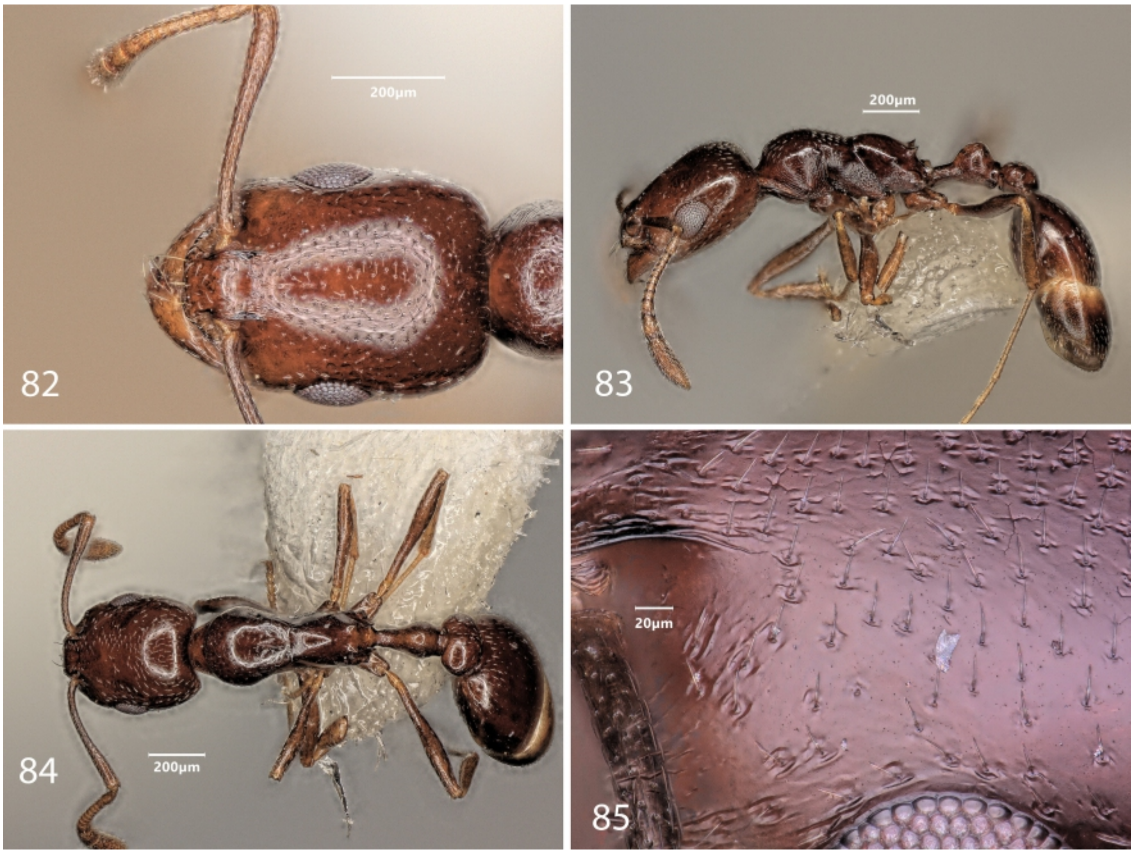
FIGURES 70–73. *Cardiocondyla kushanica*, paratype; Fig. 70: head in dorsal view; Fig. 71: lateral view (flipped horizontally); Fig. 72: dorsal view; Fig. 73: head surface between inner eye margin and paramedian vertex. Afghanistan: Darountah, 1958.01.21



FIGURES 74–77. *Cardiocondyla tenuifrons*, holotype; Fig. 74: head in dorsal view; Fig. 75: lateral view (flipped horizontally); Fig. 76: dorsal view; Fig. 77: head surface between inner eye margin and paramedian vertex (flipped horizontally). Jordan: Abdallah, 1996.03.30

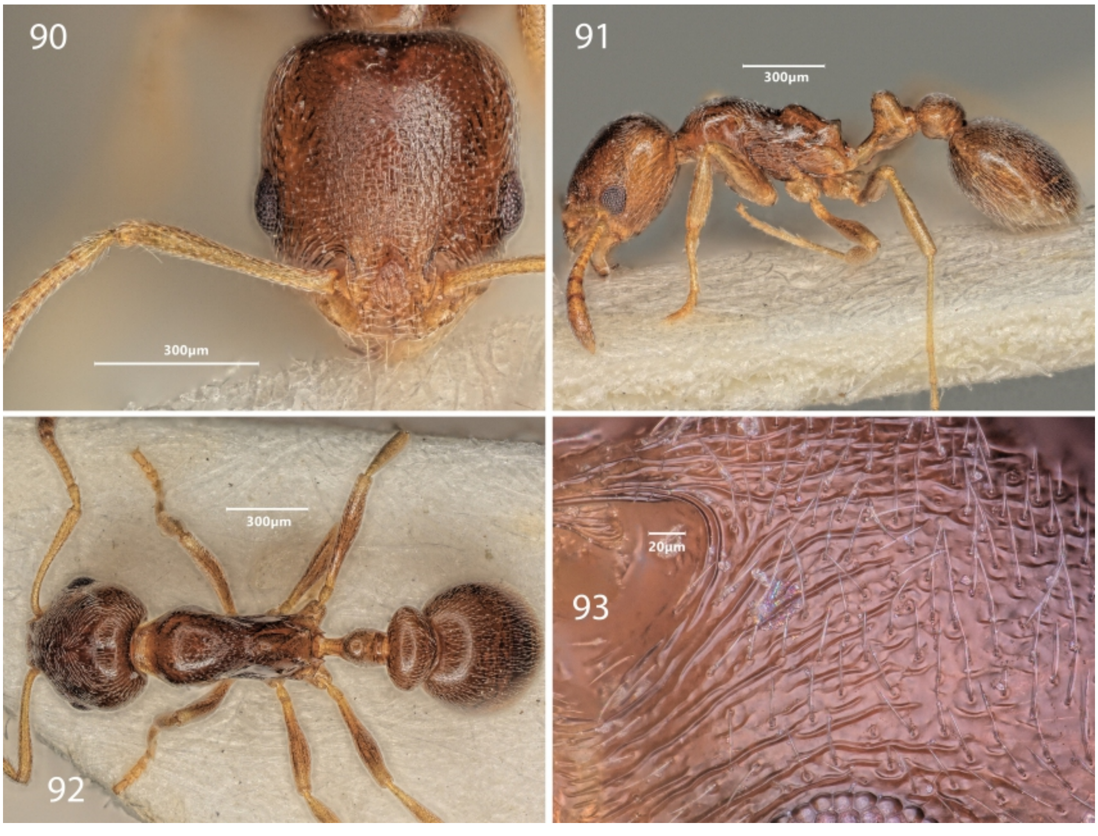


FIGURES 78–81. *Cardiocondyla nigra*; Fig. 78: head in dorsal view; Fig. 79: lateral view; Fig. 80: dorsal view; Fig. 81: head surface between inner eye margin and paramedian vertex (flipped horizontally). Cyprus: Linda Evangelista, 2003.03

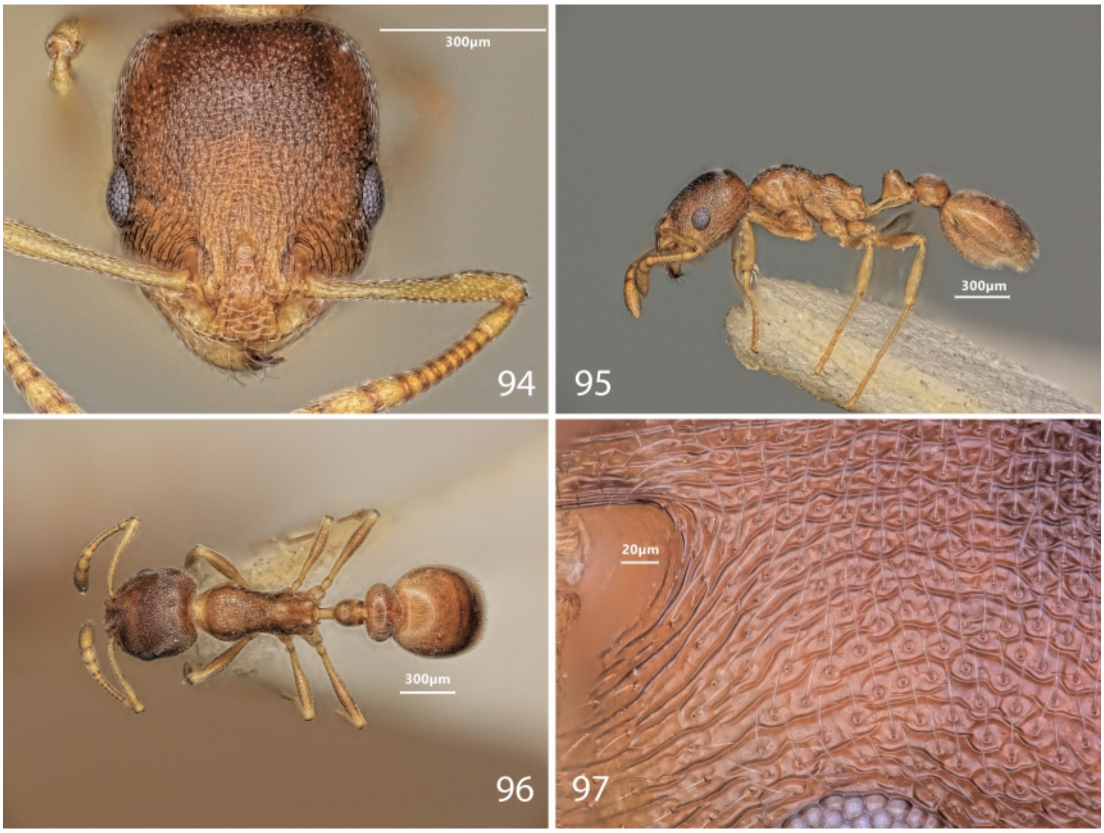


FIGURES 82–85. *Cardiocondyla verdensis* **n. sp.**, holotype; Fig. 82: head in dorsal view; Fig. 83: lateral view; Fig. 84: dorsal view; Fig. 85: head surface between inner eye margin and paramedian vertex. Cape Verde: Sao Nicolao, 2003.07.21

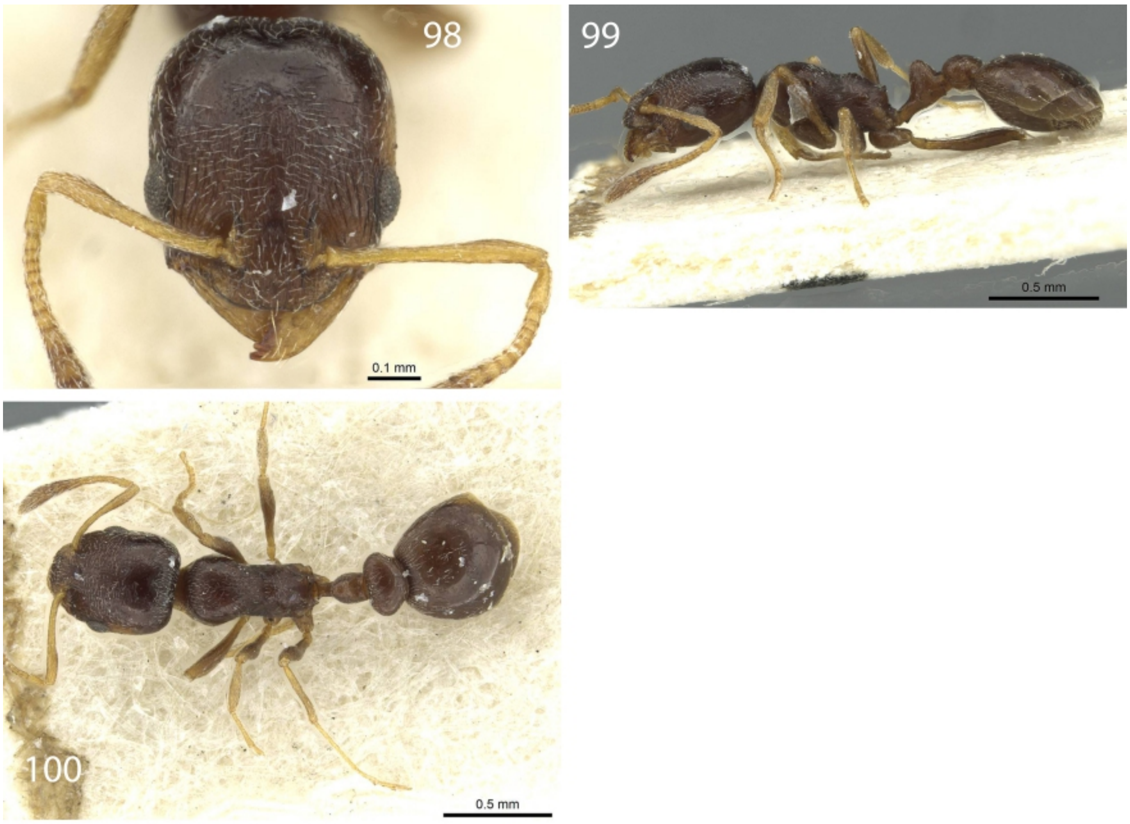
FIGURES 86–89. *Cardiocondyla stambuloffii*; Fig.86: head in dorsal view; Fig. 87: lateral view (flipped horizontally); Fig. 88: dorsal view; Fig. 89: head surface between inner eye margin and paramedian vertex. Georgia: river Podshori, 2010.08.27



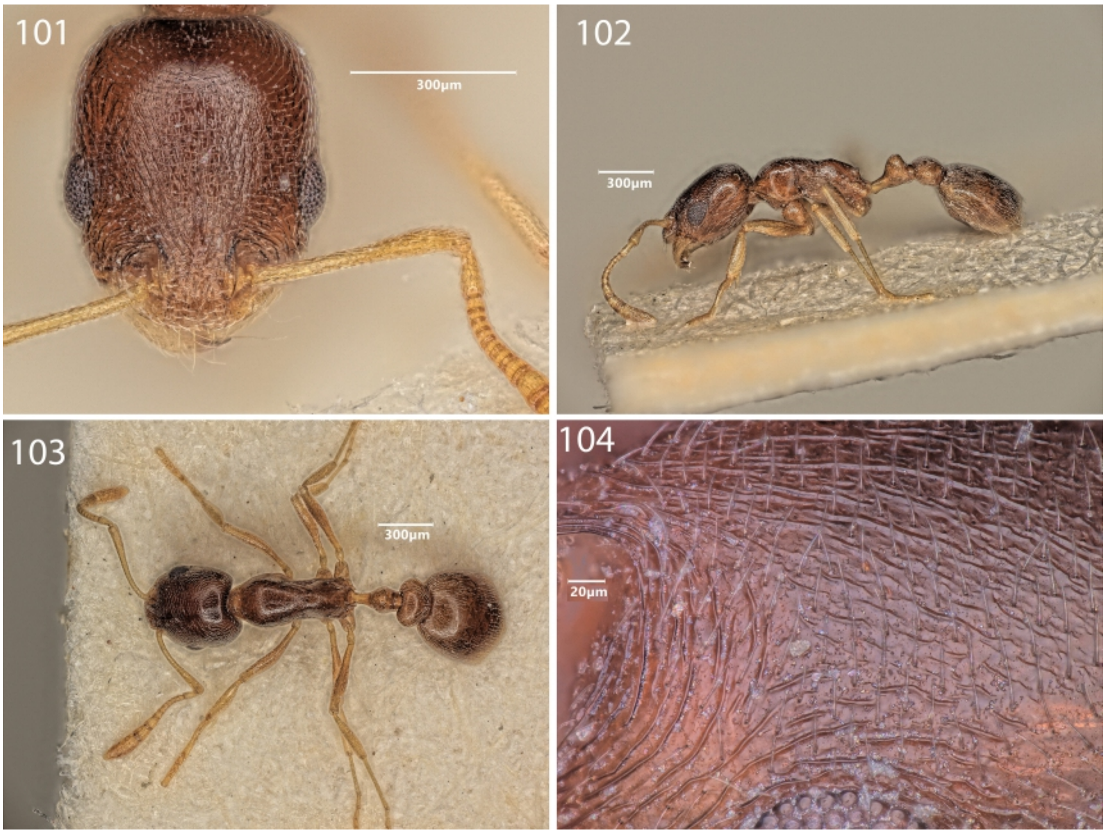
FIGURES 90–93. *Cardiocondyla koshewnikovi*; Fig. 90: head in dorsal view; Fig. 91: lateral view (flipped horizontally); Fig. 92: dorsal view; Fig. 93: head surface between inner eye margin and paramedian vertex. Kazakhstan: Sassy Kol, 2001.08.07



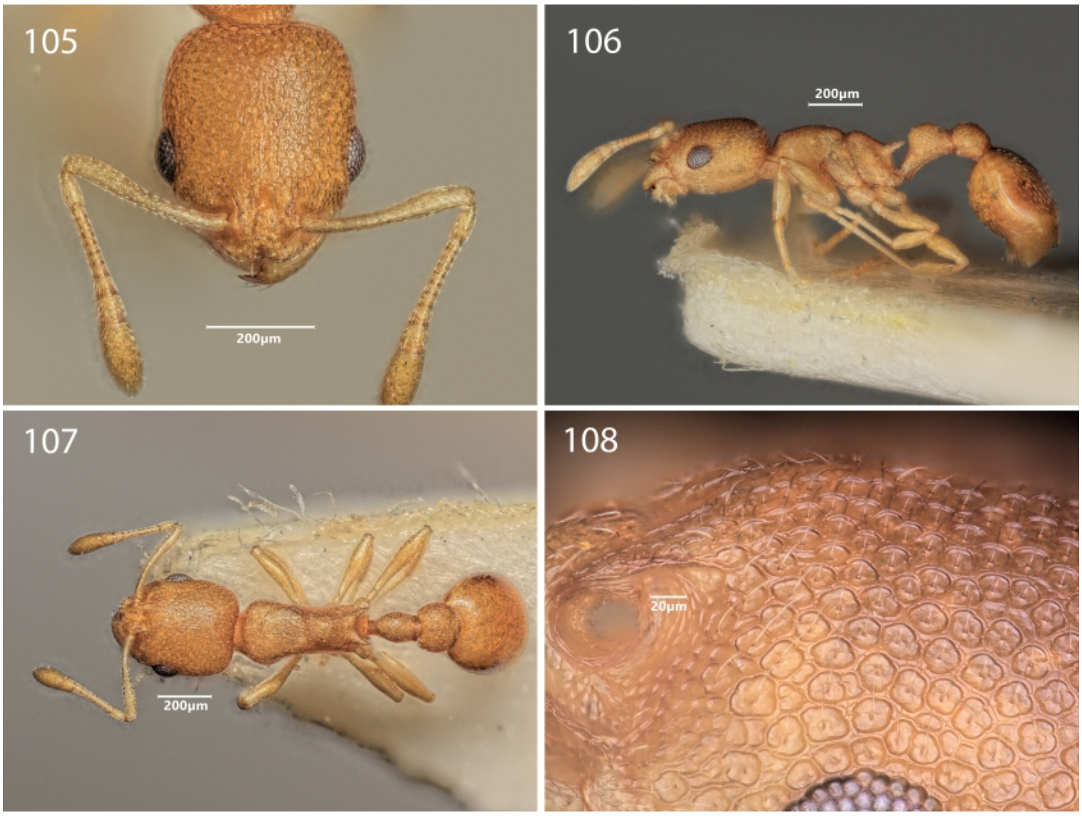
FIGURES 94–97. *Cardiocondyla rolandi* **n. sp.**, holotype; Fig. 94: head in dorsal view; Fig. 95: lateral view; Fig. 96: dorsal view; Fig. 97: head surface between inner eye margin and paramedian vertex. China: Oasis Yengisar, 2004.09.03



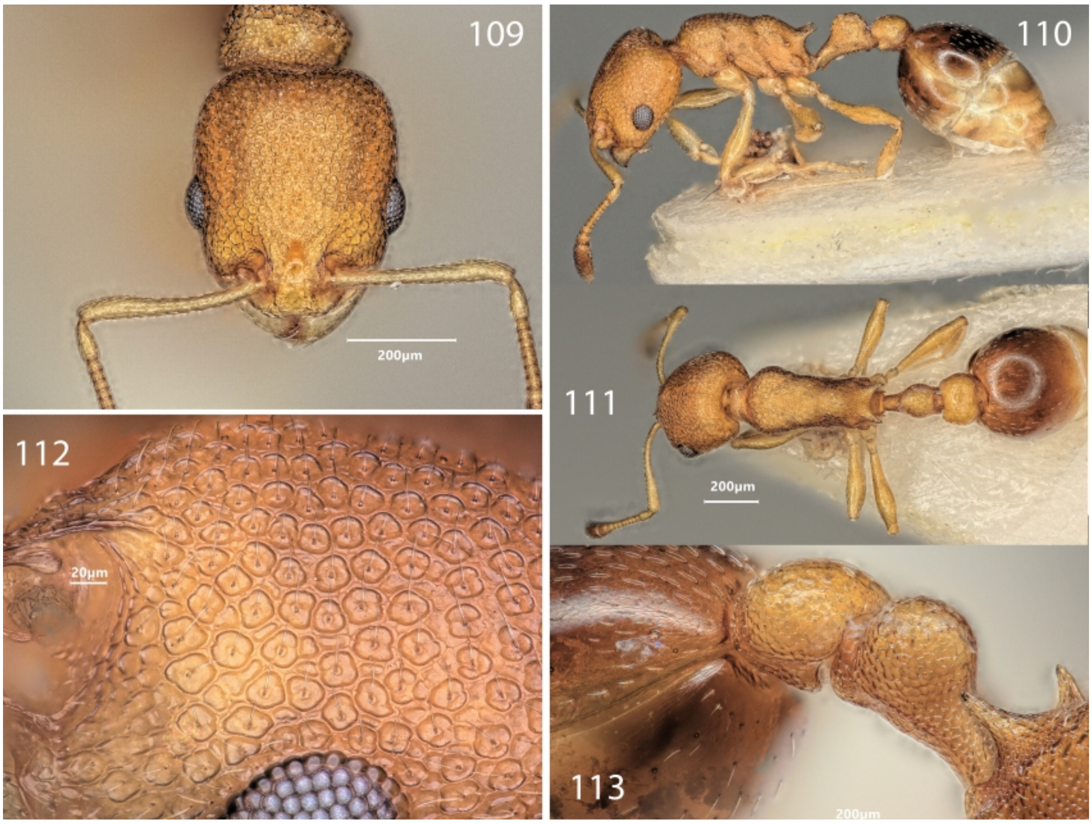
FIGURES 98–100. *Cardiocondyla gibbosa*, lectotype; Fig. 98 head in dorsal view; Fig. 99: lateral view; Fig. 100: dorsal view. Kazakhstan: Suzak, 1923.07.03



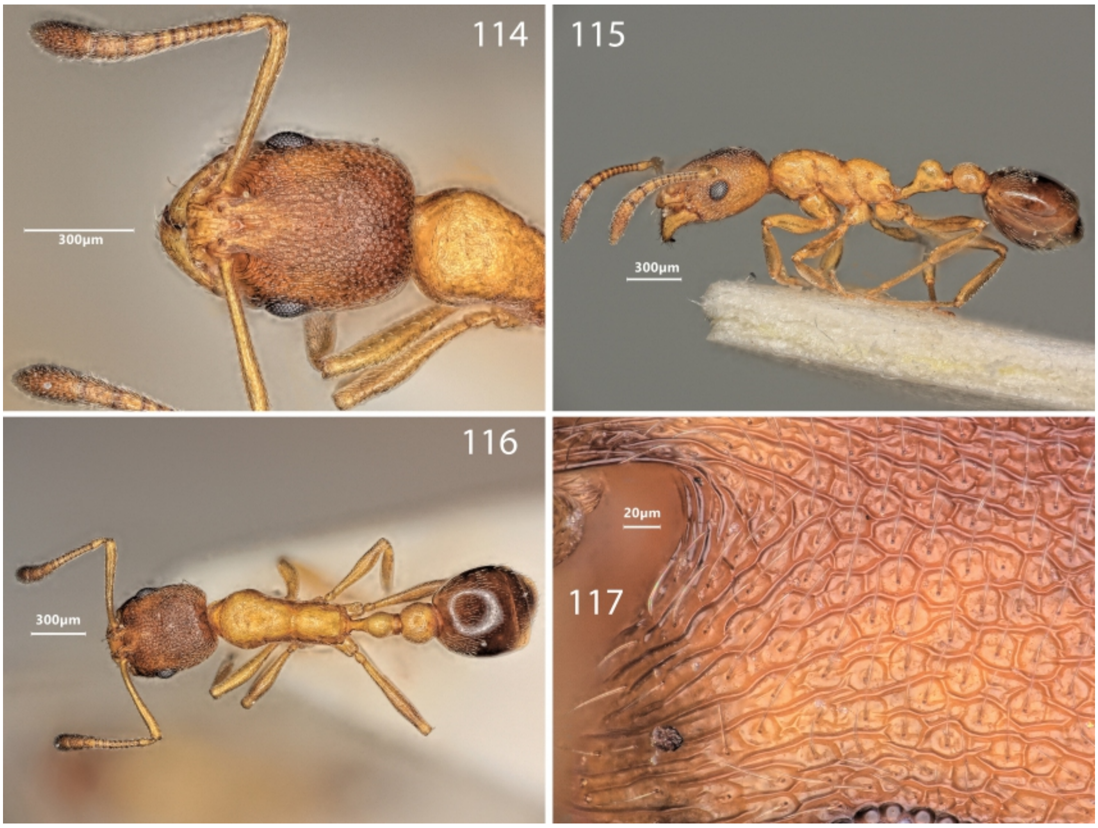
FIGURES 101–104. *Cardiocondyla tibetana*, paratype; Fig. 101: head in dorsal view; Fig. 102: lateral view (flipped horizontally); Fig. 103: dorsal view; Fig. 104: head surface between inner eye margin and paramedian vertex (flipped horizontally). China: Tarim: Ceele Station, 1966.08.26



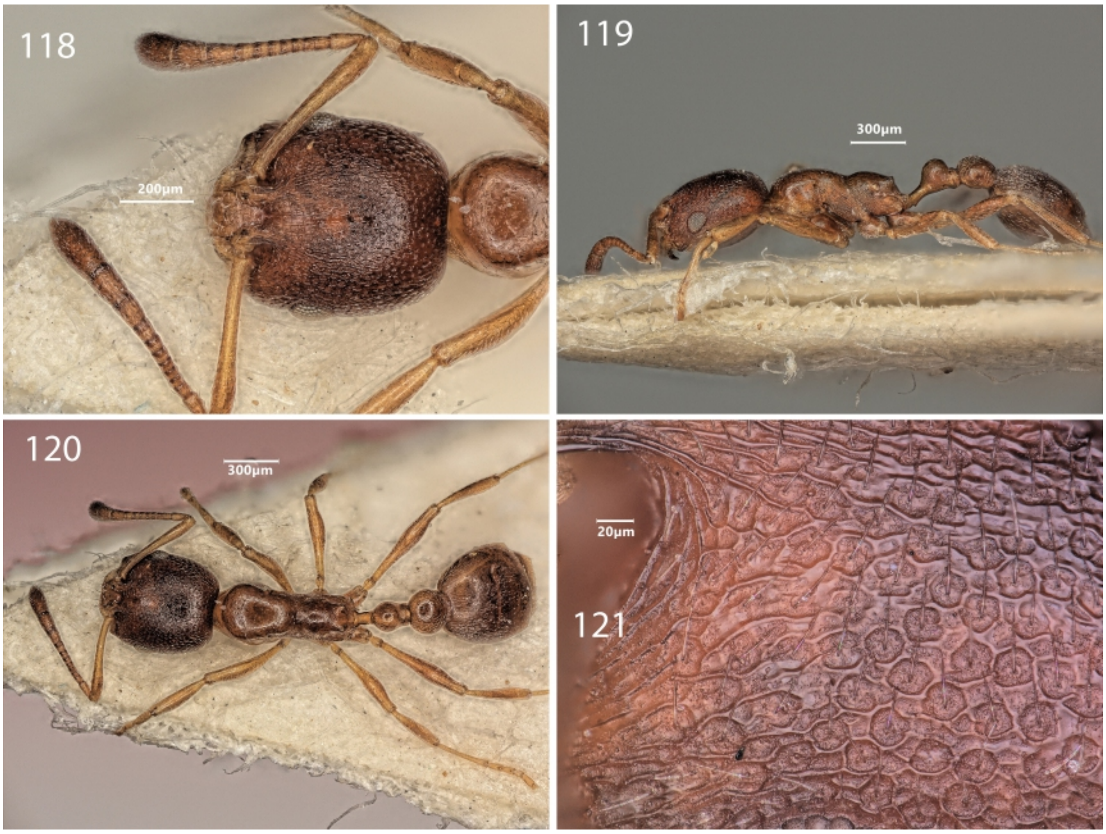
FIGURES 105–108. *Cardiocondyla wroughtonii*; Fig. 105: head in dorsal view; Fig. 106: lateral view; Fig. 107: dorsal view; Fig. 108: head surface between inner eye margin and paramedian vertex. Malaisia: Lundu, 2007.05.27



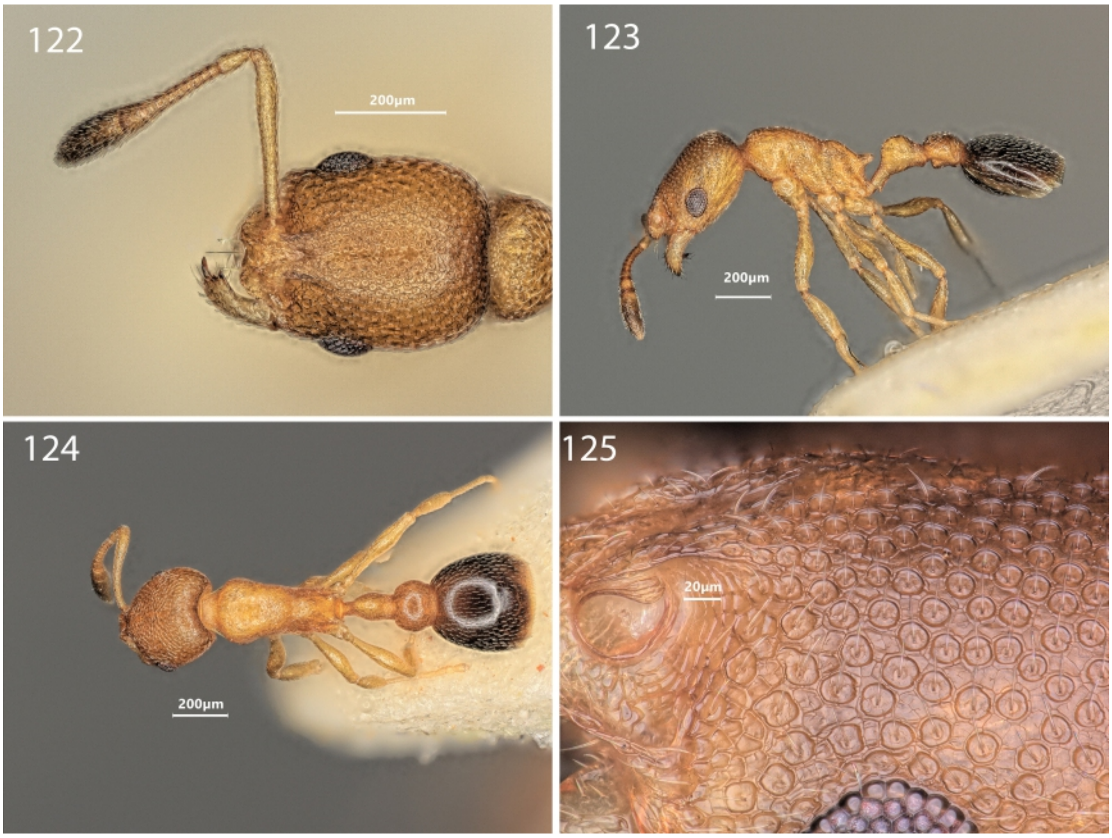
FIGURES 109–113. *Cardiocondyla obscurior*; Fig. 109: head in dorsal view; Fig. 110: lateral view; Fig. 111: dorsal view; Fig. 112: head surface between inner eye margin and paramedian vertex; Fig. 113: frontolateral aspect of waist segments. Galapagos: Santa Cruz, 2012.11.19



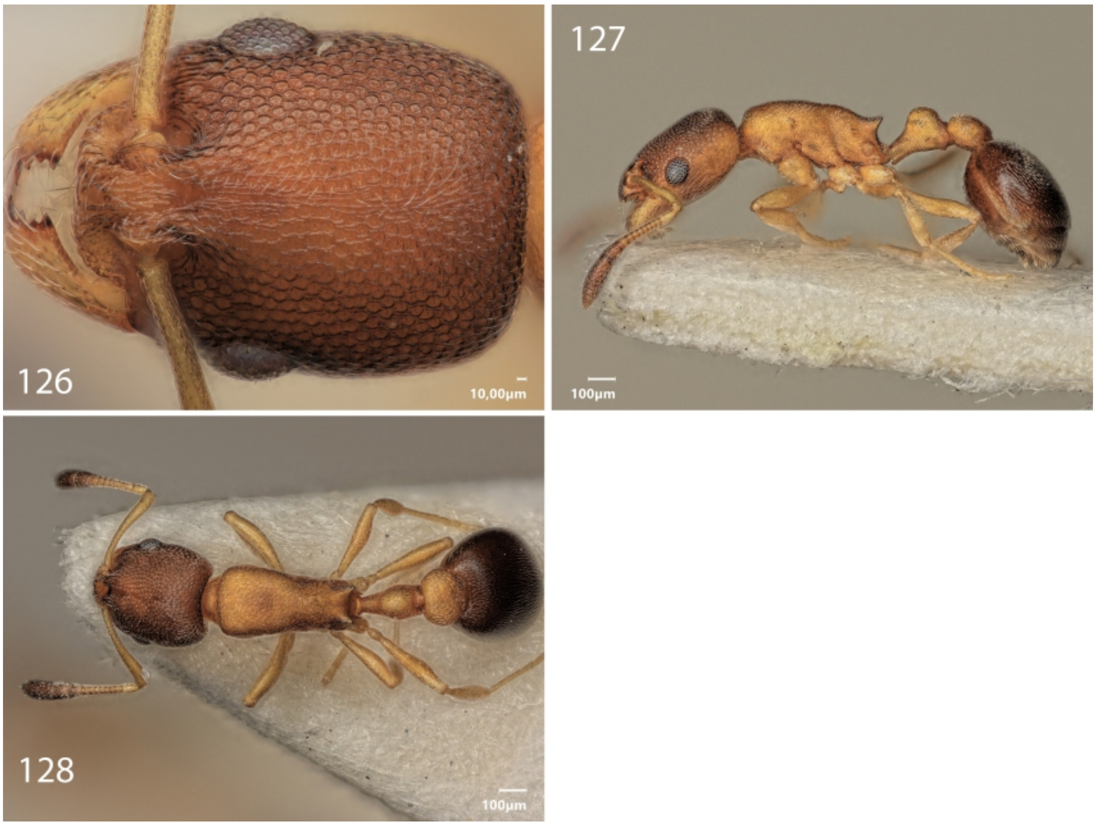
FIGURES 114–117. *Cardiocondyla fajumensis*; Fig. 114: head in dorsal view; Fig. 115: lateral view; Fig. 116: dorsal view; Fig. 117: head surface between inner eye margin and paramedian vertex. Egypt: Hurghada, 2008.04.16



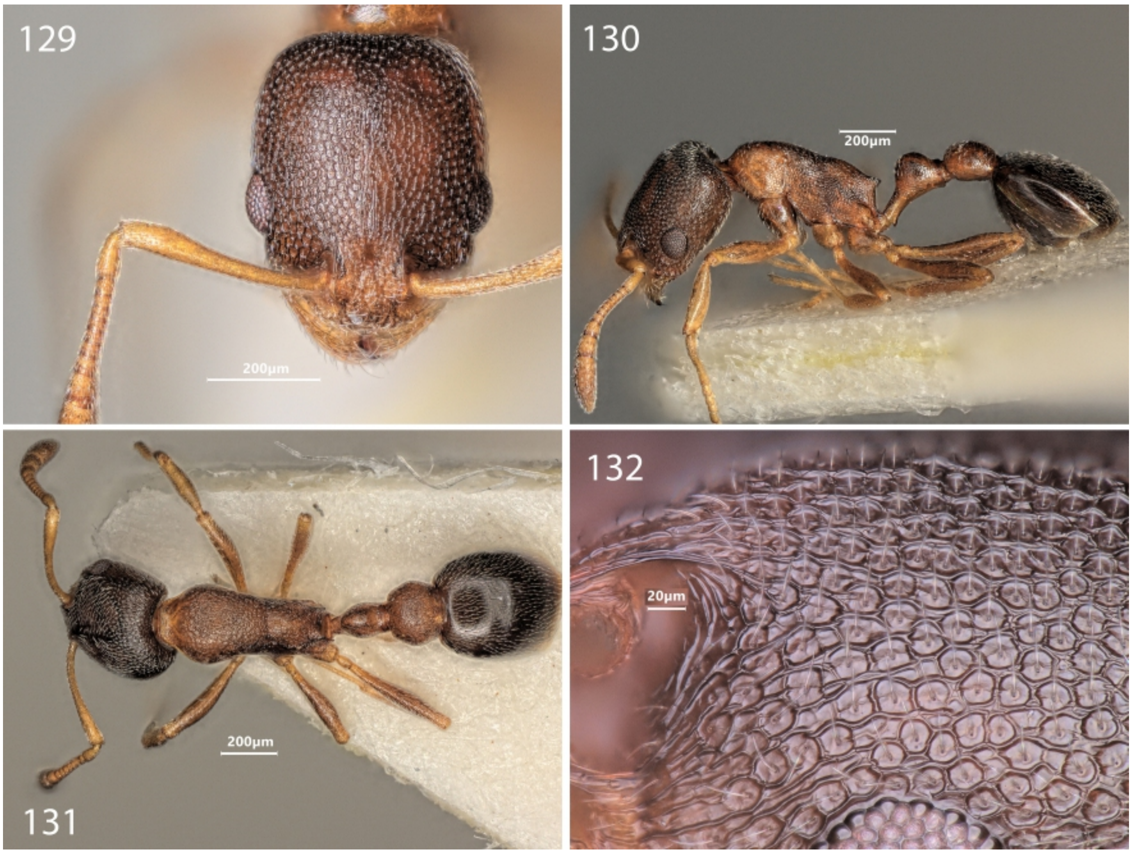
FIGURES 118–121. *Cardiocondyla unicalis*, holotype; Fig. 118: head in dorsal view; Fig. 119: lateral view; Fig. 120: dorsal view; Fig. 121: head surface between inner eye margin and paramedian vertex. Iran: Ma'amulam, 1973.08.06



FIGURES 122–125. *Cardiocondyla emeryi*; Fig. 122: head in dorsal view; Fig. 123: lateral view; Fig. 124: dorsal view; Fig. 125: head surface between inner eye margin and paramedian vertex. Angola: Candelela, 2022.02.11



FIGURES 126–128. *Cardiocondyla minutior*; Fig. 126: head in dorsal view; Fig. 127: lateral view; Fig. 128: dorsal view. Malaisia: Melina Beach-Paya, 2007.06.03



FIGURES 129–132. *Cardiocondyla mauritanica*; Fig. 129: head in dorsal view; Fig. 130: lateral view; Fig. 131: dorsal view; Fig. 132: head surface between inner eye margin and paramedian vertex. Angola: Luanda, 2022.02.0

Treatment by species

The reasons for identification of a taxon are given in square brackets after taxonomic name, author and year.

Cardiocondyla elegans Emery 1869

Cardiocondyla elegans Emery 1869 [type investigation]
The species has been described from Napoli / Italy. Investigated were one lectotype worker from MCSN Genova and five paralectotype worker from MHN Genève (a gift of Emery to Forel). The lectotype worker is labelled "Naples♀", Bosco di Capodimonte 18. VI 1866", "Cardiocondyla elegans Em. Napoli", "TYPUS", "Lectotype *Cardiocondyla elegans* Emery 1869, designated by B.Seifert 1998" and "ANTWEB CASENT 0904460".

Cardiocondyla elegans r. *santschii* Forel 1905 [type investigation]
This taxon has been described from Marseille / France. Investigated were 5 worker syntypes labelled: "C.elegans Em. r. santschii. type For. Marseille VIII. 04 (Santschi)", "TYPUS", ANTWEB CASENT 0908353"; MHN Genève. Three worker and two gynes from MHN Genève labelled by Forel "C.elegans santschii Forel, type, Candia (Biso)" have no type status as the locality Candia is not mentioned in the original description.

Cardiocondyla provincialis Bernard 1956 [type investigation]
The type locality of this taxon is Fréjus / France. Investigated were two worker syntypes labelled "Fréjus (Var) plage IX. 34 F. Bernard", "Cardiocondyla provincialis F. Bernard", "Type", "ANTWEB CASENT 0915398"; MNHN Paris.

Xenometra gallica Bernard 1957 [type investigation]
This taxon has been described from Pinsac / France. Investigated were 3 ergatoid male syntypes plus 5 workers and 5 gynes labelled "Xenometra gallica F. Bernard", "Pinsac Lepointe 1951", "Type", "ANTWEB CASENT 0915399", MNHN Paris. This taxon was erected because F. Bernard erroneously considered the ergatoid males found within a nest sample of *C. elegans* as gynes of a different socially parasitic species.

All material examined. Numeric phenotypical data were available in 50 samples (largely nest samples) with 119 workers. For details see supplementary information SI1, SI2. This material originated from France (39 samples), Italy (7) and Spain (4).
Geographic range. Spain, southern France and Italy north to 47.5°N. In northern Italy east to 13.1°E and in southern Spain ascending to 930 m.
Diagnosis: **--**Worker (Tab. 1, Figs. 6–9, key; pictures CASENT0904460, CASENT0908353, CASENT0915398 in www.antweb.org). Relatively large, CS 560 µm. Head moderately elongated, CL/CW 1.159. Postocular distance low, PoOc/CL 0.394. Scape rather long, SL/CS 0.842. Eye rather large, EYE/CS 0.252, with notable microsetae. Occipital margin suggestively concave to straight. Frons rather broad (FRS/CS 0.264), frontal carinae slightly converging immediately caudal of FRS level (FL/FR 1.051). Dorsal profile of promesonotum and of propodeum convex with a deep metanotal depression (MGr/CS 4.82 %). Spines rather short and acute (SP/CS 0.119), their axis in profile deviating by about 35° from longitudinal axis of mesosoma, their bases rather distant (SPBA/CS 0.267). Petiole rather wide and slightly lower than wide (PeW/CS 0.348, PeH/CS 0.330); in profile with a moderately long peduncle and a steep anterior slope of the node (about 65° relative to ventral profile). Postpetiole wide and moderately high (PpW/CS 0.580, PpH/CS 0.300), in dorsal view suggestively heard-shaped, with a concave anterior margin and convex sides; postpetiolar sternite convex. Head in overall impression mildly shiny. Whole vertex with shallow, feebly bicoronate foveolae of 16–18 µm diameter, foveolar distance on paramedian vertex smaller than foveolar diameter, near to eyes larger; the interspaces between foveolae shiny and in places with fragments of a very delicate microreticulum (Fig. 9). Mesosoma shiny, with weakly developed microreticulum and microrugulae, a large number of foveolae present on dorsal promesonotum, their distance approximately equal to their diameter. Dorsal propodeum glabrous but with small foveolae and a very delicate microrugosity. Dorsum of waist glabrous, with scattered fragments of very fine microreticular structures. First gaster tergite glabrous. Pubescence on whole body

long and dense, PLG/CS 7.92 %, sqPDG 3.95. Color of head, mesosoma, waist and gaster usually homogenously dark to medium brown; mandibles, scape, tibiae and tarsae yellowish brown.

Taxonomic comments and clustering results. The 85 available nest samples of the sister species *Cardiocondyla elegans* and *C. dalmatica* Soudek 1925 can be separated with a mean error of 1.2 % by the exploratory data analyses NC-Ward, NC-part.hclust, NC-part.kmeans and NC-NMDS.kmeans using the characters CS, CL/CW, PoOc/CL, EYE/CS, SL/CS, SP/CS, PeW/CS, PpW/CS, PeH/CS, PpH/CS, sqPDG, PLG/CS, MGr/CS and dFOV (Fig. 133). A LDA using the same characters classified 97.8 % of 185 worker individuals of both species correctly. In the sample mean and when run in the LDA as wild-cards, the type samples of *C. elegans*, *C. santschii*, *C. provincialis* and *C. gallica* are allocated with posterior probabilities of 0.8443, 0.9166, 0.9972 and 0.9924 to the *elegans* cluster, whereas the lectotype of *C. dalmatica* is allocated with p=0.9961 to the *dalmatica* cluster.

Biology. For a condensed description of life history see Seifert (2018) and for details Lafrechoux *et al.* (1999, 2000), Lenoir (2006), Lenoir *et al.* (2007), Mercier *et al.* (2007), and Vidal *et al.* (2021).

Cardiocondyla dalmatica Soudek 1925

Cardiocondyla elegans var. *dalmatica* Soudek 1925 [type investigation]

This taxon has been described from the Gulf of Kotor / Montenegro. Investigated was one worker from NHM Basel, labelled “Boka Kotorska, Dalmacia, 1923, Dr. Soudek” and one worker from ZIPAS Warszawa labelled “Boka Kotor, Igalo VII 1922, Dr.Soudek”. Both specimens are most similar in morphology and are allocated to the *dalmatica* cluster in a wild-card run of the LDA mentioned above with p = 1.0000 (specimen from “Boka Kotorska”) and p = 0.9961 (specimen from “Boka Kotor, Igalo”). The original description of Soudek (1925) does not give collecting dates and only reports of a single colony found “at Erceg Novi (Castelnuovo) in the Gulf of Kotor”. As the locality Igalo is a part of the town Herceg Novi, the specimen from this locality is better attributable to Soudek’s statements and is fixed herewith as lectotype.

All material examined. Numeric phenotypical data were available in 32 samples (largely nest samples) with 72 workers. For details see supplementary information SI1, SI2. This material originated from Albania (1 sample), Bulgaria (5), Cyprus (1), Greece (15), Hungary (2), Iran (1), Italy (1); Montenegro (2) and Turkey (4).

Geographic range. From N Italy (8.6°E), across the whole Balkans, Cyprus and Asia Minor east to the Iran (52.7°E). The northern range border is demarcated by 47. 78°N and 16.84°E in Austria (Zettel *et al.* 2021), 47.83°N 18.83°E in Slovakia (Bezdecka & Tetal 2013) and 48.07°N, 19.29°E in Hungary. All European sites are below 600 m but in the Iran it ascends to 1700 m (29.76°N, 52.70°E). The mean air temperature May–Aug of 29 sites is 22.23 ± 2.12 [18.7, 25.8] °C.

Diagnosis: **--**Worker (Tab. 1, Figs. 10–13, key; pictures CASENT0179878, ANTWEB1041351 in www.antweb.org). Relatively large, CS 554 µm. Head moderately elongated, CL/CW 1.156. Postocular distance low, PoOc/CL 0.399. Scape long, SL/CS 0.855. Eye rather large, EYE/CS 0.247, with notable microsetae. Occipital margin suggestively concave to straight. Frons rather broad (FRS/CS 0.258), frontal carinae slightly converging immediately caudal of FRS level (FL/FR 1.045). Dorsal profile of promesonotum and of propodeum convex with a rather deep metanotal depression (MGr/CS 3.90 %). Spines rather short and acute (SP/CS 0.109), their axis in profile deviating by about 35° from longitudinal axis of mesosoma, their bases rather distant (SPBA/CS 0.262). Petiole narrower than in *C. elegans* and slightly higher than wide (PeW/CS 0.313, PeH/CS 0.329); in profile with a moderately long peduncle and a steep anterior slope of the node (about 65° relative to ventral profile). Postpetiole rather wide and moderately high (PpW/CS 0.562, PpH/CS 0.298), in dorsal view suggestively heard-shaped, with a concave anterior margin and convex sides; postpetiolar sternite convex. Head in overall impression mildly shiny. Whole vertex with shallow, feebly bicoronate foveolae of 16–18 µm diameter, foveolar distance on paramedian vertex smaller than foveolar diameter, near to eyes larger; the interspaces between foveolae shiny and in places with fragments of a very delicate microreticulum (Fig. 13). Mesosoma shiny, with weakly developed microreticulum and microrugulae, a large number of foveolae present on dorsal promesonotum, their distance approximately equal to their diameter. Dorsal propodeum glabrous but with small foveolae and a very delicate microrugosity. Dorsum of waist glabrous, with scattered fragments of very fine microreticular structures. First gaster tergite glabrous. Pubescence on whole body long and dense, PLG/CS 7.57 %, sqPDG 4.09. Color of head, mesosoma, waist and gaster usually homogenously dark to medium brown; mandibles, scape, tibiae and tarsae yellowish brown.

Taxonomic comments and clustering results. *Cardiocondyla dalmatica* is an eastern, parapatric sibling species of *C. elegans* with a sympatric occurrence, as far as known, only in N Italy. Both species are in basic shape and surface structure extremely similar but there are significant differences in PeW, SL, MGr and PpW (Tab1.). The clear separation of both species by exploratory and hypothesis-driven data analyses is reported in the previous section (p. 29).
Biology. A strongly thermophilous species. Natural habitats are open riverine or coastal sand-gravel banks, dunes and solonchaks with very sparse herb layer. There is a considerable habitat shift to anthropogenous sites; it is frequent here at roadsides, country lanes, camping grounds etc. The simple soil nests usually show a single, very narrow entrance hole of 1.0–1.4 mm diameter which leads to a vertical duct that passes through a number of chambers down to 50 cm in habitats with low water table. A nest entrance in the solonchaks at Lake Neusiedlersee, situated within a transitional zone which is flooded for several days to weeks annually, was according to Zettel *et al.* (2021) only 15 cm above the water table. The material around this entrance was strongly cemented and the entrance could be closed when flooded. One nest excavated in Bulgaria contained 150 workers, 7 ergatoid males, 155 alate gynes and one queen and the nests are probably monogynous at the nest level. Mating and colony foundation is probably as in *C. elegans* (Seifert 2018). Gynes are polymorphic in mesosoma size and wing length—flight dispersal and independent colony foundation is supposed for macrosomatic-macropterous gynes in particular. Forages at surface temperatures up to 50°C on soil surface and in the lower herb layer. Apparently largely zoophagous. Visits nectaries. It behaves submissive and cryptic in respect to other ants.

Cardiocondyla dalmaticoides n. sp.

Etymology: because of similarity to *Cardiocondyla dalmatica*.
Type material:
Holotype plus 2 paratype workers labelled "HATAY—2km N Reyhauli 50 km E Hatay 100 mH Straßenrand 1020 Leg. Schulz 09.06.93 TÜRKEI"; one paratype worker labelled "ANTALYA 2km S Geris 40km NE Manavgat 1000 mH Straßenrand 1020 Leg. Schulz 06.06.93 TÜRKEI"; both samples deposited in SMN Görlitz; at least two paratype workers labelled "HATAY—2km N Reyhauli 50 km E Hatay 100 mH Straßenrand 1022 Leg. Schulz 09.06.93 TÜRKEI", in private collection of Andreas Schulz / Leverkusen.
All material examined. Only the three type samples with 6 workers from Asia Minor were available. For details see supplementary information SI1, SI2.
Geographic range. So far only known from two sites in Asia Minor between 100 and 1000 m a.s.l.
Diagnosis: --Worker (Tab. 1, Figs. 14–17, key). Large, CS 614 µm. Head short, CL/CW 1.126. Postocular distance low, PoOc/CL 0.399. Scape long, SL/CS 0.855. Eye medium-sized, EYE/CS 0.242. Occipital margin straight or suggestively concave. Frons rather broad (FRS/CS 0.256), frontal carinae slightly converging immediately caudal of FRS level (FL/FR 1.044). Dorsal profile of promesonotum and of propodeum convex with a deep metanotal depression (MGr/CS 4.43 %). Spines rather short but much more acute than in *C. dalmatica* and *elegans* (SP/CS 0.112), their axis in profile deviating by about 50° from longitudinal axis of mesosoma, their bases much more approached than in *C. dalmatica* (SPBA/CS 0.228). Petiole narrower than in *C. dalmatica* and *elegans* and much higher than wide (PeW/CS 0.296, PeH/CS 0.341); in profile with a long peduncle and a very steep anterior slope of the node (about 72° relative to ventral profile). Postpetiole rather wide and moderately high (PpW/CS 0.563, PpH/CS 0.291), in dorsal view suggestively heard-shaped, with a concave anterior margin and convex sides; postpetiolar sternite convex. Head in overall impression mildly shiny. Whole vertex with shallow, feebly bicoronate foveolae of 18–19 µm diameter, foveolar distance on paramedian vertex smaller than foveolar diameter, near to eyes larger; the interspaces between foveolae shiny and in places with fragments of a very delicate microreticulum (Fig. 17). Mesosoma more shiny than in *C. dalmatica*, with only suggestively developed microreticulum and microrugulae, a large number of foveolae present on dorsal promesonotum, their distance approximately equal to their diameter. Whole propodeum completely glabrous. Dorsum of waist glabrous. First gaster tergite glabrous. Pubescence on whole body long and dense, PLG/CS 6.97 %, sqPDG 3.95. Color of head, mesosoma, waist and gaster usually homogenously dark to medium brown; mandibles, scape, tibiae and tarsae yellowish brown.
Taxonomic comments and clustering results. *Cardiocondyla dalmaticoides* **n. sp.** can be safely separated from *C. dalmatica* and *C. elegans* alone by the more approached spine bases and narrower petiole (Fig. 134). The glabrous

surface of propodeum, the very acute propodeal spines and the high petiole with a very steep anterior profile of the node offer accessory means for separation.
Biology. Unknown.

Cardiocondyla brachyceps Seifert 2003

Cardiocondyla brachyceps Seifert 2003 [type investigation]
This taxon has been described from west of Shiraz / Iran. Investigated were the holotype worker and 15 worker paratypes labelled "Iran, Fars 1997 (15), 51 road-km W Shiraz, Chehel Chesmeh, 1940 m, 17.9.; leg. Schödl ", NHM Wien; 9 worker paratypes from the same sample in SMN Goerlitz. 3 worker paratypes labelled "ARTVIN—Taslica, 10 km W Artvin, 1000 mH, Laubmischwald, Steinmauer, leg. Schulz 02.07.89 TÜRKEI", SMN Goerlitz.

All material examined. Numeric phenotypical data were available in 4 samples with 13 workers. For details see supplementary information SI1, SI2. This material originated from Afghanistan (1 sample), Georgia (1) and Iran (2).
Geographic range. From S Georgia and NE Turkey (41.7°E) eastwards over the Iran to E Afghanistan (69.5°E). The altitudinal range extends from 5 m in Georgia to 2000 m in Iran.
Diagnosis: --Worker (Tab. 1, Figs. 18–21, key; pictures CASENT0919731 in www.antweb.org). Relatively large, CS 559 µm. Head rather short, CL/CW 1.131. Postocular distance very low, PoOc/CL 0.380. Scape rather long, SL/CS 0.831. Eye rather large, EYE/CS 0.251. Occipital margin suggestively concave. Frons rather broad (FRS/CS 0.257), frontal carinae slightly converging immediately caudal of FRS level (FL/FR 1.044). Dorsal profile of promesonotum and of propodeum convex with a deep metanotal depression (MGr/CS 4.39 %). Propodeal spines slightly longer and slightly thinner than in related species (SP/CS 0.128), their axis in profile deviating by about 35° from longitudinal axis of mesosoma, their bases more approached (SPBA/CS 0.237). Petiole narrower than in C. *elegans* and as high as wide (PeW/CS 0.299, PeH/CS 0.301); in profile with a long peduncle that is about 1.8fold as long as wide and an extremely steep anterior slope of the node (about 85° relative to ventral profile). Postpetiole much narrower and lower than in related species (PpW/CS 0.522, PpH/CS 0.260), in dorsal view heard-shaped, with a concave anterior margin and convex sides; postpetiolar sternite with the anteromedian portion significantly more bulging than its anteroparamedian portion; in lateral view this anteromedian bulge forms a small, obtusely-angled, rounded corner and changes into the helcium with a distinct angle. Frontal laminae, paramedian vertex, and lateral clypeus with weak longitudinal sculpture. Vertex with strongly demarcated, bicoronate foveolae of 18–21 µm diameter; interspaces narrower than foveolar diameter, near to eyes larger; the interspaces between foveolae shiny and in places with fragments of a very delicate microreticulum. Mesosoma on most of its surface shining and with very fine microreticulum. Dorsal promesonotum finely longitudinally rugulose and with scattered bicoronate foveolae. Lateral meso- and metapleurae delicately longitudinally striate-reticulate; at lower magnifications appearing duller, contrasting the shining lateral parts of mesonotum and pronotum. Dorsum of waist glabrous except for a very delicate microreticulum. First gaster tergite glabrous. Pubescence on whole body long but less dense than in related species, PLG/CS 7.96 %, sqPDG 4.65. Color variable: head medium brown to blackish brown; mesosoma and petiole usually light orange-brown, in specimens with to dark brown mesosoma an orange-yellowish color component is still visible; postpetiole and gaster dark to blackish brown.
Taxonomic comments and clustering results. *Cardiocondyla brachyceps* is obviously a member of the *C. elegans* species group but differs from *C. elegans, C. dalmatica* and *C. dalmaticoides* **n. sp.** by much narrower and lower waist segments, more dilute pubescence and the differing petiole profile (compare Figs. 7, 11, 15 and 19). In numeric terms, *C. brachyceps* is strongly separable from the other three species by a PCA of the characters PpH/CS, dFOV, SL/CS, PoOc/CL, sqPDG, SP/CS, PLG/CS and PeW/CS (Fig. 135).
Biology. The nest sample from Georgia was collected on a sandy riverbank with scattered bushes.

TABLE 1. Measurements of workers of the *Cardiocondyla elegans* group. Data are given in the sequence arithmetic mean ± standard deviation [minimum, maximum]. For characters with fewer data than indicated in the head of the columns, the number of measurements is given after the square brackets.

	elegans (n=119)	***dalmatica*** (n=66)	***dalmaticoides*** (n=6)	***brachyceps*** (n=13)
CS	560 ± 24 [511,615]	554 ± 22 [495,598]	614 ± 3 [610,618]	559 ± 25 [498,587]
CL/CW	1.159 ± 0.019 [1.112,1.224]	1.156 ± 0.017 [1.125,1.196]	1.126 ± 0.025 [1.100,1.163]	1.131 ± 0.019 [1.093,1.164]
SL/CS	0.842 ± 0.015 [0.790,0.869]	0.855 ± 0.016 [0.816,0.881]	0.861 ± 0.008 [0.849,0.870]	0.831 ± 0.019 [0.812,0.869]
PoOc/CL	0.394 ± 0.008 [0.378,0.414]	0.399 ± 0.009 [0.383,0.422]	0.399 ± 0.003 [0.395,0.401]	0.380 ± 0.010 [0.367,0.396]
EYE	0.252 ± 0.006 [0.235,0.263]	0.247 ± 0.006 [0.235,0.266]	0.242 ± 0.006 [0.237,0.253]	0.251 ± 0.005 [0.244,0.260]
dFOV	17.2 ± 0.79 [15.3,19.4]	17.3 ± 0.86 [15.5,20.1]	18.2 ± 0.42 [17.9,19.0]	19.4 ± 0.9 [18.0,21.0]
FRS/CS	0.264 ± 0.008 [0.242,0.288]100	0.258 ± 0.009 [0.232,0.277] 60	0.256 ± 0.004 [0.249,0.262]	0.257 ± 0.011 [0.235,0.273]
FL/FR	1.051 ± 0.027 [1.000,1.100] 34	1.045 ± 0.022 [1.004,1.097] 40	1.082 ± 0.028 [1.050,1.112] 4	1.044 ± 0.031 [1.000,1.096]
SPBA/CS	0.267 ± 0.012 [0.232,0.297]100	0.262 ± 0.015 [0.229,0.290] 59	0.228 ± 0.011 [0.213,0.246]	0.237 ± 0.017 [0.214,0.282]
SP/CS	0.119 ± 0.012 [0.079,0.153]	0.109 ± 0.016 [0.074,0.144]	0.112 ± 0.009 [0.101,0.125]	0.128 ± 0.009 [0.113,0.142]
PeW/CS	0.348 ± 0.026 [0.292,0.413]	0.313 ± 0.019 [0.272,0.375]	0.296 ± 0.015 [0.276,0.315]	0.299 ± 0.016 [0.265,0.322]
PpW/CS	0.580 ± 0.026 [0.526 , 0.640]	0.562 ± 0.021 [0.516 , 0.615]	0.563 ± 0.016 [0.546 , 0.585]	0.522 ± 0.029 [0.448,0.556]
PeH/CS	0.330 ± 0.016 [0.295 , 0.368]	0.329 ± 0.015 [0.298 , 0.367]	0.341 ± 0.008 [0.328 , 0.350]	0.301 ± 0.016 [0.269,0.327]
PpH/CS	0.300 ± 0.013 [0.274 , 0.344]	0.298 ± 0.015 [0.270 , 0.333]	0.291 ± 0.012 [0.275 , 0.308]	0.260 ± 0.016 [0.232,0.291]
sqrtPDG	3.95 ± 0.26 [3.47,4.61]	4.09 ± 0.25 [3.54 , 4.64]	3.95 ± 0.22 [3.52 , 4.17]	4.65 ± 0.52 [3.91,5.44]
PLG/CS [%]	7.92 ± 0.48 [6.74 , 9.00]	7.57 ± 0.58 [6.11 , 8.54]	6.97 ± 0.16 [6.80 , 7.22]	7.96 ± 0.70 [6.88,9.08]
MGr/CS [%]	4.82 ± 0.83 [0.5 , 6.2]	3.90 ± 0.65 [2.4 ,5.4]	4.43 ± 1.11 [2.8 ,5.6]	4.39 ± 1.18 [2.4,6.6]

Cardiocondyla ulianini Emery 1889

Cardiocondyla elegans var. *ulianini* Emery 1889 [type investigation]

This taxon has been described from material of the Fedchenko Expedition to "Turkestan". The geographic position of the type locality is unknown and should be somewhere in Turkmenistan, Uzbekistan or Tajikistan. Investigated were lectotype and paralectotype worker from MCSN Genova, labelled "Turkestan Fedtschenko, mus. Moscou" and "Cardiocondyla elegans var. ulianini Em." and one worker from MHN Genève, designated by Forel as "Cotype" and labelled "Cardiocondyla elegans var. ulianini Em., Turkestan".

All material examined. Numeric phenotypical data were available in 23 samples with 44 workers. For details see supplementary information SI1, SI2. This material originated from Afghanistan (3 samples), Caucasus (3), China (1), Kazakhstan (8), Kyrghistan (3), allegedly Saudi Arabia (1) and the Ukraine (3).

Geographic range. Continuously distributed across the steppe and semidesert zone from the S Ukraine (32°E) eastwards to N Xinjang (88°E). The northern range border is demarcated by 46.5°N in the Ukraine and 46.7°N in E Kazakhstan and the southern border by 34°N in Afghanistan. The altitudinal range extends from 25 m below zero in the Caspian region to 1800 m in Afghanistan. A morphologically typical sample, centrally placed in the *C. ulianini* cluster by PCA considering the 16 standard characters, allegedly from Hofuf /Saudi Arabia (25.4°N, 49.6°E), appears extremely isolated. The most likely explanation is confusion of labels after side-by-side stereomicroscopic comparison of unmounted specimens belonging to different samples as it was a frequent investigation practice by Cedric Collingwood—the donor of several samples in the SMN Görlitz collection. This putting of specimens in wrong tubes repeatedly lead to dramatic zoogeographic confusion: a male of the exclusively Himalayan *Lasius crinitus* was "transferred" by Collingwood to Spain, a worker of the exclusively Australasian *Cardiocondyla paranuda* Seifert 2003 to the Sahara desert (see Seifert *et al.* 2017) or a worker of *Cardiocondyla bulgarica*, restricted to the Balkans and Asia Minor, to inner Tunisia (see p. 37).

Diagnosis: --Worker (Tab. 2, Figs. 22–25, key). Medium-sized, CS 522 µm. Head moderately elongated, CL/CW 1.149. Postocular distance rather low, PoOc/CL 0.411. Scape moderately long, SL/CS 0.810. Eye rather large, EYE/CS 0.251. Occipital margin suggestively concave. Frons rather broad (FRS/CS 0.257), frontal carinae slightly converging immediately caudal of FRS level (FL/FR 1.060). Dorsal profile of promesonotum and of propodeum convex with a well-developed metanotal depression (MGr/CS 3.44 %). Propodeal spines rather short, more triangular than spiny, SP/CS 0.120), their axis in profile deviating by about 45° from longitudinal axis of mesosoma, their bases approached (SPBA/CS 0.236). Petiole rather narrower and much higher than wide (PeW/CS 0.290, PeH/CS 0.336), its node in dorsal aspect slightly longer than wide; in profile with a moderately long peduncle that is about 1.25fold as long as high and with a moderately steep anterior slope of the node (about 60° relative to ventral profile). Postpetiole twice as wide as high (PpW/CS 0.564, PpH/CS 0.279), in dorsal view heard-shaped, with a concave anterior margin and convex sides; postpetiolar sternite with the anteromedian portion significantly more bulging than its anteroparamedian portion; in lateral view this anteromedian bulge forms a small, obtusely-angled, rounded corner and changes into the helcium with a distinct angle. Clypeus smooth and shiny, with only suggested of microrugulae. Vertex in overall impression shiny, completely without carinulae or microrugae, very weak and fine rugulae are restricted to frontal laminae and frontolateral head (genae). Vertex with numerous foveolae the diameter of which is smaller than the width of the brilliantly shining interspaces (dFOV 13.8), the interspaces with scattered very fine stickman-like fragments of a microreticulum; outer margin of foveolae shallow, not very clearly demarcated and internal foveolar surface often with longitudinal carinulae (Fig. 25). Dorsal promesonotum and propodeum glabrous. Promesonotum with scattered and shallow foveolae of 10–12 µm diameter. Lateral meso- and metapleurae rather shiny and delicately longitudinally striate-reticulate, contrasting the glabrous parts of mesonotum and pronotum. Dorsum of waist glabrous except for a very delicate microreticulum. First gaster tergite glabrous. Pubescence on whole body rather short and dilute, PLG/CS 5.89 %, sqPDG 4.89. Color of head, mesosoma, and gaster varying from pale yellowish brown to blackish brown.

Taxonomic comments and clustering results. *Cardiocondyla ulianini* is a characteristic species that differs from members of the four species of the *C. elegans* group as well as from *C. bulgarica, C. persiana*, and *C. sahlbergi* by the structure of vertex foveolae and several morphometric differences (Tabs. 1 and 2). For differences to *C. littoralis*, *C. caspiense* **n. sp.**, *C. gallilaeica* and *C. israelica* see these species.

Biology. Habitats observed in E Dagestan, Kyrghistan and Kazakhstan were in three cases sandy river terraces with very sparse dry steppe vegetation and once a flat, salty and periodically inundated loess soil at a lake margin. Nests had one or two simple entrance holes. Two excavated nests contained two and four fully sclerotized ergatoid males with shear-shaped mandibles. The presence of more than one adult male in these nests and the fact that only one of these six males showed an injury (an amputated tibia) indicates that males of *Cardiocondyla ulianini* tend to coexist and avoid fighting at least in adult stage. Alate gynes were observed in SE Kazakhstan 7 August 2001. Marikovsky & Yakushkin (1974) described the biology of supposedly *Cardiocondyla ulianini* from SE Kazakhstan. However, a possible confusion with sympatric *C. littoralis* or *C. caspiense* **n. sp.** makes the interpretation of their findings difficult.

Cardiocondyla littoralis Seifert 2003

Cardiocondyla littoralis Seifert 2003 [types investigated]
This species has been described from SE Kazakhstan. Investigated were the holotype worker and 11 worker paratypes, all labelled "KAZ: 46.41.57 N, 80.35.00 E, 358 m, W-Ufer des Sassy Kol, Lössboden, versalzt, hart, selten überschwemmt leg. Seifert 2001.08.07-1", SMN Goerlitz.

All material examined. Numeric phenotypical data were taken in five workers of the type sample from Kazakhstan. For details see supplementary information SI1, SI2. .
Geographic range. Only known from the type locality (46.6992 °N, 80.5833 °E, 356 m).
Diagnosis: --Worker (Tab. 2, Figs. 26–29, key). Small, CS 486 µm. Head moderately elongated, CL/CW 1.167. Postocular distance much larger than in *C. ulianini* and *C. caspiense* **n. sp.** PoOc/CL 0.442. Scape shorter, SL/CS 0.792. Eye rather large, EYE/CS 0.249. Occiput in dorsal aspect with evenly rounded corners, its median third straight or weakly concave. Frons moderately broad (FRS/CS 0.241), frontal carinae slightly converging immediately caudal of FRS level (FL/FR 1.044). Dorsal profile of promesonotum and of propodeum convex with a well-developed metanotal depression (MGr/CS 3.70 %). Propodeal spines very short (SP/CS 0.087, more triangular but with sharp tips), their axis in profile deviating by about 48° from longitudinal axis of mesosoma, their bases much approached (SPBA/CS 0.223). Petiole narrow and lower than in *C. ulianini* but still higher than wide (PeW/CS 0.274, PeH/CS 0.306), its node in dorsal aspect as long as wide, tapering frontad; in lateral aspect its frontodorsal profile not concave, more directed caudad (about 50° relative to ventral profile). Postpetiole much narrower than in *C. ulianini*, less than twice as wide as high (PpW/CS 0.500, PpH/CS 0.277), in dorsal view heard-shaped, with a concave anterior margin and convex sides; postpetiolar sternite with a shallow anteromedian bulge. Clypeus between the level of the paramedian 1st order setae, smooth, its anteromedian margin straight or weakly concave. Frontal laminae and a small area posterior of them finely and densely longitudinally rugulose. Anteromedian vertex glabrous and whole vertex without longitudinal microsculpture, in overall impression similar to situation in *C. ulianini*, foveolar interspaces glabrous and on the average as wide as foveolar diameter (dFOV 13–16), the interspaces with scattered very fine stickman-like fragments of a microreticulum, internal foveolar surface often with longitudinal carinulae (Fig. 29). Dorsal mesosoma in overall impression shiny; dorsal promesonotum with shallow foveolae of 9–16 µm diameter, interspaces clearly wider than foveolar diameter; dorsal propodeum shiny but very finely microrugulose-reticulate. Caudolateral pronotum, ventrolateral mesonotum, mesopleuron, and propodeum below spiracular level finely reticulate. Lateral metapleuron with 2–4 curved longitudinal carinae. Waist segments almost smooth and shining. First gaster tergite glabrous. Pubescence on whole body rather long but dilute, PLG/CS 6.90 %, sqPDG 4.63. Color of head, mesosoma, femora, and gaster dark brown; waist segments sometimes slightly lighter with yellowish tinge.
Taxonomic comments and clustering results. The taxonomic separation of *Cardiocondyla littoralis* from those of sympatric *C. ulianini* and *C. caspiense* **n. sp.** is supported by a PCA considering the characters PoOc/CL, Pew/CS, PpH/CS and PLG/CS (Fig. 136). The type specimens clearly differed from syntopic *ulianini* by the much larger PoOc/CL, larger PeW/PpW, a lower petiole with a less steep anterior slope, and by shorter spines. *C. littoralis* shows some similarity to the W Palaearctic *gallilaeica* from which it differs by the much larger PoOc/CL and PeW/PpW, the more excavated dorsofrontal postpetiolar margin, the almost straight median third of occipital margin, and the wider frons with more curved frontal carinae.
Biology. The workers were collected when foraging on the surface of a salty loess soil with very sparse vegetation near the margin of a lake in a semidesert.

Cardiocondyla caspiense n. sp.

Etymology: name given because the of type locality situated near the shore of the Caspian Sea.
Type material:
Holotype plus 1 paratype worker on the same pin labelled "IRAN: 36.833° N, 53.450° E, Miankaleh, shrubs and grass, Paknia 2004.07.23 -561" and "Holotype (upper) paratype of *Cardiocondyla caspiense*", depository, SMN Görlitz.

All material examined. Only the type sample from Iran was available. For details see supplementary information SI1, SI2. .

Geographic range. Only known from the type locality (36.833 °N, 53.450 °E, minus 29 m).

Diagnosis: --Worker (Tab. 2, Figs. 30–33, key). Small, CS 485 µm. Head moderately elongated, CL/CW 1.144. Postocular distance much smaller than in *C. littoralis*, PoOc/CL 0.418. Scape longer, SL/CS 0.818. Eye rather large, EYE/CS 0.253. Hind margin of vertex in dorsal view suggestively concave. Frons moderately broad (FRS/CS 0.248), frontal carinae slightly converging immediately caudal of FRS level (FL/FR 1.041). Dorsal profile of promesonotum and of propodeum convex with a well-developed metanotal depression (MGr/CS 3.88 %). Propodeal spines more diverging and slightly longer than in *C. littoralis* (SP/CS 0.110), triangular but with sharp tips), their axis in profile deviating by about 45° from longitudinal axis of mesosoma, their bases much approached (SPBA/CS 0.220). Petiole extremely narrow and much higher than wide (PeW/CS 0.252, PeH/CS 0.312), its node in dorsal aspect as long as wide, tapering frontad; in lateral aspect its frontodorsal profile steeper than in *C. littoralis* (about 58° relative to ventral profile). Postpetiole as wide but much lower than in *C. littoralis*, about twice as wide as high (PpW/CS 0.502, PpH/CS 0.248), in dorsal view heard-shaped, with a concave anterior margin and convex sides; postpetiolar sternite with a shallow anteromedian bulge. Clypeus between the level of the paramedian 1st order setae, smooth, its anteromedian margin straight or weakly concave. Frontal laminae and a small area posterior of them finely and densely longitudinally rugulose. Anteromedian vertex glabrous and whole vertex without longitudinal microsculpture, in overall impression similar to situation in *C. ulianini*, foveolar interspaces glabrous and on the average as wide as foveolar diameter (dFOV 16.2 µm), the interspaces with scattered very fine stickman-like fragments of a microreticulum, internal foveolar surface often with longitudinal carinulae (Fig. 33). Dorsal mesosoma in overall impression shiny; dorsal promesonotum shiny, slightly microrugulose and with few shallow foveolae; dorsal propodeum shiny but very finely microrugulose-reticulate. Ventrolateral mesonotum, mesopleuron, and propodeum below spiracular level finely reticulate. Lateral metapleuron with 2–4 curved longitudinal carinae. Waist segments almost smooth and shining. First gaster tergite glabrous. Pubescence on whole body moderately long and dilute, PLG/CS 6.47 %, sqPDG 4.80. Color of head, mesosoma, femora, and gaster medium brown with yellowish-reddish color component.

Taxonomic comments and clustering results. *Cardiocondyla caspiense* **n. sp.** is most similar to *C. littoralis* but the strong differences in petiole width and postpetiolar height appear to be outside the usual range of intraspecific variability. The separation from *C. littoralis* and *C. ulianini* is supported by a PCA considering the characters PoOc/CL, Pew/CS, PpH/CS and PLG/CS (Fig. 136).

Biology. Unknown.

Cardiocondyla gallilaeica Seifert 2003

Cardiocondyla gallilaeica Seifert 2003 [type investigated]

This species has been described on a single worker from Israel. Investigated was the holotype worker labelled "ISRAEL Sedé Eliyyahu 6.ix.1983 Argaman", SMN Görlitz.

All material examined. Numeric phenotypical data were taken in the holotype worker. For details see supplementary information SI1, SI2.

Geographic range. Only known from the type locality (32.440 °N, 35.510 °E, minus 191 m).

Diagnosis: --Worker (Tab. 2, Figs. 34–37, key). Small, CS 480 µm. Head rather short, CL/CW 1.131. Postocular distance very small, PoOc/CL 0.403. Scape moderately long, SL/CS 0.807. Eye rather large, EYE/CS 0.254. Hind margin of vertex in dorsal view notably excavated. Frons narrower than in any species of the *C. ulianini* group (FRS/CS 0.225), frontal carinae slightly converging immediately caudal of FRS level (FL/FR 1.041). Frontal carinae immediately caudal of the FRS level almost parallel, FL/FR 1.000. Dorsal profile of promesonotum and of propodeum convex with a well-developed metanotal depression (MGr/CS 3.75 %). Pronotal corners more pronounced than in *ulianini*. Propodeal spines short but sharp (SP/CS 0.071), their axis in profile deviating by about 53° from longitudinal axis of mesosoma, their bases much approached (SPBA/CS 0.230). Petiole very narrow and distinctly higher than wide (PeW/CS 0.275, PeH/CS 0.308), its node in dorsal aspect as long as wide; in lateral aspect its frontodorsal profile slightly concave and moderately steep (about 52° relative to ventral profile). Postpetiole rather wide and high,

only slightly lower than petiole (PpW/CS 0.552, PpH/CS 0.298), in dorsal view with a slightly concave anterior margin; postpetiolar sternite with a shallow anteromedian bulge. Clypeus between the level of the paramedian 1st order setae glabrous, its anteromedian margin straight or weakly concave. Frontal laminae almost smooth and shining, with only weak fragments of microcarinulae. Vertex completely without carinulae or microrugae, in overall impression shiny and with smaller, less clearly demarcated foveolae the diameter of which is clearly smaller than the width of the brilliantly shining interspaces (dFOV 14.0); weak rugulae are restricted to genae. Dorsal mesosoma in overall impression smooth and shiny; dorsal promesonotum with scattered and shallow foveolae of 10–12 µm diameter; dorsal propodeum with fragments of very fine microrugae. Caudolateral pronotum, lateral mesonotum, mesopleuron, metapleuron, and propodeum below spiracular level rather shiny but microreticulate. Waist segments almost smooth and shining. First gaster tergite glabrous. Pubescence on whole body moderately long and dilute, PLG/CS 6.24 %, sqPDG 4.66. Color of head, mesosoma, and gaster pale yellowish brown to dark brown.
Taxonomic comments and clustering results. *Cardiocondyla gallilaeica* is unmistakable as a combination of very small frontal carinae distance, small postocular index, more concave hind margin of head, and very short but acute spines.
Biology. Unknown.

Cardiocondyla israelica Seifert 2003

Cardiocondyla israelica Seifert 2003 [type investigated]
This species has been described from Israel. Investigated was the holotype and one paratype worker, labelled "Tor (Sinai), 25.2.35, W.Wittmer"; MCZ Cambridge. Two paratype workers labelled "Neot Hakikar, Israel, 21. III. 1980, leg. Kugler" and "Ein Agrabim, Israel, 22. III 1980, leg. Kugler"; SMN Görlitz.

Note: The holotype and paratype workers from Tor (Sinai), leg. W.Wittmer 1935.02.25 were formerly labelled as syntypes of *Cardiocondyla elegans var. torretassoi* Finzi 1936. However, after lectotype fixation for *C. torretassoi* in the syntype series from Wadi Hoff, which definitely belongs to *C. nigra*, this sample was available to serve as types of *C. israelica*.

All material examined. Numeric phenotypical data were taken in 6 samples with 10 workers from Egypt (3 samples) and Israel (3). For details see supplementary information SI1, SI2.
Geographic range. So far only known from five localities in Egypt and Israel in a small area from 31°E to 36°E and 28° N to 31° N. The altitudinal range extends between 346 m below sea level and 378 m above sea level.
Diagnosis: --Worker (Tab. 2, Figs. 38–41, key, images under CASENT0913594 and ANTWEB 1040303 in www.antweb.org). Medium-sized, CS 516 µm. Head moderately elongated, CL/CW 1.145. Postocular distance rather low, PoOc/CL 0.422. Scape moderately long, SL/CS 0.816. Eye rather large, EYE/CS 0.247. Occipital margin suggestively concave. Frons very broad (FRS/CS 0.268), frontal carinae slightly converging immediately caudal of FRS level (FL/FR 1.046). Dorsal profile of promesonotum and of propodeum convex with a well-developed metanotal depression (MGr/CS 3.58 %). Spines moderately long (SP/CS 0.132), rather thin and more erected than in other species, spine axis in lateral view deviating 58° from longitudinal mesosomal axis; spine bases much approached, SPBA/CS 0.224. Petiole narrow, distinctly higher than wide (PeW/CS 0.285, PeH/CS 0.327), its node as wide as long, in profile with a moderately long peduncle that is about 1.35fold as long as high and with a moderately steep anterior slope of the node (about 58° relative to ventral profile), anteroventral petiolar dent reduced. Postpetiole relatively wide and high (PpW/CS 0.564, PpH/CS 0.303), in dorsal view heard-shaped, with a concave anterior margin and convex sides; postpetiolar sternite with weak anteromedian bulge. Median clypeus smooth and shiny, its lateral portions weakly longitudinally carinulate. Frontal laminae and anteromedian vertex longitudinally carinulate-rugulose. Vertex foveolae rather large (dFOV 17.0 µm), relatively deep and well-demarcated, bicoronate (Fig. 41), densely-packed, interspaces much smaller than foveolar diameter. Dorsal promesonotum varying from almost smooth to longitudinally carinulate-rugulose, scattered foveolae are present. Lateral mesosoma and propodeum with well-developed microreticulum, metapleuron longitudinally carinulate-rugulose. Waist segments smooth and shiny but with a delicate microreticulum. First gaster tergite glabrous. Pubescence on gaster tergites long and relatively dense, PLG/CS 7.11 %, sqPDG 4.00. Rather concolorous medium brown with yellowish tinge.
Taxonomic comments and clustering results. *Cardiocondyla israelica* can be separated from *C. ulianini*, *C.*

gallilaeica, *C. caspiense* **n. sp.** and *C. littoralis* by its deeper, well-demarcated and densely-packed vertex foveolae and the stronger longitudinal sculpture on head and is placed apart from these species by exploratory data analyses of NUMOBAT characters.
Biology. Three samples from Egypt, provided by M.R. Sharaf, were collected from "a wild area with *Tamarix* bushes and *Phragmites* within a cultivated, insecticide polluted surrounding."

Cardiocondyla bulgarica **Forel 1892**

Cardiocondyla elegans var. *bulgarica* Forel 1892 [types investigated]
This species has been described from Bulgaria. Investigated were 4 worker syntypes, labelled "C.elegans var. bulgarica Forel, 16 VIII, Anchialo (Bulgarien)", MHN Genève; one worker syntype, labelled "Anchialo", NHM Wien; five worker syntypes, labelled "Sozopolis 15 VIII, type bulgarica ", NHM Basel.

Cardiocondyla elegans var. *eleonorae* Forel 1911 [types investigated]
This taxon has been described from Smyrna (Izmir) in Turkey. Investigated were four worker syntypes, labelled "C.e. var. eleonorae Forel, type, Plage de Cocarimali pr. Smyrne", MHN Genève.

All material examined. Numeric phenotypical data were taken in 40 samples with 102 workers from Bulgaria (8 samples), Greece (3), North Makedonia (1), Turkey (27) and unknown locality (1). For details see supplementary information SI1, SI2. One fully typical worker specimen of *Cardiocondyla bulgarica* was placed by Cedric Collingwood together with 2 workers of *C. nigra* into a tube labelled "30 km S of Medenine / Tunisia". Whereas the occurrence of *C. nigra* at this locality is certainly a matter of fact, it appears impossible that a Balkan-Turkish ant, not showing any tramp species properties, might occur in small village in the Sahara Desert. The most probable reason for this disturbing observation is that Collingwood transferred the *C. bulgarica* worker after side-by-side stereomicroscopic comparison with unmounted specimens from other localities into a wrong tube.
Geographic range. *C. bulgarica* is so far only known from a comparably small area in the S Balkans and Asia Minor but it is the most abundant *Cardiocondyla* species in this region. The findings range from the 21.7°E to 41.1°E, 36.2°N to 42.6°N and from sea level up to 1800 m.
Diagnosis: --Worker (Tab. 2, Figs. 42–45, key; images CASENT0179879, CASENT0904462, CASENT0908338, and CASENT0908339 in www.antweb.org). Medium-sized, CS 512 µm. Head much elongated, CL/CW 1.201. Postocular distance very large, PoOc/CL 0.451. Scape moderately long, SL/CS 0.809. Eye medium-sized, EYE/CS 0.240. Median third of hind margin of head straight or slightly concave. Frons broad (FRS/CS 0.260), frontal carinae immediately caudal of FRS level usually parallel, sometimes slightly diverging, rarely converging (FL/FR 1.007). Dorsal profile of promesonotum and of propodeum convex with a well-developed metanotal depression (MGr/CS 3.32 %). Spines rather short (SP/CS 0.112), usually triangular in lateral view with the spine axis deviating 42° from longitudinal mesosomal axis; spine bases widely distant, SPBA/CS 0.279. Petiole very wide and as high as wide (PeW/CS 0.338, PeH/CS 0.337), its node wider than long, in profile with a moderately long peduncle that is about 1.6fold as long as high and with a rather steep anterior slope of the node (about 63° relative to ventral profile). Postpetiole relatively wide and high (PpW/CS 0.557, PpH/CS 0.311) but only 1.65fold as wide as petiole and not heart-shaped in dorsal view; postpetiolar sternite with weak anteromedian bulge. Clypeus rather smooth, weak lateral carinulae and suggestions of foveolae may be present. Frontal laminae, area posterior of frontal lobes and genae finely longitudinally carinulate-rugulose. Vertex with shallow but well-demarcated foveolae of 17.0 µm mean diameter; interspaces about as wide as foveolae, glabrous and with fragments of very fine stickman-like structures (Fig. 45). Mesosoma in overall impression more or less glabrous, only with very delicate reticular structures; promesonotum with scattered, shallow foveolae; meso- and metapleurae with suggestions of longitudinal carinulae. Waist segments smooth and shiny. First gaster tergite glabrous. Pubescence on gaster tergites short and dilute, PLG/CS 5.66 %, sqPDG 5.02. Head usually medium brown with a warm yellowish tinge, sometimes dark brown. Mesosoma and petiole varying between yellow and medium brown, but warm yellowish tinge even in darkest specimens always visible. Postpetiole yellowish brown to dark brown. Gaster dark brown. Pigmentation contrast between dorsal head and mesosoma usually clearly expressed, PigCap/PigMes 1.38 ±0.24 [1.0,2.0].
Taxonomic comments and clustering results. On the nest sample level and without selection among all 17

available NUMOBAT characters, 40 samples of *Cardiocondyla bulgarica* are separable from 48 samples of the similar species *C. sahlbergi* and *C. persiana* by five exploratory data analyses with a mean error of 0.45% (Fig. 137). All type specimens of *C. bulgarica* and *C. eleonorae* were allocated by a LDA to the *C. bulgarica* cluster with $p > 0.999$.
Biology. *Cardiocondyla bulgarica* seems to use a wider habitat spectrum than other species. It was found in xerothermous grasslands, a sandy salt marsh, a forest-covered stream course and in a woodland-steppe with *Pinus*.

Cardiocondyla sahlbergi Forel 1913

Cardiocondyla elegans var. *sahlbergi* Forel 1913 [type investigation]
This taxon has been described from eastern Caucasus. Investigated was the lectotype gyne labelled *"C.elegans var. sahlbergi Forel,* $ *type, Caucase (Ruszky)*" and on a second label "*Aralokaspigebiet*", MHN Genève. If both labels are true, the terra typica should be the eastern Caucasus (present Dagestan or Azerbaijan). Three worker paratypes, placed in the box with the lectotype gyne of *C. sahlbergi* and with similar labelling by Forel ("C.elegans var. sahlbergi Forel, type, Caucase (Ruszky) / Aralokaspigebiet") do not belong to *C. sahlbergi* and are instead typical *C. ulianini* in both structure and morphometry.

All material examined. Numeric phenotypical data were available in 39 samples (largely nest samples) with 77 workers. For details see supplementary information SI1, SI2. This material originated from Afghanistan (1 sample), Azerbaijan (1), Georgia (9), Iran (10), Israel (1), Kazakhstan (1), Kyrgystan (1), Russia (3), "Turkestan" (2), and Turkey (8).
Geographic range. Touches Europe by the westernmost site at Altunkent (41.01°N, 28.67°E). Distributed eastwards over Asia Minor, the Great Caucasus, the Caspian region, the Iran, and Afghanistan to Kyrgistan (42.9°N, 74.6°E). The southernmost sites are in the Iran (29.59°N, 51.99°E) and in Israel (32.95°N, 35.63°E). The altitudinal range varies from minus 29 m in the Caspian region to 2000 m at the southernmost site in the Iran.
Diagnosis: --Worker (Tab. 2, Figs. 46–49, key; pictures CASENT0908341 (paralectotype *sahlbergi*), CASENT0917364 (wrong neotype des. Radchenko of *Cardiocondyla bogdanovi*, see p. 48 *C. stambuloffii*) in www.antweb.org). Medium-sized, CS 522 µm. Head moderately elongated, CL/CW 1.176. Postocular distance large, PoOc/CL 0.439. Scape moderately elongated, SL/CS 0.798. Eye rather small, EYE/CS 0.231, with notable microsetae. Occipital margin weakly concave. Frons rather broad (FRS/CS 0.256), frontal carinae slightly converging immediately caudal of FRS level (FL/FR 1.058). Dorsal profile of promesonotum and of propodeum convex with a rather deep metanotal depression (MGr/CS 3.83 %). Spines rather short and acute (SP/CS 0.125), their axis in profile deviating by about 35° from longitudinal axis of mesosoma, their bases rather distant (SPBA/CS 0.279). Petiole rather wide and slightly higher than wide (PeW/CS 0.331, PeH/CS 0.351); in profile with a rather long peduncle and moderately steep anterior and posterior slopes of the node (about 65° and 62° relative to ventral profile—i.e. rather symmetric). Postpetiole wide and moderately high (PpW/CS 0.565, PpH/CS 0.305), in dorsal view suggestively heard-shaped, with a concave anterior margin and convex sides. Head in overall impression shiny. Whole vertex with shallow, feebly bicoronate foveolae of 16–18 µm diameter, foveolar distance on central vertex larger than foveolar diameter, near to eyes about equal to foveolar diameter, the interspaces very shiny and with very delicate stickman-like microstructures (Fig. 49). Mesosoma shiny, microreticulum and microrugulae very weakly developed, a few foveolae are present on dorsal promesonotum. Waist segments very shiny with barely visible microreticulum. Pubescence on whole body rather short and dilute, PLG/CS 6.4 %, sqPDG 4.64. Color of head, mesosoma, waist and gaster usually homogenously dark brown; mandibles, scape, tibiae and tarsae pale yellowish brown.
Taxonomic comments and clustering results. In his original description of *C. sahlbergi*, Forel explicitly referred only to a gyne from "Palestine (Sahlberg)" and a gyne from "Caucase (Ruzsky)". The first specimen could not be discovered during a search in the collections of Forel in Lausanne, Genève, and Basel but the latter gyne is present in the MHN Genève collection under the labelling "C.elegans Em. v. sahlbergi type For. , Caucase (Ruszky)", "Aralokaspigebiet N2", "Typus" [printed red label] and "ANTWEB CASENT 098340". This specimen was fixed by Seifert (2003) as lectotype. A worker specimen with the same labelling but "ANTWEB CASENT 098341" was not directly investigated but is in any character shown by the images in www.antweb.org consistent with the worker

concept of *C. sahlbergi* presented here. The gynes of *C. sahlbergi*, *C. persiana* and *C. bulgarica* are separated by a PCA of the characters CS, CL/CW, PoOc/CL, SL/CS, PeW/CS, PpW/CS, SP/CS, sqPDG, PLG/CS, PeH/CS, PpH/CS, dFOV, ML/CS with the type specimens being allocated to their corresponding clusters (Fig. 138). This is in agreement with the clustering of workers.

The workers of *C. sahlbergi* are similar to those of *C. persiana* but differ from the latter by shorter microsetae on clypeus (compare Figs. 46 and 50), shorter pubescence on all body parts, smaller, less densely packed vertex foveolae (compare Figs. 49 and 53), wider waist segments, the petiole node in lateral view being more symmetric (compare Figs. 47 and 51) and a frequently darker mesosoma. A character-reduced LDA using the characters CS, SL/CS, PeW/CS, sqPDG, dFOV, PigCon, EYE/CS classifies 99.0 % of 103 worker individuals of both species correctly and provides a strong separation on the nest sample level (Fig. 139).

Biology. Unknown.

Cardiocondyla persiana Seifert 2003

Cardiocondyla persiana Seifert 2003 [type investigation]

This taxon has been described from Iran. Investigated was the holotype worker labelled "IRAN, Fars 1997 (1), Shiraz, ca. 1570 m; 13.-22.9.; leg. Schödl", NHM Wien; 1 worker paratype with same labelling, SMN Görlitz. 6 worker paratypes labelled "IRAN, Fars 1997 (29), 80 km NW Shiraz, Chesmeh Bozghan, 2000 m; 22.9.; leg. Schödl", SMN Görlitz; 7 worker paratypes with same label NHM Wien. 3 worker paratypes labelled "IRAN, Fars 1997 (17), Barnoo NP, 7 km NE Shiraz, Chesmeh Mehrab, 1800 m; 18.9.; leg. Schödl", SMN Görlitz.

All material examined. Numeric phenotypical data were available in 10 samples (largely nest samples) with 26 workers. For details see supplementary information SI1, SI2. This material originated from Georgia (2 samples) and Iran (8).

Geographic range. From W Georgia (41.8°E) east to Central Iran (54.0°E). The most southern and northern sites are in Iran at. 29.2°N and in Georgia at 41.8°N. The altitudinal range varies from 5 m in W Georgia to 2000 m in Central Iran.

Diagnosis: --Worker (Tab. 2, Figs. 50–53, key; images under ANTWEB1041250 and CASENT0919736 in www.antweb.org). Medium-sized, CS 536 µm. Head moderately elongated, CL/CW 1.165. Postocular distance large, PoOc/CL 0.441. Scape moderately elongated, SL/CS 0.794. Eye rather small, EYE/CS 0.233, with notable microsetae. Median third of hind margin of head suggestively concave. Frons rather broad (FRS/CS 0.254), frontal carinae slightly converging immediately caudal of FRS level (FL/FR 1.056). Dorsal profile of promesonotum and of propodeum convex with a deep metanotal depression (MGr/CS 4.30 %). Spines rather short and acute (SP/CS 0.125), their axis in profile deviating by about 48° from longitudinal axis of mesosoma, their bases rather distant (SPBA/CS 0.270). Petiole narrower than in *C. sahlbergi* and distinctly higher than wide (PeW/CS 0.316, PeH/CS 0.347), the node is slightly wider than long; petiole in profile with a moderately long peduncle and moderately steep anterior and very steep posterior slope of the node (about 63° and 88° relative to ventral profile—i.e. more asymmetric than in *C. sahlbergi*). Postpetiole wide, but narrower than in *C. sahlbergi* and moderately high (PpW/CS 0.543, PpH/CS 0.297), in dorsal view suggestively heard-shaped, with a concave anterior margin and convex sides; postpetiolar sternite with weak anteromedian bulge. Head in overall impression less shiny than in *C. sahlbergi*. Whole vertex with densely-packed, large (dFOV 19.4 µm) and well-demarcated foveolae showing an inner corona; the interspaces much smaller than foveolar diameter (Fig. 53). Median and paramedian clypeus and a small stripe on median vertex smooth; lateral clypeus and frontal laminae usually shining and finely longitudinally carinulate. Mesosoma due to more developed foveolae and carinulae less shiny than in *sahlbergi.* Waist segments very shiny with barely visible microreticulum. Pubescence on whole body distinctly longer than in *sahlbergi* and moderately dense, PLG/CS 6.77 %, sqPDG 4.36. Dorsal head often bicolored: anterior head back to the antennal socket level dirty yellowish, remaining vertex dark dirty brown. Mesosoma usually dirty yellowish brown to dirty brown. Waist, gaster, and hind- and midfemora often blackish brown. This color pattern is typical but not consistent throughout the population.

Taxonomic comments and clustering results. The separation from *C. sahlbergi* and *C. bulgarica* has been presented in sections treating these species (p. 37, p. 38).

Biology. Unknown.

TABLE 2. Measurements of workers of the *Cardiocondyla ulianini* group. Explanation of data arrangement as in Tab. 1

	galli-laeica (n=1)	***ulianini*** (n=44)	***caspiense*** (n=2)	***littoralis*** (n=5)	***israelica*** (n=10)	***persiana*** (n=26)	***sahlbergi*** (n=77)	***bulgarica*** (n=102)
CS	480	522 ± 22 [490,568]	485 ± 3 [482,487]	486 ± 14 [468,501]	516 ± 14 [483,528]	536 ± 20 [495,566]	522 ± 20 [468,564]	512 ± 18 [460,560]
CL/CW	1.131	1.149 ± 0.018 [1.098,1.181]	1.144 ± 0.015 [1.134,1.155]	1.167 ± 0.015 [1.152,1.190]	1.145 ± 0.020 [1.119,1.182]	1.165 ± 0.026 [1.123,1.216]	1.176 ± 0.019 [1.110,1.254]	1.201 ± 0.010 [1.150,1.272]
SL/CS	0.807	0.810 ± 0.017 [0.768,0.847]	0.818 ± 0.013 [0.809,0.828]	0.792 ± 0.008 [0.780,0.800]	0.816 ± 0.009 [0.804,0.828]	0.794 ± 0.017 [0.764,0.827]	0.798 ± 0.014 [0.764,0.829]	0.809 ± 0.015 [0.752,0.839]
PoOc/CL	0.403	0.411 ± 0.008 [0.397,0.432]	0.418 ± 0.006 [0.413,0.422]	0.442 ± 0.009 [0.431,0.454]	0.422 ± 0.008 [0.410,0.431]	0.441 ± 0.008 [0.429,0.458]	0.439 ± 0.008 [0.414,0.453]	0.451 ± 0.009 [0.424,0.469]
EYE	0.254	0.251 ± 0.004 [0.242,0.262]	0.253 ± 0.000 [0.253,0.253]	0.249 ± 0.004 [0.244,0.253]	0.247 ± 0.003 [0.244,0.255]	0.233 ± 0.007 [0.224,0.246]	0.231 ± 0.006 [0.215,0.244]	0.240 ± 0.007 [0.222,0.255]
dFOV	14.0	13.8 ± 1.0 [12.0,16.0]	16.2 ± 0.8 [15.7,16.8]	15.0 ± 1.2 [13,16]	17.0 ± 0.98 [15.6,19.0]	19.4 ± 0.96 [17.8,21.0]	17.3 ± 0.79 [15.0,19.0]	17.0 ± 1.00 [14.0,19.0]
FRS/CS	0.225	0.257 ± 0.007 [0.243,0.272]	0.248 ± 0.002 [0.247,0.250]	0.241 ± 0.005 [0.234,0.248]	0.268 ± 0.009 [0.257,0.282]	0.254 ± 0.009 [0.235,0.268]	0.256 ± 0.009 [0.236,0.275] 69	0.260 ± 0.009 [0.237,0.282] 84
FL/FR	1.000	1.060 ± 0.027 [1.000,1.120] 29	1.041 ± 0.014 [1.031,1.051]	1.044 ± 0.022 [1.024,1.081]	1.046 ± 0.057 [1.038,1.051] 6	1.056 ± 0.031 [1.005,1.127]25	1.058 ± 0.029 [1.000,1.124] 53	1.007 ± 0.014 [1.000,1.069] 54
SPBA/CS	0.230	0.236 ± 0.010 [0.204,0.255]	0.220 ± 0.002 [0.219,0.222]	0.223 ± 0.012 [0.206,0.238]	0.224 ± 0.007 [0.217,0.238]	0.270 ± 0.015 [0.240,0.294	0.279± 0.015 [0.253,0.322]	0.279 ± 0.012 [0.249,0.315] 84
SP/CS	0.071	0.120 ± 0.012 [0.099,0.149]	0.110 ± 0.006 [0.105,0.114]	0.087 ± 0.019 [0.066,0.113]	0.132 ± 0.010 [0.119,0.149]	0.125 ± 0.015 [0.097,0.157]	0.125 ± 0.013 [0.085,0.155]	0.112 ± 0.012 [0.084,0.136]
PeW/CS	0.275	0.290 ± 0.018 [0.261,0.336]	0.252 ± 0.013 [0.243,0.262]	0.274 ± 0.009 [0.263,0.286]	0.285 ± 0.011 [0.270,0.303]	0.316 ± 0.025 [0.278,0.355]	0.331 ± 0.022 [0.292,0.401]	0.338 ± 0.022 [0.281,0.382]
PpW/CS	0.552	0.564 ± 0.025 [0.494,0.626]	0.502 ± 0.020 [0.488,0.516]	0.500 ± 0.011 [0.487,0.514]	0.564 ± 0.013 [0.548,0.585]	0.543 ± 0.033 [0.478,0.593]	0.565 ± 0.025 [0.509,0.654]	0.557 ± 0.023 [0.513,0.642]
PeH/CS	0.308	0.336 ± 0.012 [0.310,0.364]	0.312 ± 0.008 [0.306,0.317]	0.306 ± 0.004 [0.299,0.310]	0.327 ± 0.010 [0.311,0.345	0.347± 0.019 [0.316,0.382]	0.351± 0.014 [0.323,0.388]	0.337 ± 0.015 [0.292,0.370]
PpH/CS	0.298	0.279 ± 0.010 [0.255,0.299]	0.248 ± 0.002 [0.247,0.250]	0.277 ± 0.006 [0.271,0.286]	0.303 ± 0.009 [0.286,0.313]	0.297 ± 0.014 [0.278,0.323]	0.305 ± 0.012 [0.281,0.331]	0.311 ± 0.015 [0.276,0.357]
sqrtP-DG	4.66	4.89 ± 0.29 [4.29,5.67]	4.80 ± 0.16 [4.69,4.91]	4.63 ± 0.38 [4.20,5.07]	4.00 ± 0.11 [3.78,4.17]	4.36 ± 0.26 [3.64,4.90]	4.64 ± 0.27 [3.97,5.27]	5.02 ± 0.36 [4.28,6.12]
PLG/CS [%]	6.24	5.89 ± 0.37 [5.04,6.69]	6.47 ± 0.48 [6.13,6.81]	6.90 ± 0.18 [6.74,7.13]	7.11 ± 0.24 [6.82,7.53]	6.77 ± 0.39 [5.61,7.38]	6.37 ± 0.54 [5.18,8.06]	5.66 ± 0.36 [4.96,6.52]
MGr/CS [%]	3.75	3.44 ± 0.66 [2.4,5.4]	3.88 ± 0.51 [3.5,4.2]	3.70 ± 0.56 [3.3,4.7]	3.58 ± 0.99 [2.0,5.3]	4.30 ± 0.58 [3.2,5.6]	3.83 ± 0.83 [2.3,6.6]	3.32 ± 0.71 [1.5,5.3]
PigCap						9.33 ± 0.92 [8.0,11.0]	10.09 ± 1.17 [7.0,12.0]	9.12 ± 1.45 [6.0,12.0]
PigMes						8.07 ± 1.36 [6.0,11.0]	9.59 ± 1.29 [6.0,12.0]	6.87 ± 1.87 [4.0,12.0]
PigCon						1.17 ± 0.14 [0.90,1.50]	1.06 ± 0.07 [0.95,1.33]	1.38 ± 0.24 [1.00,2.00]

Cardiocondyla batesii Forel 1894

Cardiocondyla batesii Forel 1894 [type investigation]
This taxon has been described from Algeria. Investigated were 5 worker syntypes labelled "C. Batesii, € type, Perregaux Algerie 29 III", and 4 gyne syntypes labelled "C. Batesii, $ type, Perregaux Algerie 29 III", both in MHN Genève.

All material examined. Numeric phenotypical data were available in 18 samples (largely nest samples) with 37 workers. For details see supplementary information SI1, SI2. This material originated from Algeria (1 sample), Morocco (3) and Spain (14).
Geographic range. Based on determined vouchers distributed from N Morocco (6.8°W) east to NE Algeria (6.6°E) and from S Spain north to 41.8°N. In S Spain ascending to 930 m. Unverified records presented in antmaps.org include S Morocco, Tunisia and the Balearic Islands.
Diagnosis: --Worker (Tab. 3, Figs. 54–57, key; images under CASENT 0908335 in www.antweb.org). Medium-sized, CS 518 µm. Head moderately elongated, CL/CW 1.177. Postocular distance small, PoOc/CL 0.383. Scape moderately elongated, SL/CS 0.791. Eye large, EYE/CS 0.264. Median third of hind margin of head slightly concave. Frons moderately broad (FRS/CS 0.244), frontal notably converging immediately caudal of FRS level (FL/FR 1.077). Dorsal profile of promesonotum and of propodeum convex with a deep metanotal depression (MGr/CS 3.82 %). Spines rather short and blunt, more triangular (SP/CS 0.117), their axis in profile deviating by about 43° from longitudinal axis of mesosoma, their bases rather distant (SPBA/CS 0.257). Petiole distinctly higher than wide (PeW/CS 0.282, PeH/CS 0.330); with characteristic profile, showing a short peduncle, a rather straight to weakly convex anterior face and an ample node with the anterior slope less steep than the caudal slope (about 60° respectively 75° relative to ventral profile). Petiole in dorsal view with elongated node that gradually merges with the anterior peduncle. Postpetiole wide (PpW/CS 0.533, PpW /PeW 1.89, PpH/CS 0.286), in dorsal view suggestively heard-shaped, with a concave anterior margin and convex sides; postpetiolar sternite completely flat. Median and paramedian clypeus smooth; lateral clypeus with 1–2 longitudinal rugulae. Dorsal head almost without longitudinal sculpture; weak longitudinal carinulae are present on and posterior of the frontal laminae. Vertex with very shallow foveolae of 15–16 µm diameter; the margins of foveolae often breached by microrugulae running partially or entirely through the foveolae; the interspaces on average wider than foveolar diameter, shiny and with fragments of a very delicate microreticulum (Fig. 57). Dorsal mesosoma shiny, but finely microreticulate; meso- and metapleurae finely rugulose-reticulate. Waist segments very shiny, with barely visible microreticulum. Pubescence on gaster tergites moderately long and dense, PLG/CS 5.55 %, sqPDG 4.84. The typical color pattern is bicolored: dorsal head medium brown, mesosoma and waist light orange brown, gaster dark brown. This distinct color contrast may be lost in rarely occurring specimens with darker brown mesosoma.
Taxonomic comments and clustering results. The only species with sympatric occurrence related to *Cardiocondyla batesii* is *C. nigra. C. batesii* is strongly separable on the worker individual level by a PCA considering all the 14 morphometric characters shown in Tab. 3 as available for all 132 individuals (Fig. 112). All classifications, including the single *batesii* worker displaced by the PCA, are confirmed with p > 0.97 by a LOOCV-LDA reduced to the 10 characters CS, CL/CW, SL/CS, PoOc/CS, dFOV, PeW/CS, PeH/CS, PpH/CS, sqPDG, and PLG/CS in order to avoid character overfitting. The type series of *C. nigra*, *C. torretassoi* and *C. bicoronata* are allocated to the *nigra* cluster with p = 1.000 and the type series of *C. batesii* with p = 1.000 to the *batesii* cluster. A simpler way for a perfect separation, using six primary measurements given in mm, is offered by a linear discriminant

D(6) = 63.22*CL-63.18*PoOc+55.89*SL+64.64*PeW-184.93*PeH-93.82*PpH-11.19.
C. batesii D(6) -2.459 ± 0.892 [-4.11, -0.53] n=37
C. nigra D(6) 2.786 ± 1.038 [0.53, 5.20] n=95

Allopatric species with similarities to *C. batesii* are *C. semirubra* from Asia Minor and *C. kushanica* from Afghanistan. Non-overlapping morphometric data and structural differences provide arguments to treat these taxa as heterospecific in addition to the geographic argument (see the sections treating these species, p. 43, p. 45).
Biology. The biology of populations in southern Spain was investigated by Heinze *et al.* (2002) and Schrempf *et al.* (2005): Nests were found in cavities in the soil down to a depth of more than 1 m in very sunny and dry

places. Colony density was high, with up to one nest per square meter. Nest populations contained 10–120 workers, were strictly monogynous and could contain 1–3 ergatoid males. Winged males were not observed. Workers never tolerated the presence of more than one inseminated, fertile gyne. Gynes mated in the nest in autumn, with mean mating frequencies of 1.52 ± 0.65 [1–3], and dispersed on foot to found their own colonies in spring. Gynes were dimorphic in mesosoma size which was correlated with wing length (brachyptery vs. macroptery). Yet, flight musculature was not sufficiently developed in both brachy- and macropterous gynes to allow flying. This reduced dispersal capacity explained the high inbreeding coefficient and the close genetic relatedness between queens and their mates and it was suggested that 83% of all matings were between brothers and sisters. As expected from local mate competition theory, sex ratios were extremely female biased, with more than 85% of all sexuals produced being young gynes.

Cardiocondyla semirubra Seifert 2003

Cardiocondyla semirubra Seifert 2003 [type investigation]
This taxon has been described from Asia Minor. Investigated were the holotype worker and 2 paratype workers labelled "TURKEY: Sanliurfa 20 km S Steppe, 500 m, leg. A.Schulz 1993.06.12, No 1036" and 1 paratype worker labelled "TURKEY: Sanliurfa 25 km E, Camlidere, Steppe, 500 m, leg. A. Schulz 1993.06.13, No 1045", all in SMN Görlitz.

All material examined. Numeric phenotypical data were available for two samples with four workers. For details see supplementary information SI1, SI2. This material originated from Turkey (2 samples).
Geographic range. The two known samples from Asia Minor were collected at 36.94°N, 38.91°E, 400 m and 37.20°N, 39.00° E, 600 m. They are about 30 km apart.
Diagnosis: --Worker (Tab. 3, Figs. 58–61, key). Rather large, CS 552 µm. Head moderately elongated, CL/CW 1.168. Postocular distance very small, PoOc/CL 0.374. Scape rather short, SL/CS 0.782. Eye rather large, EYE/CS 0.256. Median third of hind margin of head slightly concave. Frons broad (FRS/CS 0.258), frontal notably converging immediately caudal of FRS level (FL/FR 1.069). Dorsal profile of promesonotum and of propodeum convex with a deep metanotal depression (MGr/CS 4.38 %). Spines short and blunt, more triangular (SP/CS 0.096), their axis in profile deviating by about 47° from longitudinal axis of mesosoma, their bases rather distant (SPBA/CS 0.254). Petiole very wide, nearly as wide as high (PeW/CS 0.322, PeH/CS 0.326); in profile with short peduncle, a rather straight to weakly convex anterior face and an ample node with the anterior slope less steep than the caudal slope (about 58° respectively 69° relative to ventral profile). Petiole node in dorsal view as wide as long and not gradually merging with the anterior peduncle. Postpetiole only 1.61-fold as wide as petiole and rather low (PpW/CS 0.518, PpH/CS 0.267), in dorsal view suggestively heard-shaped, with a concave anterior margin and convex sides; postpetiolar sternite completely flat. Lateral and paramedian clypeus, frontal laminae, and area posterior of frontal laminae finely longitudinally carinulate. Dorsal head almost without longitudinal sculpture , a small stripe on median vertex often glabrous. Vertex with shallow foveolae of 16–19 µm mean diameter, the margins of foveolae often breached by microrugulae running partially or entirely through the foveolae; the interspaces on average wider than foveolar diameter, shiny and with fragments of a very delicate microreticulum (Fig. 61). Mesosoma moderately shining, finely microreticulate. Median promesonotum finely longitudinally carinulate-rugulose. Lateral meso- and metapleuron finely longitudinally carinulate-rugulose. Waist segments very shiny, with barely visible microreticulum. Pubescence on gaster tergites moderately long and moderately dense, PLG/CS 5.39 %, sqPDG 5.37. Dorsal head, gaster, coxae, femora, and tibiae dark to blackish brown; mesosoma and petiole reddish brown; postpetiole, scape, and antennal club dark brown.
Taxonomic comments and clustering results. The extremely wide petiole is the outstanding character of *Cardiocondyla semirubra*. The only similar species with zoogeographic proximity is *C. nigra* which has a narrower frons and petiole and often a darker mesosomal pigmentation. A PCA considering FRS, PeW and PigMes separates the four workers of *semirubra* from the *nigra* cluster (Fig. 141).
Biology. Unknown.

Cardiocondyla opistopsis Seifert 2003

Cardiocondyla opistopsis Seifert 2003 [type investigation]
This taxon has been described from Kuwait. Investigated were the holotype worker and one paratype worker labelled "KUWAIT: Burgan, 1988 W.Büttiker" and 3 worker paratypes labelled "KUWAIT: 1985", all in SMN Görlitz.

All material examined. Numeric phenotypical data were available for two samples with four workers. For details see supplementary information SI1, SI2. This material originated from Kuwait (2 samples).
Geographic range. The species is only known from the type locality.
Diagnosis: --Worker (Tab. 3, Figs. 62–65, key). Rather large, CS 553 µm. Head moderately elongated, CL/CW 1.171. Postocular index lower than in any species considered here, PoOc/CL 0.316. Hind margin of vertex rather straight or weakly concave. Scape rather long, SL/CS 0.825. Eye very large, EYE/CS 0.280. Median third of hind margin of head slightly concave. Frons moderately broad (FRS/CS 0.241), frontal carinae strongly converging immediately caudal of FRS level (FL/FR 1.122); dorsal extension of scape joint capsule in dorsal aspect strongly surpassing the frontal carinae laterad. Dorsal profile of promesonotum and of propodeum convex with a rather shallow metanotal depression (MGr/CS 2.15 %). Spines very short and blunt, triangular (SP/CS 0.073), their assumed axis in profile deviating by about 50° from longitudinal axis of mesosoma, their bases more approached (SPBA/CS 0.234). Petiole very low, lower than wide (PeW/CS 0.283, PeH/CS 0.271); in profile with a more distinct peduncle and a semicircular node with the anterior slope appearing less steep than the caudal slope; node in dorsal aspect as wide as long and almost circular. Postpetiole narrower than in any related species and but not very low (PpW/CS 0.463, PpH/CS 0.259), in dorsal view not heard-shaped, with feebly concave anterior margin and convex sides; postpetiolar sternite completely flat. Clypeus rather smooth, with 4–5 weak longitudinal carinulae. Frontal laminae rather smooth, very delicately microreticulate-carinulate. Vertex with numerous bicoronate foveolae of 17–19 µm diameter, the margins of foveolae only rarely breached by microrugulae running partially or entirely through the foveolae, foveolar interspaces about as wide as foveolar diameter, glabrous, with scattered fragments of fine cross-branched structures or microcarinulae. A narrow median stripe on vertex perfectly smooth, paramedian vertex only in its anterior part weakly longitudinally microcarinulate. Despite of microsculpture all parts of mesosoma and waist appear in overall impression rather shiny. Dorsal promesonotum irregularly microreticulate-carinulate, with scattered suggestions of foveolae. Whole lateral mesosoma reticulate but moderately shiny. Region of the metapleural gland bulla with 2–4 short and weak longitudinal carinae. Propodeum and petiole microreticulate; Postpetiole more shiny, with very delicate microreticulum. Pubescence on gaster tergites moderately long and moderately dense, PLG/CS 5.13 %, sqPDG 5.34. Whole body dark to medium brown.
Taxonomic comments and clustering results. As a combination of extremely small postocular index, petiolar height and postpetiolar width *Cardiocondyla opistopsis* is unmistakable.
Biology. Unknown

Cardiocondyla rugulosa Seifert 2003

Cardiocondyla rugulosa Seifert 2003 [type investigation]
This taxon has been described from Yemen. Investigated was the holotype worker labelled "Yemen, Sana'a, 1991.05, leg. A.van Harten", SMN Görlitz.

All material examined. Only the holotype specimen was available for examination. For details see supplementary information SI1, SI2. This material originated from Yemen (1 sample).
Geographic range. So far only known from the type locality Sana'a (15.37°N, 44.19°E, 2265 m).
Diagnosis: --Worker (Tab. 3, Figs. 66–69, key). Rather large, CS 576 µm. Head moderately elongated, CL/CW 1.168. Postocular index low, PoOc/CL 0.344. Median third of hind margin of head notably concave. Scape rather short, SL/CS 0.789. Eye large, EYE/CS 0.267. Frons moderately broad (FRS/CS 0.249), frontal carinae slightly converging immediately caudal of FRS level (FL/FR 1.027). Mesosoma in lateral view characteristic: dorsal profile of promesonotum only weakly convex, metanotal depression shallow (MGr/CS 2.1 %) and dorsal profile of propodeum more strongly convex and more strongly sloping down to spine base than in related species. Spines

short (SP/CS 0.101), acute and weakly erected, their axis in profile deviating by about 33° from longitudinal axis of mesosoma, their bases more approached (SPBA/CS 0.240). Petiole distinctly higher than wide (PeW/CS 0.276, PeH/CS 0.329), in profile with a short peduncle, a rather straight to weakly convex anterior face and an ample node with the anterior slope less steep than the caudal slope, petiole in dorsal view with elongated node that gradually merges with the anterior peduncle. Postpetiole wide (PpW/CS 0.537, PpW /PeW 1.95, PpH/CS 0.286), in dorsal view suggestively heard-shaped, with a concave anterior margin and convex sides; postpetiolar sternite completely flat. Clypeus and frontal laminae finely longitudinally rugulose. Whole vertex densely and finely longitudinally rugulose, the numerous foveolae of 14–18 µm diameter are not eye-catching because of being embedded within the rugosity, foveolar interspaces on paramedian vertex about as wide as foveolar diameter and glabrous (Fig.69). Dorsal promesonotum with scattered foveolae and weakly microreticulate between superimposed longitudinal rugulae. Propodeum irregularly microreticulate. Lateral pronotum moderately shiny but on whole surface microreticulate. Lateral mesonotum and mesopleuron reticulate and longitudinally rugulose. Lateral metapleuron with 5–7 weak, longitudinal carinae. Petiole irregularly microreticulate. Postpetiole more shiny, with very delicate microreticulum. Pubescence on gaster tergites moderately long and moderately dense, PLG/CS 5.41 %, sqPDG 5.48. Head, gaster, femora, and tibiae dark brown to blackish brown. Mesosoma and postpetiole dark brown with reddish component. Petiole orange brown.

Taxonomic comments and clustering results. *C. rugulosa* is morphometrically similar to *nigra*. The most diagnostic character of *rugulosa* is the strong longitudinal rugulae or carinulae on whole surface of dorsal head. The much more dense and stronger sculpture produces a mat surface appearance on head, mesosoma and petiole. The mesosomal shape is also characteristic: a feebly convex dorsal profile of promesonotum is contrasted by the more strongly convex dorsal profile of propodeum which is more strongly sloping down to spine base than in related species.

Biology. Unknown

Cardiocondyla kushanica Pisarski 1967

Cardiocondyla kushanica Pisarski 1967 [type investigation]

This taxon has been described from Afghanistan. Investigated was the holotype worker (ZM Lund) and one paratype worker (SMN Görlitz), both labelled "Afghanistan: Darountah, A 231 (Djelalabad), 4 et 24.1.1958, leg. K.Lindberg".

All material examined. Only the type specimens were available for examination. For details see supplementary information SI1, SI2. This material originated from Afghanistan (1 sample).

Geographic range. So far only known from the type locality Darountah (34.477°N, 70.365°E, 592 m).

Diagnosis: --Worker (Tab. 3, Figs. 70–73, images under CASENT0917207 in www.antweb.org, key). Rather small, CS 508 µm. Head moderately elongated, CL/CW 1.162. Postocular index small, PoOc/CL 0.373. Median third of hind margin of head slightly concave. Scape rather long, SL/CS 0.828. Eye large, EYE/CS 0.270. Frons broad (FRS/CS 0.262), frontal carinae clearly converging immediately caudal of FRS level (FL/FR 1.099). Dorsal profile of promesonotum only very weakly convex, metanotal depression shallow (MGr/CS 2.56 %), dorsal profile of propodeum moderately convex. Spines rather short (SP/CS 0.100), steeper and more acute than in *semirubra* and *batesii,* their angle differing by 53° from longitudinal axis of mesosoma; their bases more approached (SPBA/CS 0.248). Petiole distinctly higher than wide (PeW/CS 0.269, PeH/CS 0.306), in profile with a short peduncle, a rather straight to weakly convex anterior face and an ample node with the anterior slope less steep than the caudal slope; petiole node in dorsal aspect much longer than wide and gradually merging with the anterior peduncle. Postpetiole wide, twice as wide as petiole and rather high (PpW/CS 0.532, PpW /PeW 1.98, PpH/CS 0.287), in dorsal view with a weakly concave anterior margin and convex sides; postpetiolar sternite completely flat. Clypeus on whole surface longitudinally carinulate, in anterior part 5–6 stronger carinulae, in posterior part 6–7 finer carinulae. Paramedian vertex with bicoronate foveolae of 16–17 µm diameter, the margins of foveolae not regularly circular but often kinked; the interspaces with perifoveolar rugae or with cross-branched carinulae that are significantly stronger than in *batesii* and *nigra* (Fig. 73)—consequently the overall surface impression is less shining. Mesosoma finely and irregular rugulose-reticulate; lateral meso- and metapleurae longitudinally rugulose. Petiole very finely irregular

rugulose-reticulate. Dorsum of postpetiole in overall impression smooth and shining but clearly microreticulate. Pubescence on gaster tergites longer than in any related species and moderately dense, PLG/CS 6.89 %, sqPDG 4.73. Head blackish brown; mesosoma and petiole reddish brown; postpetiole and gaster brown.
Taxonomic comments and clustering results. As a combination of very long tergite pubescence, high postpetiole and characteristic head sculpture with irregular foveolar margins *Cardiocondyla kushanica* should be unmistakable.
Biology. Unknown

Cardiocondyla tenuifrons Seifert 2003

Cardiocondyla tenuifrons Seifert 2003 [type investigation]
This taxon has been described from Jordan. Investigated was the holotype worker and two worker paratypes labelled "JORDANIA: Abdallah zw. Shobek und Wadi Musa, 1996.03.30, No 1, leg. Chr. Dietrich", SMN Görlitz.

All material examined. Only the type series with three workers was available for examination. For details see supplementary information SI1, SI2. This material originated from Jordan (1 sample).
Geographic range. So far only known from the type locality situated at (34.477°N, 70.365°E, 592 m).
Diagnosis: --Worker (Tab. 3, Figs. 74–77, images under CASENT0917207 in www.antweb.org, key). Rather small, CS 509 µm. Head rather long, CL/CW 1.205. Postocular index larger than in any member of the *batesii* group, PoOc/CL 0.413. Median third of hind margin of head straight. Scape moderately long, SL/CS 0.804. Eye large, EYE/CS 0.267. Frons narrow (FRS/CS 0.238), frontal carinae strongly converging immediately caudal of FRS level (FL/FR 1.149). Dorsal profile of promesonotum moderately convex, metanotal depression shallow (MGr/CS 2.00 %), dorsal profile of propodeum moderately convex. Propodeal spines short (SP/CS 0.093), acute, and very steep, their angle differing by 50° from longitudinal axis of mesosoma; their bases more approached (SPBA/CS 0.237). Petiole distinctly higher than wide (PeW/CS 0.272, PeH/CS 0.325), in profile with a short but rather thin peduncle, a straight to weakly convex anterior face and the anterior and posterior slopes of the node equally inclined—as result the node profile is symmetric. Petiole node wedge-shaped in dorsocaudal view. Postpetiole moderately wide and rather high (PpW/CS 0.516, PpW /PeW 1.90, PpH/CS 0.288), in dorsal view with a straight anterior margin and roughly trapezoidal—when tilted caudad as in Fig. 76, anterior margin concave; postpetiolar sternite completely flat. Clypeus on whole surface rather smooth and shiny but very finely longitudinally carinulate. Frontal lobes and area posterior of the frontal lobes longitudinally rugulose-carinulate. Foveolae on vertex shallow, of 13–15 µm diameter, with an inner corona, foveolar margins not ideally circular, often kinked or breached by short microrugulae running partially or entirely through the foveolae; foveolar interspaces wider than foveolar diameter, shiny and with fine cross-branched to semireticulate microstructures (Fig. 77). Dorsal mesosoma shiny, with shallow foveolae and fine cross-branched microstructures. Ventrolateral mesosoma with well-developed microreticulum, metapleuron with few longitudinal carinulae. Petiole and postpetiole smooth and shiny but delicately microreticulate. Pubescence on gaster tergites short and dilute, PLG/CS 5.37 %, sqPDG 5.57. Head and gaster dark brown. Mesosoma and waist medium brown, with yellowish-red component.
Taxonomic comments and clustering results. As a combination of very high FL/FR and very high PoOc/CL, *Cardiocondyla tenuifrons* can be separated from any closely related species.
Biology. Unknown

Cardiocondyla nigra Forel 1905

Cardiocondyla batesii var. *nigra* Forel 1905 [type investigation]
This taxon has been described from Tunisia. Investigated were 5 worker syntypes labelled "C. Batesii For. var. nigra, Kairouan (Santschi) 159", MHN Genève.

Cardiocondyla elegans var. *torretassoi* Finzi 1936; type investigation]
This taxon has been described from Egypt. Investigated were the worker lectotype and 3 worker paralectotypes, labelled "Wadi Hoff.Eg., 8.3.33, C.Koch " and "MCZ Cotype 28812", MCZ Cambridge.

Cardiocondyla bicoronata Seifert 2003, n.syn. [type investigation]
This taxon has been described from Jordan. Investigated were the holotype worker and two paratype workers labelled "JORDANIA:1996.03.21, Shaumari Wildlife Reserve, 31.47N 36.42E, leg. Dietrich No 5" and three paratype workers labelled " JORDANIA:1996.03.21, Shaumari Wildlife Reserve, 31.47N 36.42E, leg. Dietrich No 6"; SMN Görlitz.

All material examined. Forty-five samples with 95 workers were morphometrically investigated. For details see supplementary information SI1, SI2. This material originated from Algeria (1 sample), Cape Verde (1), Cyprus (8), Egypt (2), Iran (4), Israel (7), Jordan (7), Morocco (1), Portugal (1), "Turkestan" (1), Tunisia (10), Turkey (1) and Yemen (1).
Geographic range. Probably continuously distributed from Portugal and Morocco (9.2°W) over Algeria, Tunisia and Egypt east to the Iran (56.2°E). The southernmost and northermost sites are in Yemen at 15.4°N and in Portugal at 38.8°N. The altitudinal distribution ranges from 213 m below to 2254 m above sea level. One isolated site is from the island Sao Vicente of the Cape Verde Archipelago.
Diagnosis: --Worker (Tab. 3, Figs. 78–81; images under CASENT0281805, CASENT0908336 in www.antweb.org; key). Polymorphic. Rather small, CS 538 µm. Head moderately long, CL/CW 1.174. Postocular index small, PoOc/CL 0.366. Median third of hind margin of head slightly excavated. Scape moderately long, SL/CS 0.813. Eye large, EYE/CS 0.263. Frons rather narrow (FRS/CS 0.243), frontal carinae moderately converging immediately caudal of FRS level (FL/FR 1.067). Dorsal profile of promesonotum moderately convex, metanotal depression moderately deep (MGr/CS 3.65 %), dorsal profile of propodeum moderately convex. Propodeal spines short (SP/CS 0.098); in lateral view varying from short triangular to longer and acute with their axis differing by 47° from longitudinal axis of mesosoma; spine bases approached (SPBA/CS 0.229). Petiole distinctly higher than wide (PeW/CS 0.266, PeH/CS 0.300), in profile with a rather short peduncle, a straight to weakly convex anterior face and the anterior slope of the node slightly less inclined than the posterior one. Petiole node in dorsal view varying between longer than wide in the *bicoronata* morph to as long as wide in the *nigra* morph. Postpetiole moderately wide and rather low (PpW/CS 0.503, PpW /PeW 1.89, PpH/CS 0.259), in dorsal view with a straight to weakly concave anterior margin; postpetiolar sternite completely flat. Clypeus overall rather smooth and shiny, lateral clypeus longitudinally carinulate. Frontal lobes and area posterior of the frontal lobes longitudinally rugulose-carinulate. Longitudinal sculpture on dorsal head in the *nigra* morph weaker and restricted to the area posterior of the frontal laminae, in the *bicoronata* morph stronger developed; a rather narrow median stripe on vertex is in both morphs smooth and shiny. Foveolae on vertex shallow, of 14–19 µm diameter, with an inner corona that is weakly visible in the *nigra* morph, foveolar margins not ideally circular, sometimes kinked or breached by short microrugulae running partially or entirely through the foveolae; foveolar interspaces as wide or wider than foveolar diameter, shiny and with fine cross-branched to semireticulate microstructures (Figs. 81 and 85). Dorsal promesonotum in the *bicoronata* morph with shallow foveolae and finely microreticulate-carinulate, these structures are in the *nigra* morph absent or much weaker. Lateral meso- and metapleuron in the *bicoronata* morph with relatively strong and in the *nigra* morph with weak longitudinal rugosity. Petiole and postpetiole smooth and shiny but delicately microreticulate. Pubescence on gaster tergites short and dilute, PLG/CS 5.46 %, sqPDG 5.08. Strong color polymorphism. Head and gaster usually dark to blackish brown but pigmentation of mesosoma and waist varying from dark to blackish brown to light reddish brown. Concolorous dirty yellowish brown workers were observed in the sample from Turkestan.
Taxonomic comments and clustering results. There is much polymorphism in morphometric and pigmentation data, petiole shape and sculpture within the 45 nest samples investigated here and classified as *Cardiocondyla nigra*. Yet, none of the five forms of exploratory data analyses run was able to reasonably dissolve separate clusters. As result, the taxa *C. bicoronata* and *C. torretassoi* were synonymized with *C. nigra*. Seifert (2003) proposed a character combination of more clearly bicoronate foveolae, stronger microsculpture on head and mesosoma as well as a longer petiole node as diagnostic to separate *C. bicoronata* from *C. nigra*. As these three characters were not numerically recorded, no objective testing of their real value is possible. The clear separation of *C. batesii* from the taxa synonymized here under *C. nigra* has been shown in the section treating the former species (p. 41) and in Fig. 112.
Biology. Nest populations collected in Cyprus and observed in the laboratory may contain several ergatoid males which did not fight (Schrempf 2014).

Cardiocondyla verdensis n. sp.

Etymology: name referring to the type locality—an island within the Cape Verde Archipelago.
Type material:
Holotype plus 1 paratype on the same pin labeled " C.VERDE: 16.588°N, 24.328°W, Sao Nicolao, 385 m, 1 km SW Cabecalinho, trees, CV-192, J.Wetterer 2003.07.21"; depository: collection of X. Espadaler.
All material examined. Only the type sample was available. For details see supplementary information SI1, SI2.
Geographic range. Only known from the type locality.
Diagnosis: --Worker (Tab. 3, Figs. 82–85). Rather small, CS 503 µm. Head longer than in any species of the *C. batesii* group, CL/CW 1.247. Postocular index rather small, PoOc/CL 0.371. Median third of hind margin of head feebly concave. Scape longer than in any species of the *C. batesii* group, SL/CS 0.860. Eye large, EYE/CS 0.266. Frons moderately wide (FRS/CS 0.254), frontal carinae very weakly converging immediately caudal of FRS level (FL/FR 1.042). Dorsal profile of promesonotum convex, metanotal depression deep (MGr/CS 4.50 %), dorsal profile of propodeum convex. Propodeal spines short (SP/CS 0.096) but very acute and moderately steep, their angle in lateral view differing by 45° from longitudinal axis of mesosoma; their bases approached (SPBA/CS 0.230). Petiole distinctly higher than wide (PeW/CS 0.271, PeH/CS 0.312); in profile with a short but rather thin peduncle, a straight to weakly convex anterior face and a strongly convex dorsal profile. Postpetiole moderately wide and rather low (PpW/CS 0.519, PpW /PeW 1.92, PpH/CS 0.264), in dorsal view with a slightly concave anterior margin; postpetiolar sternite completely flat. Clypeus on whole surface smooth and shiny but its lateral areas finely longitudinally carinulate. Frontal lobes and area posterior of the frontal lobes smooth but areas adjacent to frontal carinae longitudinally carinulate. Vertex with the smallest foveolae seen in the *C. batesii* group (dFOV 8.0 µm), the interspaces between the foveolae completely smooth, in places with very delicate stickman-like microstructures (Fig. 85). Dorsal mesosoma smooth and shiny, with very small foveolae and delicate stickman-like microstructures. Meso- and metapleurae shiny but notably microreticulate, surface of the bulla glandulae metapleuralis longitudinally carinulate. Petiole and postpetiole very smooth and shiny but very delicately microreticulate. Pubescence on gaster tergites short and more dilute than in other species of the *C. batesii* group, PLG/CS 5.24 %, sqPDG 5.90. Head, mesosoma and gaster concolorous dark brown.
Taxonomic comments and clustering results. Despite the isolated position of the Cape Verde Archipelago 600 kilometers off the African continent, these islands are apparently not poor in species. Within only nine samples available from Cape Verde, the author could detect four species: *Cardiocondyla emeryi* Forel 1881, *C. fajumensis* Forel 1913, *C. nigra* Forel 1905 and *C. verdense* **n. sp.** Most likely all these species (or their ancestors) were introduced from Africa. Passive anthropogenous introduction, beginning with the Portuguese colonization in the 15th century, should have played a major role. *Cardiocondyla verdensis* **n. sp.** is interpreted here as an endemic island species having developed extreme shape characters as a consequence of genetic bottle necking after introduction. According to data in Tab. 3, *C. verdense* **n. sp.** is a combination of extreme values of CL/CW, SL/CS, dFOV and of large sqPDG. The type sample is placed widely separate from the *C. nigra* cluster in a PCA considering the 14 characters CS, CL/CW, SL/CS, PoOc/CS, EYE/CS, dFOV, SP/CS, PeW/CS, PpW/CS, PeH/CS, PpH/CS, sqPDG, PLG/CS and MGr/CS (Fig. 142). Apart from its extreme morphometrics it is in overall impression similar to the dark and shiny morph of *C. nigra* of which the next place of occurrence is the island Sao Vicente, 50 km overseas from Sao Nicolao.
Biology. The type sample was collected in a garden with trees within a semidesert landscape.

Cardiocondyla stambuloffii Forel 1892

Cardiocondyla stambuloffii Forel 1892 [types investigated]
This taxon has been described from Bulgaria. Investigated were 3 worker syntypes labelled "C.stambuloffii Forel, type, 17 VIII, Anchialo (Bulgarien)", MHN Genève; 3 worker syntypes labelled "Anchialo, 17 VIII ", NHM Wien; 2 worker syntypes labelled "Anchialo 17 VIII, type stambuloffii", NHM Basel.
***Cardiocondyla bogdanovi* Ruzsky 1905** [description and topotypical specimen]
This taxon has been described from Armenia (now Turkey) in a sample collected by K.A.Satunin: "Erivansk. Gub., Aralych, about 3000 feet, worker, gyne 7.IX.1900 ". Type specimens were not detectable in the collections of ZMLU

Moskva and ZM St. Petersburg. Investigated was one worker from the type locality labelled “Caucasus Aralich Horváth 1893 \ Cardiocondyla bogdanovi Ruzsk. det. B.Pisarski \ Inst.Zool.P.A.N. Warszawa 92/60 \ topotype”, ZIPAS Warszawa. This specimen is not a type but a candidate for neotype fixation. Seifert (2003) presented a comprehensive, data-based argumentation why Ruzsky’s unusually detailed description indicates a synonymy with *C. stambuloffii* and that the unjustified neotype fixation for *C. bogdanovi* published by Radchenko (1995) was performed in *C. sahlbergi* (sample No 465 in SI1 and SI2). A synonymy of *C. bogdanovi* with *C. koshewnikovi* is rather unlikely by zoogeography and Ruzsky’s statement “postpetiole more than twice as wide as petiole” also favors a synonymy with *stambuloffii*.

***Cardiocondyla montandoni* Santschi 1912** [types investigated]
This taxon has been described from Romania. Investigated were three worker syntypes labelled “Cardiocondyla montandoni, Lacu Sarat, Roumanie, Montandon”, depository MHN Genève and two worker syntypes labelled “Roumanie, Lacu Sarat, A.L.Montandon”, depository NHM Basel.

Cardiocondyla stambuloffi [sic!] **ssp. *taurica* Karavajev 1927** [topotypical material investigated]
This taxon has been described from Crimea / Ukraine. Karavajev (1927) gave the sampling data “Strand der Janitschary-Bucht in der Nähe von Koktebel, Karawajew (Nr. 2818), vom 29. IX bis 17.X 1919”. According to these data, two worker specimens on separate pins, deposited in SIZ Kiev, labelled “ssp. Taurica \ Enishary bl. Koktebelya 16.VI. 1920 Karavajev \ 4357. coll. Karavaievi \ Cardiocondyla stambuloffi ssp. taurica Karaw. Typus” and “4357. coll. Karavaievi” cannot be considered as primary type specimens. “Enishary bl. Koktebelya”, written in Russian, means in English “Jenizary near Koktebel”. Hence, the collecting sites and collector are fully coincident and because the investigator is also the same, these specimens have a strong indicative value. Furthermore, a synonymy of *taurica* with the most related species *C. koshewnikovi* is most unlikely for zoogeographical reasons.

All material examined. NUMOBAT data were recorded in 34 samples with 82 worker specimens. For details see supplementary information SI1, SI2. This material originated from Armenia (1 sample), Bulgaria (6), Georgia (4), Greece (1), Iran (1), Romania (4), Russia (5), Turkey (8), Ukraine (4).
Geographic range. From the westernmost site in Greece (22.6 °E) distributed northeast and east over the lowlands along the Black Sea, Asia Minor and Georgia to the western shores of the Caspian Sea (48.6°E). The southernmost site is at 37.62°N in southern Asia Minor and the northernmost one in the southern Ukraine at 46.47°N. The altitudinal range extends from 28 m below the sea level at the Caspian coast to 1700 m a.s.l. in Asia Minor.
Diagnosis: --Worker (Tab. 4, Figs. 86–89; images in www.antweb.org with specimen identifiers CASENT0901756, CASENT0904463, CASENT0908347, CASENT0916970, CASENT0917797, FOCOL0296, FOCOL0297, FOCOL0693, FOCOL0783, FOCOL0784, FOCOL1608, FOCOL1609, FOCOL1610, FOCOL2904, FOCOL2905, FOCOL2906; key). Rather small, CS 524 µm. Head rather short, CL/CW 1.162. Postocular index large, PoOc/CL 0.444. Hind margin of head convex, sometimes with a weak concavity in the median level. Scape short, SL/CS 0.780. Eye small, EYE/CS 0.226. Frons very broad (FRS/CS 0.323), frontal carinae not or very weakly converging immediately caudal of FRS level (FL/FR 1.008). Dorsal profile of promesonotum convex, metanotal depression rather deep (MGr/CS 3.50 %), dorsal profile of propodeum posterior of metanotal depression linear. Propodeal spines short, reduced to blunt dents (SP/CS 0.074), their supposed axis in lateral view differing by 48° from longitudinal axis of mesosoma; the distance of their bases is the largest within the *stambuloffii* group (SPBA/CS 0.285). Petiole less than half as wide as postpetiole and much higher than wide (PeW/CS 0.292, PeH/CS 0.373), in profile with a rather short peduncle and the node with very steep and linear anterior and posterior slopes having similar inclination—as result the node profile is symmetric. Area of petiole node in dorsal view small and almost circular. Postpetiole very wide, twice as wide as high (PpW/CS 0.602, PpW /PeW 2.06, PpH/CS 0.305), in dorsal aspect with a weak concavity in anterior margin, its width nearly twice its length, ratio PpW/ maximum median length 1.81, postpetiolar sternite rather flat, with a weak anteromedian bulb. Clypeus and frontal laminae on whole surface longitudinally carinulate; the carinulae continue over the whole vertex but are reduced in the occipital region which is more shiny. Clear foveolae or reticular structures on vertex completely lacking; occasionally (as in the topotypical sample of *taurica*) semireticular structures are present on paramedian vertex. The interspaces between carinulae are shiny with small flat tubercles of 6–10 µm diameter which have the base of a pubescence hair in their center (Fig. 89). The pronotum at least but usually whole dorsal mesosoma smooth and shiny, few

weak carinulae and flat tubercles may be present. Lateral mesosoma in overall impression shiny but meso- and metapleurae longitudinally carinulate. Petiole and postpetiole smooth and shiny. Pubescence on gaster tergites long and dense, PLG/CS 6.46 %, sqPDG 3.51. Whole body concolorous brown, dark brown, or blackish brown.

Taxonomic comments and clustering results. *Cardiocondyla stambuloffii*, *C. koshewnikovi* and *C. rolandi* **n. sp.** are similar semipatric species with probably rather small sympatric zones. Range overlap between *stambuloffii* and *koshewnikovi* occurs in the western Caspian region and between *koshewnikovi* and *rolandi* **n. sp.** in eastern Kazakhstan and northern Mongolia. Considering the 13 characters CS, CL/CW, SL/CS, PoOc/CS, EYE/CS, dFOV, FRS/CS, SPBA/CS, PeW/CS, PpW/CS, PeH/CS, PpH/CS and sqPDG, the three species are safely separated on the nest sample level by five exploratory data analyses with a classification error of 0 % (Fig. 143). If run as wild-cards in a LDA, the type samples of *C. stambuloffii*, *C. montandoni* and *C. taurica* are allocated with p=1.000 to the *stambuloffii* cluster and those of *C. koshewnikovi* and *rolandi* **n. sp.** with p=1.000 to their corresponding clusters.

Biology. All nest sites were in open, very sun-exposed habitats with sparse, lacunose herb layer. Twelve reports on habitat name xerothermous sandy habitats, frequently along sea coast (here also aeolic sand dunes), along rivers or at margins of lakes. Three nests were in coastal sedimentary soil of moderate salinity (solonchak) and one nest in rocky soil. The males are ergatoid and have shear-shaped mandibles. One nest found by the author in the root bale of a composite plant in a coastal sand dune in Bulgaria contained in October one queen, two adult males and about 300 workers. Arnoldi (1926) reported a maximum of 400–500 workers in nests that extended more than 50 cm down into the soil. The males in the Bulgarian nest did not show any scars or signs of injury suggesting that adult males do not fight. Mutual tolerance between at least adult males is also confirmed by laboratory observations in a population from Georgia (J. Heinze, pers. comm. 2022) and the big number of 10 or 20 ergatoid males observed by Arnoldi (1926) in nests from the northern coast of the Black Sea.

Cardiocondyla koshewnikovi Ruzsky 1902

Cardiocondyla koshewnikovi Ruzsky 1902 [types investigated]

This taxon has been described from Kazakhstan in the region where the river Syr Darya entered in 1902 into the then Lake Aral. M. Ruzsky sent type specimens to A. Forel and the late G. Mayr which are still present in the collections of MHN Genève and NHM Wien. These ants were mounted by Forel and Mayr in a different way but the original labels of Ruzsky written with a pencil and the high morphometric (coefficient of variation in CS, SL/CS, PoOc, EYE, PeW/SC, PpW/CS only 1.3–1.5 %) and structural similarity indicate that all 5 syntypes in MHN Genève and NHM Wien came from the same source. In detail these types are: worker lectotype labelled by Ruzsky “Card. koshewnikovi Umg.d.Aralsees” and “1902 M.R.” and carrying a blue printed label “Cotypus”, “Lectotype Cardiocondyla koshewnikovi Ruzsky 1902 (des. B. Seifert 1999)” and “ANTWEB CASENT 0908348” ; 1 paralectotype worker, originally from the same pin but transferred by the author to another pin and labelled with a laser printer and identical text “Card. koshewnikovi Umg.d.Aralsees 1902 M.R.”, both in MHN Genève; 1 paralectotype worker labelled by Forel “Card. stambuloffii koshewnikovi Ruzsky Umgbg.d.Aralsees (Ruzsky)” and carrying a blue printed label “Cotypus”; MHN Genève. 1 worker paralectotype labelled by Ruzsky with a pencil “Card. koshewnikovi, Aralsee” and “W 5.” and by G. Mayr in ink “Aralsee Ruzsky”, NHM Wien; 1 worker paralectotype with same mode of preparation labelled by G. Mayr “Aralsee, Coll. G.Mayr” and “stambuloffi v. koshasnikovi [writing error, B.S.] Ruzsky, Type”, NHM Wien. The published type locality “gefunden an den Ufern des Aralsees und der Mündung des Syr-Darja” (Ruzsky 1902)” does not contradict to the labelling “Umgebung des Aralsee”. Hence, all these specimens can be accepted as types of Ruzsky. The lectotype fixation by Seifert was published in Seifert (2003). A lectotype label attached by Radchenko to a pin belonging to true type material of Ruzsky “LECTOTYPUS top specim. des. Radch.” is depicted in www.antweb.org under the specimen identifier CASENT 0904464. This lectotype fixation has not been published.

All material examined. NUMOBAT data were recorded in 9 samples with 22 worker specimens. For details see supplementary information SI1, SI2. This material originated from Kazakhstan (4 samples), Mongolia (4) and Russia (1).

Geographic range. From western coast of Caspian Sea (44.53°N, 46.69°E, here in contact with *C. stambuloffii*) over Kazakhstan east to Mongolia (45.14°N, 100.90°E, here in contact with *C. rolandi* **n. sp.**). All sites are between 37.62°N and 46.47°N and from 26 m below up to 1230 m above sea level.

TABLE 3. Measurements of workers of the *Cardiocondyla batesii* group. Explanation of data arrangement as in Tab. 1

	batesii (n=37)	***semirubra*** (n=4)	***opistopsis*** (n=4)	***tenuifrons*** (n=3)	***verdensis*** (n=2)	***nigra*** (n=95)	***kushanica*** (n=2)	***rugu-losa*** (n=1)
CS	518 ± 10 [499,548]	552 ± 10 [540,560]	553 ± 14 [540,569]	509 ± 3 [506,512]	503 ± 20 [489,518]	538 ± 18 [488,582]	508 ± 5 [504,512]	576
CL/CW	1.177 ± 0.016 [1.143,1.210]	1.168 ± 0.023 [1.137,1.190]	1.171 ± 0.017 [1.149,1.189]	1.205 ± 0.005 [1.199,1.209]	1.247 ± 0.013 [1.238,1.256]	1.174 ± 0.022 [1.125,1.227]	1.162 ± 0.002 [1.161,1.163]	1.168
SL/CS	0.791 ± 0.011 [0.776,0.814]	0.782 ± 0.010 [0.773,0.795	0.825 ± 0.009 [0.812,0.831]	0.804 ± 0.004 [0.802,0.809]	0.860 ± 0.009 [0.854,0.867]	0.813± 0.017 [0.776,0.856]	0.828 ± 0.009 [0.821,0.834]	0.789
PoOc/CL	0.383 ± 0.009 [0.369,0.408]	0.374 ± 0.006 [0.366,0.379	0.316 ± 0.004 [0.311,0.320]	0.413 ± 0.005 [0.409,0.418]	0.371 ± 0.001 [0.370,0.372]	0.366 ± 0.010 [0.342,0.397]	0.373 ± 0.007 [0.368,0.378]	0.344
EYE	0.264 ± 0.006 [0.251,0.277]	0.256 ± 0.003 [0.252,0.258]	0.280 ± 0.002 [0.278,0.283]	0.267 ± 0.001 [0.266,0.268]	0.266 ± 0.006 [0.262,0.271]	0.263 ± 0.008 [0.246,0.282]	0.270 ± 0.006 [0.265,0.274]	0.267
dFOV	15.5 ± 0.7 [14,17]	17.3 ± 1.3 [16,19	18.0 ± 0.8 [17,19]	14.0 ± 1.0 [13,15]	8.0 ± 1.5 [7.0, 9.1]	16.7 ± 1.0 [14.0,19.0]	16.5 ± 0.7 [16,17]	17.7
FRS/CS	0.244 ± 0.005 [0.232,0.252] 17	0.258 ± 0.006 [0.251,0.264]	0.241 ± 0.006 [0.234,0.247]	0.238 ± 0.005 [0.234,0.243]	0.254 ± 0.002 [0.252,0.255]	0.243 ± 0.009 [0.223,0.267] 74	0.256 ± 0.008 [0.250,0.262]	0.249
FL/FR	1.077 ± 0.024 [1.024,1.109] 15	1.069 ± 0.009 [1.061,1.082]	1.122 ± 0.024 [1.105,1.158]	1.149 ± 0.015 [1.134,1.163]	1.042 ± 0.031 [1.020,1.064]	1.067 ± 0.018 [1.028,1.101] 47	1.099 ± 0.01 [1.098,1.100]	1.027
SPBA/CS	0.257 ± 0.009 [0.242,0.271] 17	0.254 ± 0.011 [0.245,0.268]	0.234 ± 0.008 [0.224,0.242	0.237 ± 0.005 [0.232,0.241]	0.230 ± 0.004 [0.228,0.233]	0.229 ± 0.013 [0.195,0.259] 74	0.240 ± 0.011 [0.232,0.248]	0.240
SP/CS	0.117 ± 0.008 [0.100,0.130]	0.096 ± 0.010 [0.083,0.106]	0.073 ± 0.005 [0.069,0.081]	0.093 ± 0.009 [0.083,0.101]	0.100 ± 0.015 [0.090,0.111]	0.098 ± 0.012 [0.069,0.126]	0.100 ± 0.004 [0.098,0.103]	0.101
PeW/CS	0.282 ± 0.011 [0.256,0.301]	0.322 ± 0.032 [0.300,0.369]	0.283 ± 0.009 [0.272,0.295]	0.272 ± 0.001 [0.272,0.273]	0.271 ± 0.001 [0.270,0.272]	0.266 ± 0.016 [0.232,0.311]	0.269 ± 0.004 [0.266,0.272]	0.276
PpW/CS	0.533 ± 0.011 [0.509,0.556]	0.518 ± 0.015 [0.501,0.536]	0.463 ± 0.006 [0.454,0.467]	0.516 ± 0.004 [0.511,0.519]	0.519 ± 0.017 [0.507,0.531]	0.503 ± 0.019 [0.460,0.551]	0.532 ± 0.001 [0.531,0.532]	0.537
PeH/CS	0.330 ± 0.008 [0.315,0.346]	0.326 ± 0.027 [0.303,0.363]	0.271 ± 0.018 [0.246,0.286]	0.325 ± 0.001 [0.324,0.326]	0.312 ± 0.010 [0.305,0.319]	0.300 ± 0.009 [0.279,0.320]	0.306 ± 0.010 [0.299,0.313]	0.329
PpH/CS	0.286 ± 0.008 [0.262,0.299]	0.267 ± 0.013 [0.252,0.284]	0.259 ± 0.010 [0.244,0.267]	0.288 ± 0.006 [0.282,0.293]	0.264 ± 0.001 [0.263,0.264]	0.259 ± 0.010 [0.232,0.284]	0.287 ± 0.003 [0.285,0.289]	0.289
sqrtPDG	4.84 ± 0.30 [4.41,5.61]	5.37 ± 0.59 [4.84,6.21]	5.34 ± 0.29 [4.94,5.61]	5.57 ± 0.48 [5.12,6.07]	5.90 ± 0.03 [5.88,5.92]	5.08 ± 0.35 [4.13,6.04]	4.73 ± 0.01 [4.72,4.74]	5.48
PLG/CS [%]	5.55 ± 0.32 [4.48,6.02]	5.39 ± 0.22 [5.18,5.71]	5.13 ± 0.34 [4.85,5.62]	5.37 ± 0.21 [5.13,5.51]	5.24 ± 0.16 [5.13,5.36]	5.46 ± 0.40 [4.54,6.59]	6.89 ± 0.07 [6.84,6.94]	5.41
MGr/CS [%]	3.82 ± 0.60 [2.7,5.6]	4.38 ± 0.95 [3.3,5.4]	2.15 ± 0.95 [0.9,3.2]	2.00 ± 0.20 [1.8,2.2]	4.50 ± 0.05 [4.5,4.5]	3.65 ± 0.83 [2.2,5.6]	2.56 ± 0.25 [2.4,2.7]	2.10
PigCon	1.42 ± 0.25 [1.00,2.25]	1.57 ± 0.11 [1.43,1.71]	1.06 ± 0.12 [1.00,1.25]	1.26 ± 0.06 [1.22,1.33]	1.00 ± 0.00 [1.00,1.00]	1.17 ± 0.26 [0.89,2.00]	1.32 ± 0.09 [1.25,1.38]	1.10
PigCap	9.9 ± 1.4 [8.0,12.0]				11.0 ± 0.0 [12.0,12.0]	10.8 ± 1.3 [8.0,12.0]		
PigMes	7.1 ± 1.2 [6.0,10.0]				11.0 ± 0.0 [12.0,12.0]	9.5 ± 1.7 [6.0,12.0]		

Diagnosis: --Worker (Tab. 4, Figs. 90–93; images in www.antweb.org with specimen identifiers CASENT0904464 and CASENT0908348; key): Larger than *stambuloffii*, CS 568 µm. Head rather short, CL/CW 1.168. Postocular index large, PoOc/CL 0.450. Hind margin of head convex, sometimes with a weak concavity in the median level. Scape short, SL/CS 0.780. Eye very small, EYE/CS 0.213. Frons very broad (FRS/CS 0.331), frontal carinae not or weakly converging immediately caudal of FRS level (FL/FR 1.027). Dorsal profile of promesonotum strongly convex, metanotal depression rather deep (MGr/CS 3.20 %), dorsal profile of propodeum posterior of metanotal depression linear. Propodeal spines short, but more acute than in *stambuloffii* (SP/CS 0.076), their supposed axis in lateral view differing by 51° from longitudinal axis of mesosoma; the distance of their bases is large (SPBA/CS 0.264). Petiole less than half as wide as postpetiole and much higher than wide (PeW/CS 0.306, PeH/CS 0.384), in profile with a rather long peduncle and the node with very steep and linear anterior and posterior slopes, the anterior one slightly less inclined—as result the node profile is not fully symmetric. Petiole node in dorsal view slightly wider than long. Postpetiole wide, less than twice as wide as high (PpW/CS 0.598, PpW /PeW 1.95, PpH/CS 0.319), in dorsal aspect with a rather straight anterior margin, its width nearly twice its length, ratio PpW/ maximum median length 1.70, postpetiolar sternite rather flat, but with a weak anteromedian bulb. Whole clypeus, frontal laminae, and anteromedian vertex longitudinally carinulate-rugulose. Remaining vertex strongly longitudinally rugulose; sometimes these rugulae form together with weaker anostomosae a semi-reticulum (in other specimens the reticulum is almost lacking). The interspaces between rugulae are shiny with small flat tubercles of 6–9 µm diameter which have the base of a pubescence hair in their center (Fig. 93). Anterior pronotum transversely rugulose. Dorsal mesosoma on most of its surface longitudinally carinulate-rugulose; rugae usually stronger than in *stambuloffii*; a triangular area anterior of the spine bases or whole dorsal propodeum glabrous and only with very fine superficial reticulum. Lateral mesonotum, mesopleurae, lateral propodeum, and metapleurae longitudinally rugulose. Petiole and postpetiole smooth and shiny. Pubescence on gaster tergites shorter than in *stambuloffii* but more dense, PLG/CS 5.83 %, sqPDG 3.23. Concolorous medium to dark brown with yellowish tinge.
Taxonomic comments and clustering results. The strong separation of *C. koshewnikovi* from *C. stambuloffii* and *C. rolandi* **n. sp.** has already been demonstrated in the section above (p. 49).
Biology. Moister spots in deserts or semideserts, which are frequently salty and situated at the margins of lakes or rivers, are reported as habitats of this species. Two nests were completely dug out by the author in the Saissan Depression 25 July 2001 in a moist *Phragmites* stand in the dune valley of a semidesert. One or two simple entrances (in one nest hidden under fragments of dead *Phragmites* leaves) led to one vertical duct that passed through three levels of horizontal galleries or chambers in the upper 10 cm of soil. One nest (SaNo 207 in SI2) contained 7 ergatoid males, 5 freshly eclosed alate gynes, 35 gyne pupae, 5 gyne prepupae and 440 workers and another nest contained 409 workers and as much as 27 dealate gynes the reproductive status of which was not checked. The fact that the seven males found in one nest did not show any signs of injury indicates that males do not fight for reproductive dominance.

Cardiocondyla rolandi n. sp.

Etymology: the name dedicated to the collector Roland Schultz who substantially contributed to the knowledge of Middle and Central Asian ants.
Type material:
Holotype plus 2 paratype worker labeled "CHI:41.9739°N, 84.4906°E, Tarim Basin, 1038 m, edge of oasis Yengisar, below poplar, Schultz 2004.09.03—091"; 3 paratype workers labelled "CHI:41.2374°N, 84.4421°E, Tarim Basin, 914 m, edge of occasionally flooded area, Schultz 2004.09.08—128"; 3 paratype workers, two paratype males and two paratype gynes labelled "CHI:41.8173°N, 86.1880°E, Tian Shan, 993 m, near brook, below stone, Schultz 2004.09.08—121"; all material, including a big number of unmounted paratypes, deposited in SMN Görlitz.
All material examined. NUMOBAT data were recorded in 21 samples with 49 worker specimens. For details see supplementary information SI1, SI2. This material originated from China (17 samples), Kazakhstan (1), Mongolia (2) and "Turkestan" (1).
Geographic range. Southeast Kazakhstan (46.7°N, 80.6°E), southern Mongolia (43.2°N, 99.0°E), the north of the Chinese province Xinjiang (i.e., the ranges between Tarim River and East Tianshan and the Bogda Shan). The altitudinal distribution ranges between 358 and 1060 m. If Gustav Mayr's samples labelled "Tibet" should apply to

the margin of the Tibetan Plain with the Tarim Basin, the geographical range should extend south to 38°N and the altitudinal range could surpass 2000 m.
Diagnosis: --Worker (Tab. 4, Figs. 94–97; key): Smaller than *koshewnikovi*, CS 538 µm. Head short, CL/CW 1.149. Postocular index smaller than in *koshewnikovi*, PoOc/CL 0.439. Hind margin of head convex, sometimes with a weak concavity in the median level. Scape longer than in *koshewnikovi*, SL/CS 0.815. Eye small, EYE/CS 0.222. Frons very broad (FRS/CS 0.319), frontal carinae not or weakly converging immediately caudal of FRS level (FL/FR 1.036). Dorsal profile of promesonotum strongly convex, metanotal depression deep (MGr/CS 4.06 %), dorsal profile of propodeum posterior of metanotal depression linear. Propodeal spines very short, in lateral view triangular and blunt (SP/CS 0.065), their supposed axis in lateral view differing by 55° from longitudinal axis of mesosoma; the distance of their bases is moderately large (SPBA/CS 0.253). Petiole less than half as wide as postpetiole and much higher than wide (PeW/CS 0.276, PeH/CS 0.372), in profile with a shorter peduncle than in *koshewnikovi* and the node with very steep and linear anterior and posterior slopes, the anterior one slightly less inclined—as result the node profile is not fully symmetric. Petiole node in dorsal view wider than long. Postpetiole wide, less than twice as wide as high (PpW/CS 0.565, PpW /PeW 2.05, PpH/CS 0.313), in dorsal aspect with a rather straight anterior margin, postpetiolar sternite rather flat, but with a weak anteromedian bulb. Microsculpture stronger than in *koshewnikovi*. Whole clypeus, frontal laminae, and anterior vertex longitudinally carinulate-rugulose. Remaining vertex strongly longitudinally rugulose with the rugulae often fusing to form a reticulum. The interspaces between rugulae are shiny with small flat tubercles of 6–10 µm diameter which have the base of a pubescence hair in their center (Fig. 97). Dorsal mesosoma on most of its surface longitudinally carinulate-rugulose; sculpture usually stronger than in *koshewnikovi*. Lateral promesonotum slightly and mesopleurae, lateral propodeum and metapleurae more strongly longitudinally carinulate-rugulose. Petiole and postpetiole smooth and shiny. Pubescence on gaster tergites longer than in *koshewnikovi* but similarly dense, PLG/CS 6.60 %, sqPDG 3.28. Concolorous light to medium brown with yellowish tinge.
Taxonomic comments and clustering results. The strong separation of *C. rolandi* **n. sp.** from *C. koshewnikovi* and *C. stambuloffii* has already been demonstrated in the section treating the latter species (p. 49).
Biology. Habitats are moister spots in semideserts or dry steppe, oases in deserts, and open riverbanks. Males are ergatoid and have shear-shaped mandibles with a strongly developed apical dent. Excavation of complete nest populations was not intended by the collector. Hence, the largest sample containing 180 workers should certainly not represent the upper limit of population size. Four nest samples contained 1, 2, 4 and 4 adult males which did not show signs of any injury. Thus it seems, as in *stambuloffii* and *koshewnikovi*, that at least the adult males do not perform injury or lethal fightings. Alate gynes were seen in the nests between 31 August and 10 September 2004.

Cardiocondyla gibbosa Kuznetzov-Ugamsky 1927

Cardiocondyla elegans gibbosa Kuznetzov-Ugamsky 1927 [types investigated]
This taxon has been described from Kazakhstan. 1 worker lectotype (by present designation) and 2 worker paralectotypes labelled “Cardiocondyla elegans gibbosa nov. 1927, Suzak 3 VII 1923”, “Turkestan Suzak Kusnezov” and “ANTWEB CASENT 0912878”; depository NHM Basel. One paratype worker labelled only “Turkestan Suzak Kusnezov”, depository not recorded (NHM Genève?).

All material examined. NUMOBAT data were recorded in two samples with 4 worker specimens from the type sample. For details see supplementary information SI1, SI2. This material originated from Kazakhstan (2 samples).
Geographic range. Only known from the type locality (44.140°N, 68.467°E, 322 m).
Diagnosis: --Worker (Tab. 4, Figs. 98–100; images in www.antweb.org with specimen identifier CASENT 0912878; key): Smaller than *koshewnikovi* (CS 518 µm) and head longer (CL/CW 1.191). Postocular index large, PoOc/CL 0.458. Anterior clypeal margin convex to straight. Hind margin of head convex, sometimes with a weak concavity in the median level. Scape short, SL/CS 0.800. Eye very small, EYE/CS 0.218. Frons broad (FRS/CS 0.311), frontal carinae not or weakly converging immediately caudal of FRS level (FL/FR 1.052). Dorsal profile of promesonotum strongly convex, metanotal depression deep (MGr/CS 4.02 %), dorsal profile of propodeum posterior of metanotal depression rather linear. Propodeal spines short, reduced to obtusely-angled dents (SP/CS 0.058), the distance of their bases is rather low (SPBA/CS 0.244). Petiole less than half as wide as postpetiole and

much higher than wide (PeW/CS 0.282, PeH/CS 0.374), in profile with a rather long peduncle and the node with the anterior slope less inclined than the posterior slope—as result the node profile is slightly asymmetric. Petiole node in dorsal view slightly narrower than long. Postpetiole wide, less than twice as wide as high (PpW/CS 0.570, PpW /PeW 2.02, PpH/CS 0.306), in dorsal aspect with a moderately concave anterior margin, its width less than twice its length, postpetiolar sternite rather flat. Clypeus, frontal laminae, and anterior vertex (about 60 % of total vertex surface) longitudinally carinulate-rugulose; the strongest rugae mediad and mediofrontad of the eyes. The interspaces between rugae relatively smooth, foveolae of any size are completely absent; tiny pits around the bases of pubescence hairs are occasionally just visible with high-resolution stereomicroscopy; tiny pits of 4–5 µm diameter are well-visible on the perfectly smooth posterior 40 % of vertex surface. Mesosoma in overall impression shining, with more profuse pubescence than in most other species. Frontal and dorsolateral pronotum and dorsal propodeum glabrous. Ventrolateral pronotum, whole mesonotum, ventrolateral propodeum, mesopleurae, and metapleurae to a differing degree longitudinally rugulose with shining interspaces; the strongest rugae on meso- and metapleurae. Waist segments entirely smooth. Pubescence on gaster tergites longer than in related species and less dense, PLG/CS 7.62 %, sqPDG 3.74. More or less concolorous medium to dark brown.
Taxonomic comments and clustering results. *C. gibbosa* is similar to *koshewnikovi* and intraspecific variability in the latter is not known very well. However, the unique type of head sculpture, the much longer pubescence, the more elongated head and a separate clustering in a PCA considering the characters CS, CL/CW, SL/CS, PoOc/CS, EYE/CS, dFOV, SP/CS, PeW/CS, PpW/CS, PeH/CS, PpH/CS, sqPDG, PLG/CS and MGr/CS (Fig. 144) are arguments against a synonymization.
Biology. unknown

Cardiocondyla tibetana Seifert 2003

Cardiocondyla tibetana Seifert 2003 [types investigated]
This taxon has been described from the southern margin of Taklamakan Desert. Investigated were the holotype worker (the specimen with CW=510) and 2 paratype workers labelled “CHINA: Xinjang, Tarim Basin, Ceele Station, leg. H. Heatwole, 1966.08.26 “, SMN Goerlitz; 2 paratype workers pierced on minute pins in the same block of *Sambucus* pith and labelled “Tibet coll. G.Mayr”, NHM Wien.

All material examined. NUMOBAT data were recorded in 4 samples with 11 worker specimens. For details see supplementary information SI1, SI2. All material originated from China.
Geographic range. Three findings with precise site records are at the southern and northern margin of the Taklamakan desert (37.015°N, 80.729°E, 1366 m; 41.175°N, 84.232°N, 920 m). The precise locality of Gustav Mayr’s sample is unclear but probably at the margin of the Tarim Basin with the Tibetan Plain.
Diagnosis: --Worker (Tab. 4, Figs. 101–104; images ANTWEB1041252 and CASENT0919737 in www.antweb.org key): Rather small, CS 540 µm. Head short, CL/CW 1.159. Postocular index smaller than in other members of the *stambuloffii* group, PoOc/CL 0.424. Hind margin of head with a suggested concavity in the median third. Scape longer than in other members of the *stambuloffii* group, SL/CS 0.838. Eye larger than in other members of the *stambuloffii* group, EYE/CS 0.248. Frons narrower than in other members of the *stambuloffii* group (FRS/CS 0.280), frontal carinae weakly converging immediately caudal of FRS level (FL/FR 1.047). Dorsal profile of promesonotum convex, metanotal depression rather shallow (MGr/CS 3.14 %), dorsal profile of propodeum slightly convex. Propodeal spines reduced to obtuse angled corners, SP/CS 0.044), the distance of their bases much smaller than in other members of the *stambuloffii* group (SPBA/CS 0.219). Petiole more than half as wide as postpetiole and distinctly higher than wide (PeW/CS 0.271, PeH/CS 0.310), in profile with a moderately short peduncle and the anterior slope of the node much less inclined than the posterior slope (58° vs. 71° relative to ventral petiole profile)—as result the node profile is strongly asymmetric. Petiole node in dorsal view wider than long. Postpetiole much narrower and lower than in other members of the *stambuloffii* group and less than twice as wide as high (PpW/CS 0.510, PpH/CS 0.265), in dorsal aspect with a rather straight anterior margin, postpetiolar sternite completely flat. Clypeus, frontal laminae, and anterior 70% of median and paramedian vertex very densely longitudinally carinulate-rugulose; distance between carinulae on central vertex only 4–5 µm. Carinulae on lateral vertex interrupted and with much larger, more or less shining interspaces. Poorly visible hair base punctures of only 5–7 µm diameter are

scattered in the interspaces; many of the hair bases without surrounding micropunctures (Fig. 104). Posterior third of head almost glabrous, only scattered hair base punctures present. Foveolae of any size and type on whole head completely absent. Pronotum glabrous. Dorsal parts of mesonotum and propodeum mainly smooth and shining, longitudinal carinulae may be present. Lateral mesonotum with interrupted, meso- and metapleurae with stronger, more continuous longitudinal rugulosity. Petiole and postpetiole smooth and shiny. Pubescence on gaster tergites moderately long and dense, PLG/CS 6.39 %, sqPDG 3.54. Whole body rather concolorous medium to blackish brown, appendages and sometimes clypeus lighter with yellowish tinge.

TABLE 4. Measurements of workers of the *Cardiocondyla stambuloffii* group. Explanation of data arrangement as in Tab. 1

	gibbosa (n=4)	***stambuloffii*** (n=82)	***koshewnikovi*** (n=22)	***rolandi* n. sp.** (n=49)	***tibetana*** (n=11)
CS	518 ± 9 [508,526]	524 ± 17 [484,583]	568 ± 19 [525,613]	538 ± 20 [504,593]	512 ± 17 [495,552]
CL/CW	1.191 ± 0.020 [1.176,1.219]	1.162 ± 0.020 [1.108,1.206]	1.168 ± 0.020 [1.123,1.199]	1.149 ± 0.016 [1.120,1.188]	1.159 ± 0.013 [1.139,1.180]
SL/CS	0.800 ± 0.016 [0.784,0.823]	0.786 ± 0.015 [0.744,0.815]	0.780 ± 0.015 [0.751,0.815]	0.815 ± 0.020 [0.776,0.854]	0.838 ± 0.014 [0.818,0.865]
PoOc/CL	0.458 ± 0.004 [0.455,0.464]	0.444 ± 0.008 [0.428,0.466]	0.450 ± 0.009 [0.434,0.467]	0.439 ± 0.008 [0.425,0.458]	0.424 ± 0.004 [0.416,0.429]
EYE	0.218 ± 0.006 [0.214,0.228]	0.226 ± 0.005 [0.209,0.235]	0.213 ± 0.006 [0.203,0.225]	0.222 ± 0.006 [0.205,0.235]	0.248 ± 0.005 [0.240,0.257]
dFOV	4.8 ± 0.5 [4,5.0]	8.3 ± 0.6 [7.0,10.0]	7.7 ± 0.8 [6.0,9.0]	8.3 ± 0.7 [7.0,10.0]	7.2 ± 0.7 [6.0,8.0]
FRS/CS	0.311 1	0.323 ± 0.010 [0.295,0.353]	0.331 ± 0.010 [0.314,0.352]	0.319 ± 0.008 [0.300,0.336]	0.280 ± 0.006 [0.269,0.291]
FL/FR	1.052 (from image) 1	1.008 ± 0.009 [1.000,1.038] 42	1.027 ± 0.021 [1.000,1.070] 17	1.036 ± 0.016 [1.009,1.077] 38	1.042 ± 0.011 [1.026,1.069] 9
SPBA/CS	0.244 1	0.285 ± 0.012 [0.251,0.317]	0.264 ± 0.008 [0.249,0.281]	0.253 ± 0.015 [0.232,0.308]	0.219 ± 0.012 [0.201,0.241]
SP/CS	0.058 ± 0.013 [0.041,0.068]	0.074 ± 0.009 [0.053,0.096]	0.076 ± 0.008 [0.060,0.087]	0.068 ± 0.013 [0.044,0.101]	0.044 ± 0.012 [0.027,0.065]
PeW/CS	0.282 ± 0.014 [0.266,0.294] 3	0.292 ± 0.014 [0.270,0.334]	0.306 ± 0.017 [0.278,0.348]	0.276 ± 0.014 [0.244,0.314]	0.271 ± 0.015 [0.249,0.300]
PpW/CS	0.570 ± 0.010 [0.559,0.581]	0.602 ± 0.020 [0.548,0.664]	0.598 ± 0.023 [0.567,0.646]	0.565 ± 0.027 [0.521,0.647]	0.510 ± 0.022 [0.474,0.545]
PeH/CS	0.374 ± 0.005 [0.368,0.377] 3	0.373 ± 0.013 [0.343,0.405]	0.384 ± 0.012 [0.353,0.406]	0.372 ± 0.017 [0.337,0.414]	0.310 ± 0.011 [0.293,0.326]
PpH/CS	0.306 ± 0.006 [0.300,0.315]	0.305 ± 0.010 [0.283,0.350]	0.319 ± 0.012 [0.297,0.345]	0.313 ± 0.017 [0.283,0.354]	0.262 ± 0.012 [0.243,0.278]
sqrtPDG	3.74 ± 0.32 [3.40,4.09]	3.51 ± 0.21 [3.11,4.06]	3.23 ± 0.17 [2.87,3.56]	3.28 ± 0.20 [2.93,3.85]	3.54 ± 0.16 [3.28,3.77]
PLG/CS[%]	7.62 ± 0.33 [7.29,7.99]	6.46 ± 0.46 [5.47,7.36]	5.83 ± 0.47 [4.57,6.59]	6.60 ± 0.39 [5.57,7.37]	6.39 ± 0.37 [5.81,6.90]
MGr/CS[%]	4.02 ± 0.96 [2.7,4.9]	3.50 ± 0.69 [2.2,5.3]	3.20 ± 0.68 [1.9,4.4]	4.06 ± 0.89 [1.9,6.2]	3.14 ± 0.74 [1.6,4.1]

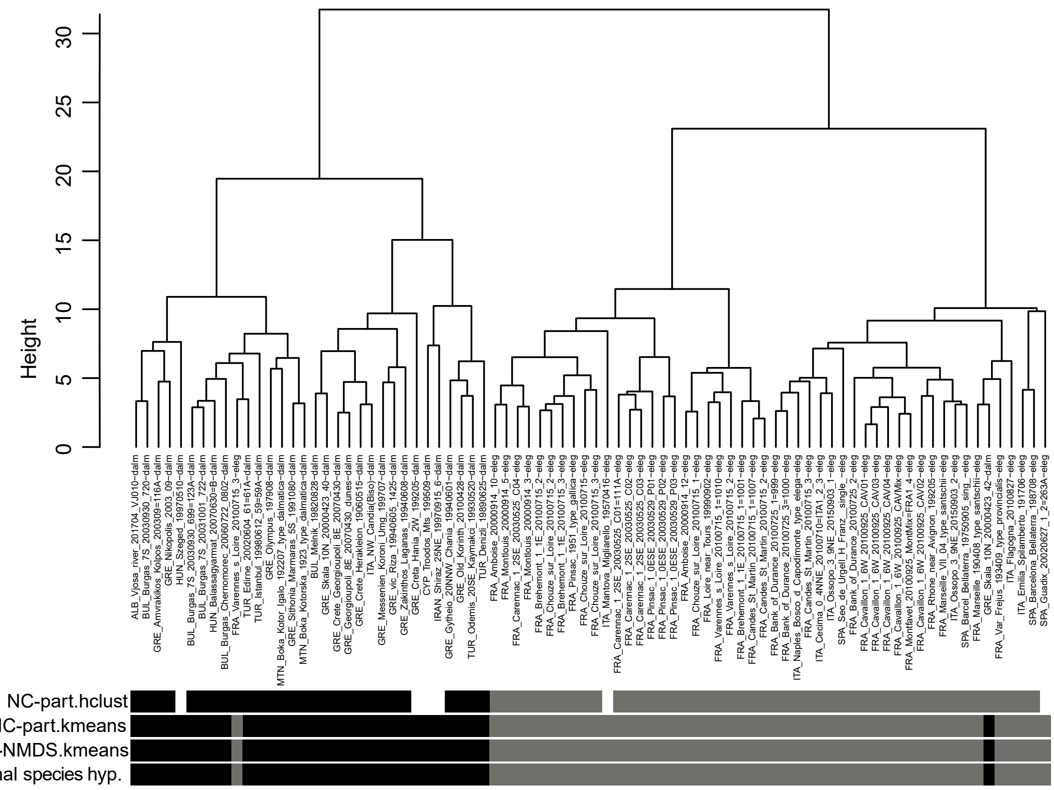


FIGURE 133. Separation of nest samples of *Cardiocondyla elegans* (grey bars) and *C. dalmatica* (black bars) by NC-Ward, NC-part.hclust, NC-part.kmeans and NC-NMDS.kmeans clustering. White bars indicate outliers in NC-part.hclust. The mean classification error of the four exploratory data analyses relative to the controlling linear discriminant analysis is 1.2%. Fourteen phenotypic characters were considered. The bimodality within both species' clusters represents an intraspecific dimorphism (Seifert 2016).

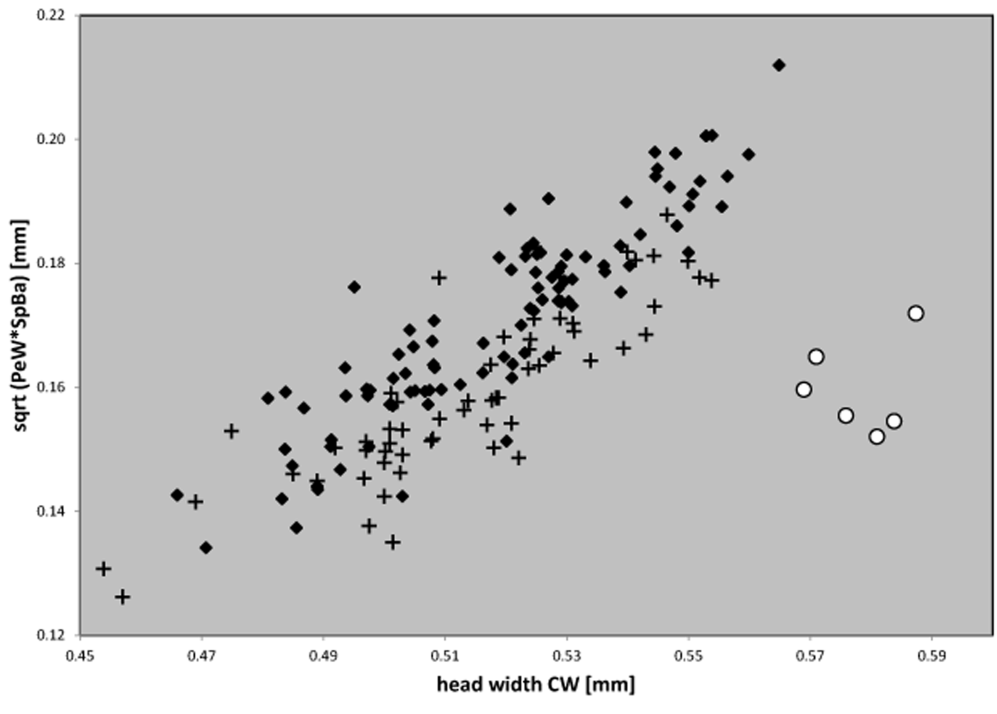


FIGURE 134. Plotting of the square root of the product of petiole width PeW and spine base distance SPBA against head width CW in worker individuals of *Cardiocondyla dalmaticoides* **n. sp.** (white dots), *C. dalmatica* (crosses) and *C. elegans* (rhombs).

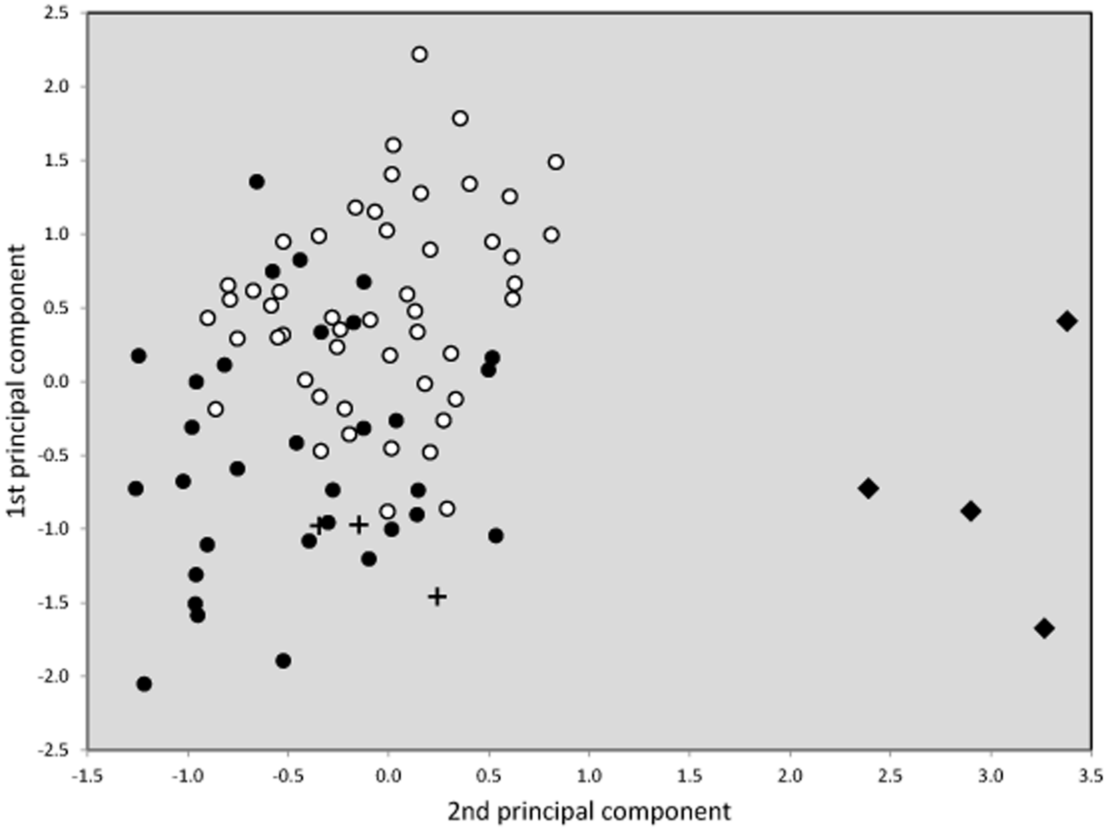


FIGURE 135. Separation of nest samples of *Cardiocondyla brachyceps* (black rhombs, n=4), *C. dalmatica* (black dots, n=32), *C. dalmaticoides* **n. sp.** (crosses, n=3) and *C. elegans* (white dots, n=50) by a principal component analysis considering the morphometric characters PpH/CS, dFOV, SL/CS, PoOc/CL, sqPDG, SP/CS, PLG/CS and PeW/CS.

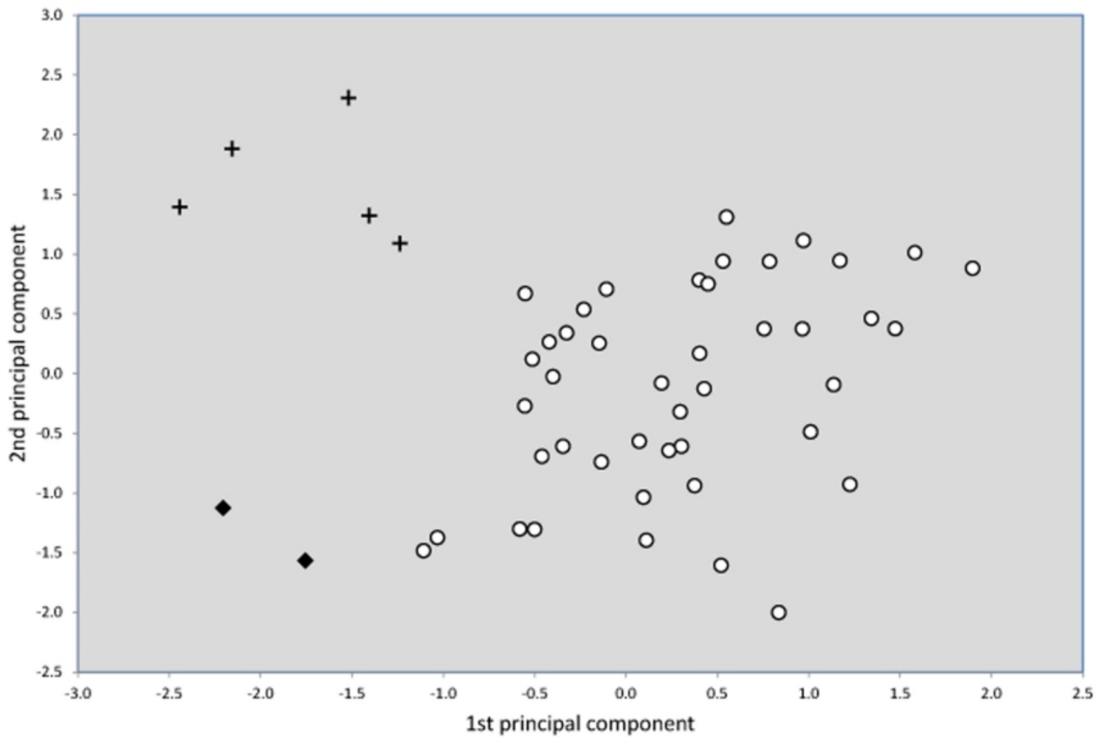


FIGURE 136. Separation of individual workers of *Cardiocondyla caspiense* **n. sp.** (black rhombs, n=2), *C. ulianini* (white dots, n=44) and *C. littoralis* (crosses, n=5) by a principal component analysis considering the morphometric characters PoOc/CL, PeW/CS, PpH/CS and PLG/CS.

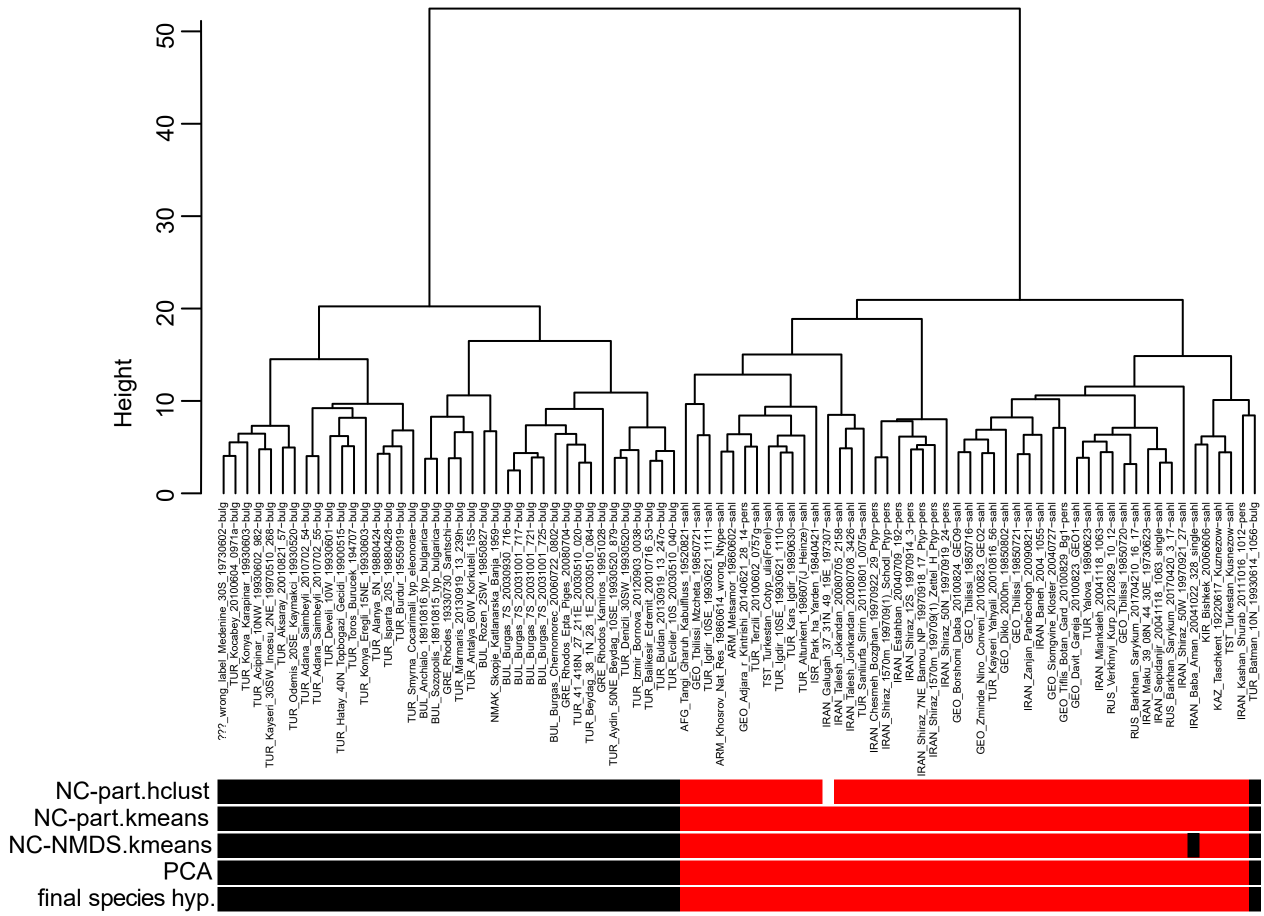


FIGURE 137. Separation of nest samples of *Cardiocondyla bulgarica* (black bars) from a combined cluster of *C. sahlbergi* and *C. persiana* (red bars) by NC-Ward, NC-part.hclust, NC-part.kmeans, NC-NMDS.kmeans clustering and a principal component analysis . The white bar indicates an outlier in NC-part.hclust. The mean classification error of the four exploratory data analyses relative to the controlling linear discriminant analysis is 0.45%. All 17 available NUMOBAT characters were processed without character selection.

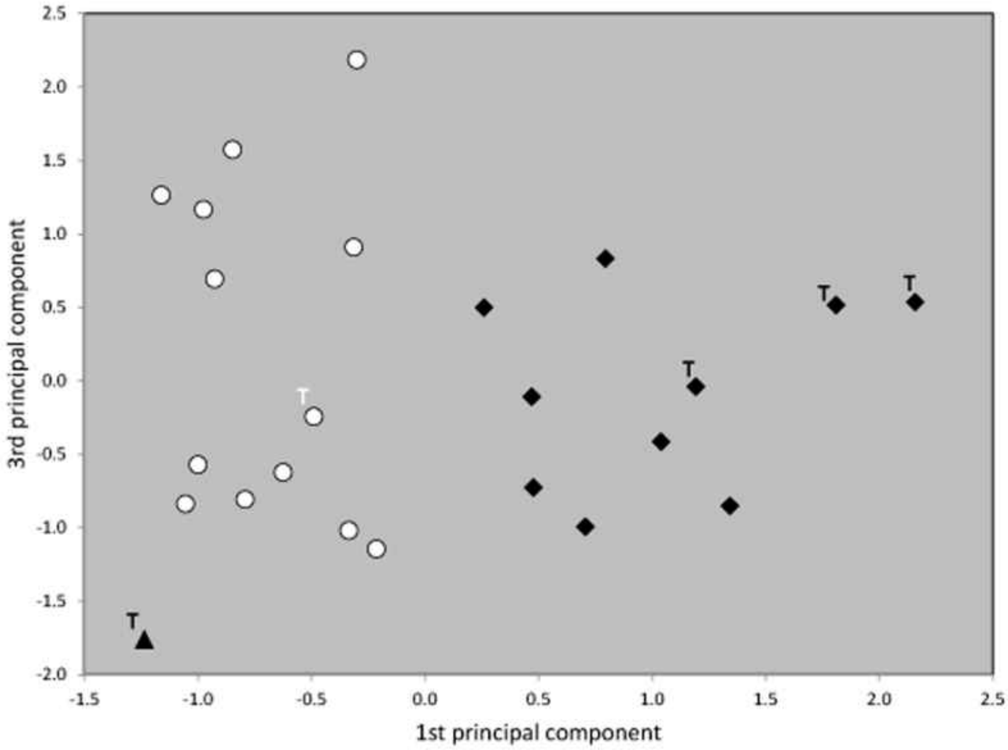


FIGURE 138. Separation of gyne individuals of *Cardiocondyla persiana* (black triangle, n=1), *C. sahlbergi* (white dots, n=13) and *C. bulgarica* (black rhombs, n=10) by a principal component analysis considering the morphometric characters CS, CL/CW, PoOc/CL, SL/CS, PeW/CS, PpW/CS, SP/CS, sqPDG, PLG/CS, PeH/CS, PpH/CS, dFOV, ML/CS. The type specimens are marked by a "T".

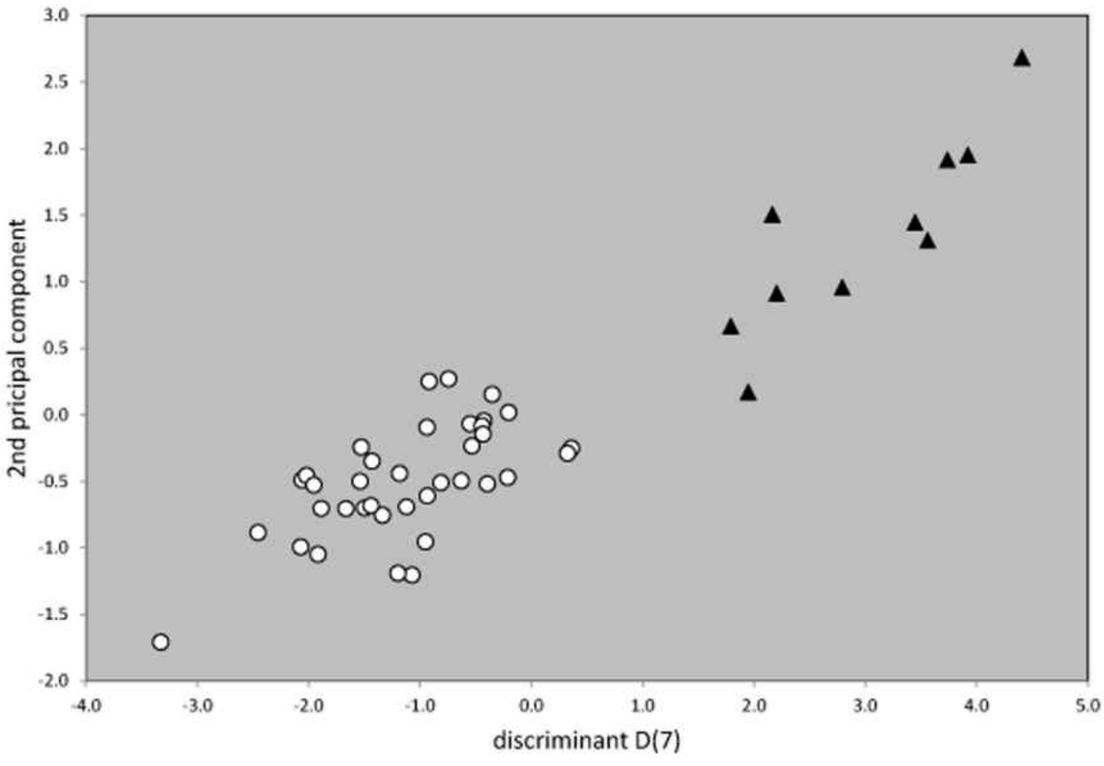


FIGURE 139. Separation of nest samples of *Cardiocondyla sahlbergi* (white dots, n=38) and *C. persiana* (black triangles, n=10) by a linear discriminant and a principal component analysis considering the morphometric characters CS, SL/CS, PeW/CS, sqPDG, dFOV, PigCon, EYE/CS.

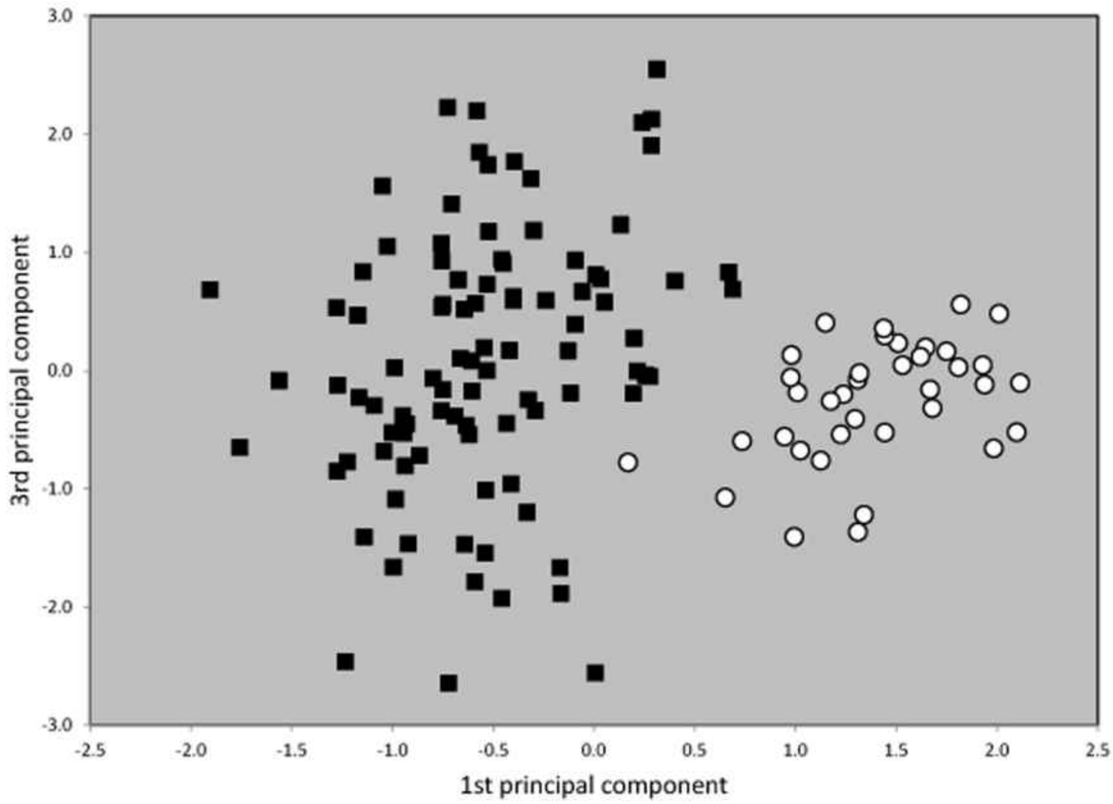


FIGURE 140. Separation of individual workers of *Cardiocondyla nigra* (black squares, n=95) and *C. batesii* (white dots, n=37) by a principal component analysis considering the morphometric characters CS, CL/CW, SL/CS, PoOc/CS, EYE/CS, dFOV, SP/CS, PeW/CS, PpW/CS, PeH/CS, PpH/CS, sqPDG, PLG/CS and MGr/CS.

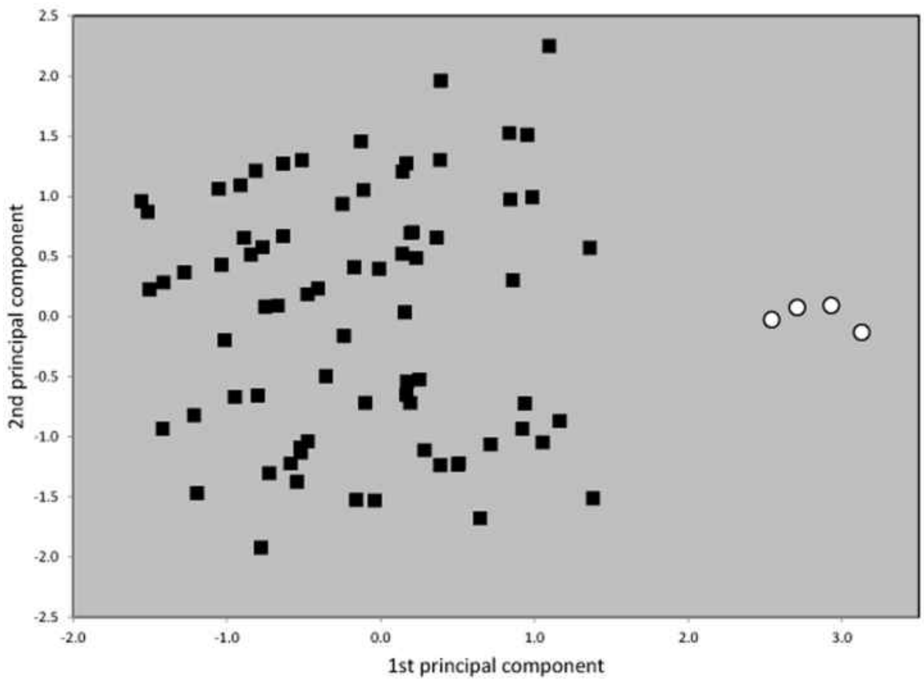


FIGURE 141. Separation of individual workers of *Cardiocondyla nigra* (black squares, n=95) and *C. semirubra* (white dots, n=4) by a principal component analysis considering the morphometric characters FRS/CS, PeW/CS and PigMes.

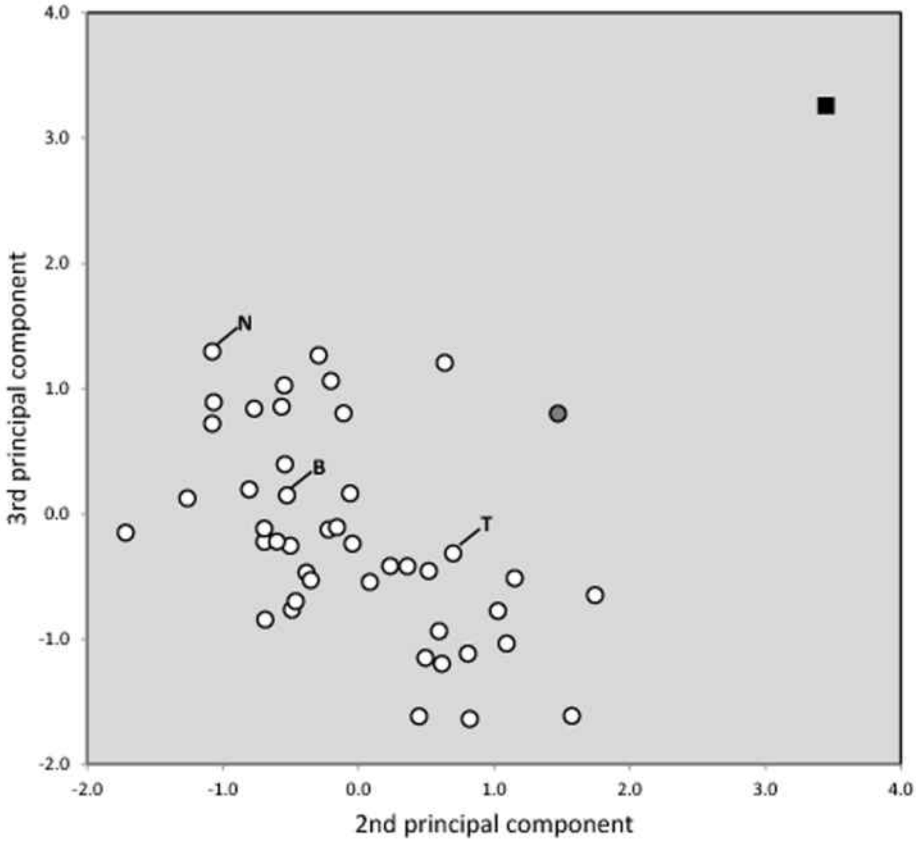


FIGURE 142. Separation of nest samples of *Cardiocondyla nigra* (white dots, n=45) and *C. verdense* (black square, n=1) by a principal component analysis considering the morphometric characters CS, CL/CW, SL/CS, PoOc/CS, EYE/CS, dFOV, FRS/CS, SPBA/CS, SP/CS, PeW/CS, PpW/CS, PeH/CS, PpH/CS, sqPDG, PLG/CS and MGr/CS. The grey dot represents a *C. nigra* sample from the Cape Verde island Sao Vicente. The type samples of *C. bicoronata*, *C. nigra* and *C. torretassoi* are marked by the letters B, N and T.

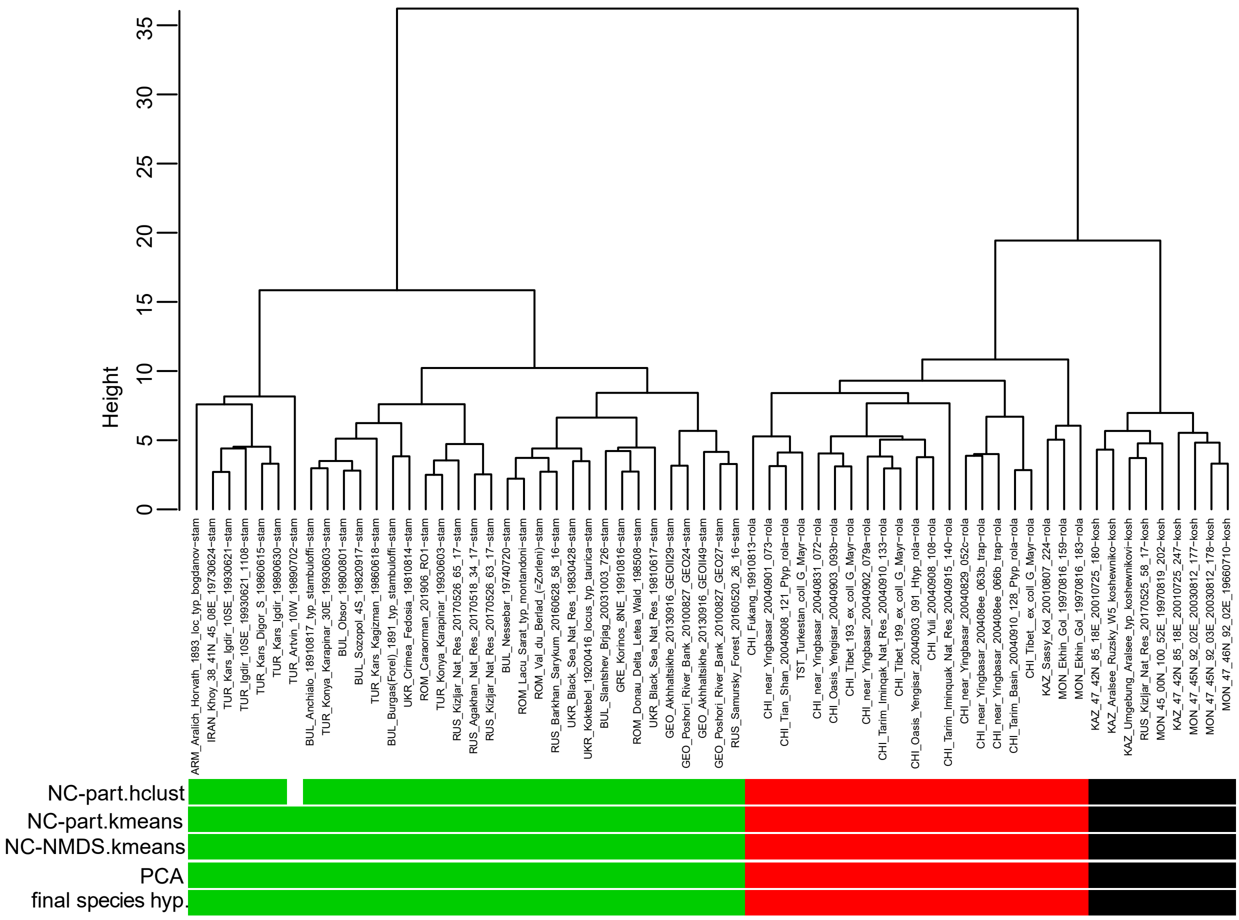


FIGURE 143. Separation of nest samples of *Cardiocondyla stambuloffii* (green bars), *C. rolandi* **n. sp.** (red bars) and *C. koshewnikovi* (black bars) by NC-Ward, NC-part.hclust, NC-part.kmeans, NC-NMDS.kmeans clustering and a principal component analysis considering 13 NUMOBAT characters. The mean classification error of the five exploratory data analyses relative to the controlling linear discriminant analysis is 0%. The white bar indicates an outlier in NC-part.hclust.

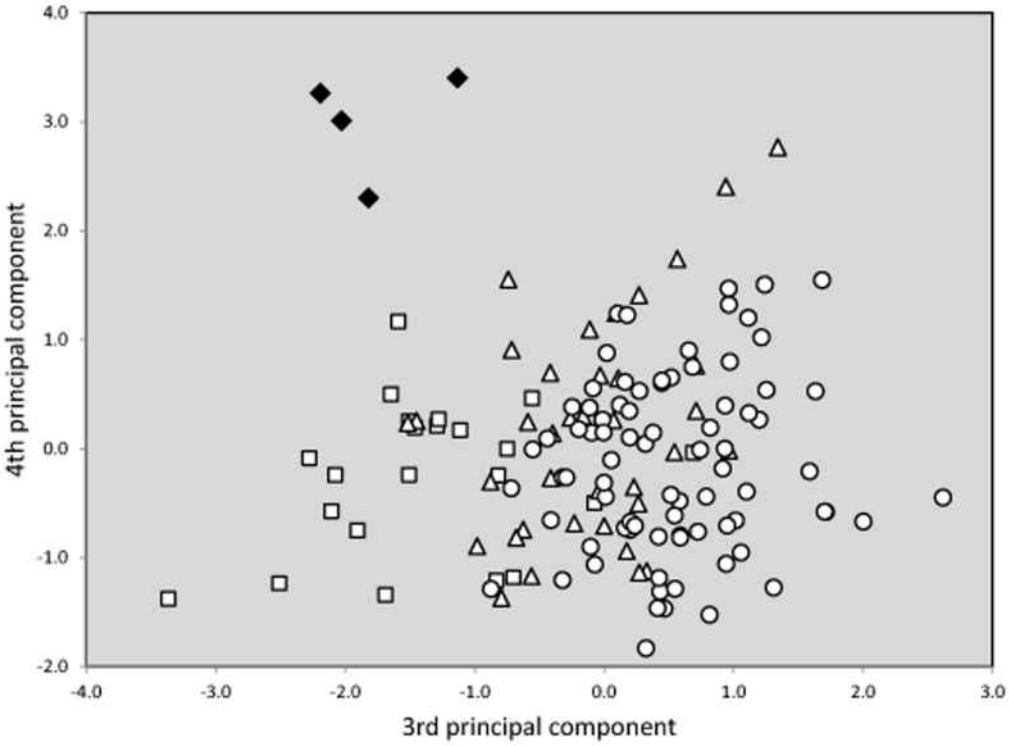


FIGURE 144. Separation of individual workers of *Cardiocondyla gibbosa* (black rhombs) and *C. koshewnikovi* (white squares), *C. rolandi* **n. sp.** (white triangles) and *C. stambuloffii* (white circles) by a principal component analysis considering the morphometric characters CS, CL/CW, SL/CS, PoOc/CS, EYE/CS, dFOV, SP/CS, PeW/CS, PpW/CS, PeH/CS, PpH/CS, sqPDG, PLG/CS and MGr/CS.

Taxonomic comments and clustering results. The character combination of *Cardiocondyla tibetana* is unique and enables a safe distinction from any known Palaearctic species both by morphometry, body shape, and microstructures. The minute or absent hair base punctures and full absence of any foveolae on vertex, as well as spine and postpetiolar shape were the reasons for placing *tibetana* in the *stambuloffii* group. However, the larger eye size, the narrower frons, and the lower petiole height and postpetiole width also indicate affinities to the *elegans* or *ulianini* groups.

Biology. Two nests were found by Roland Schultz in a semidesert zone in an area with clay or loamy soil occasionally flooded by the river Tarim and covered by light tamarisk stands.

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