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A taxonomic revision of the ants of the *Cardiocondyla wroughtonii* group (Hymenoptera: Formicidae) with a checklist of the *Cardiocondyla* species of the world

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Abstract

A revision of the *Cardiocondyla wroughtonii* group of the ant genus *Cardiocondyla* Emery 1869 is presented. The group is separable from other members of the genus by the character combination of a concave shape of postpetiolar sternite and a mesosoma not being stout and humpbacked. Eleven species were collected in this group – among these nine previously described species: *Cardiocondyla wroughtonii* Forel 1890, *C. obscurior* Wheeler 1929, *C. shagrinata* Seifert 2003, *C. nana* Seifert 2003, *C. allonivalis* Seifert 2023, *C. yemeni* Collingwood & Agosti 1996, *C. yoruba* Rigato 2001, *C. neferka* Bolton 1982 and *C. weserka* Bolton 1982. *Cardiocondyla heinzei* n.sp. is described as new from Ivory Coast whereas a species coded as *Cardiocondyla* sp. SPIT was only morphologically characterized without being validly described. The species are imaged in four standard viewing positions and data of 16 morphometric characters are presented. The heterospecific status of the closely related cosmopolitan tramp species *Cardiocondyla wroughtonii* and *obscurior* is confirmed by exploratory and hypothesis-driven data analyses based on 84 samples with 205 worker individuals. These analyses also confirmed, by investigation of type specimens, the junior synonymy of *Cardiocondyla wroughtonii* var. *hawaiensis* Forel 1899, *C. wroughtonii* subsp. *quadraticeps* Forel 1912, *C. wroughtonii* var. *bimaculata* Wheeler 1929, *C. emeryi* subsp. *chlorotica* Menozzi 1930, *C. longispina* Karavajev 1935 and *C. yamauchii* Terayama 1999 with *C. wroughtonii* and of *C. bicolor* Donisthorpe 1930 with *C. obscurior*. A checklist of the *Cardiocondyla* species of the world, including 128 published names of which 81 refer to valid species, is given at the end of the paper.

Keywords Cryptic species | numeric morphology-based alpha-taxonomy | checklist *Cardiocondyla*

Content

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1. Introduction

The members of the ant genus *Cardiocondyla* Emery 1869 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. The genus received a strong attention by sociobiologists during the last 45 years because of a striking character extremely rare within ants: All species develop ergatoid (=worker-like wingless) males with a presumedly lifelong spermiogenesis, which try to eliminate competing males in order to monopolize all intranidal matings with female sexuals. This is accompanied by a remarkable, highly asymmetric reduction of male dimorphism in *Cardiocondyla*: winged males were lost in many species but only a single species is known that has retained winged males but lost wingless males (Oettler et al. 2010, Heinze 2017, Heinze et al. 2021, Oettler 2021). These features in combination with small colony size, allowing observation of single-individual life histories, and easy laboratory rearing have made these ants very attractive objects for the study of diverse sociobiological questions (Hamilton 1979, Kinomura & Yamauchi 1987, Stuart et al. 1987, Heinze & Hölldobler 1993).

Species-level taxonomy of the genus, however, remained under-investigated for a long time. More recently, Bolton (1982) and Rigato (2002) described five species from Africa but did not consider these within a revisionary context. The revision of nine species groups of the ant genus *Cardiocondyla* by Seifert (2003) was the first attempt of a broad-scale revision of this genus in this millenium. Development of new analytical methods and new ant material investigated thereafter led to the publication of three follow-up revisionary works dealing with particular species groups. Seifert et al. (2017) revised the *Cardiocondyla nuda* group and recognized eight species. Seifert (2023a) considered the species groups with Oriental and Australasian origin and Seifert (2023b) the species groups with Palaearctic origin. Among the 14 informal species groups and three monotypical clades of the genus delimited by Seifert (2023a) which contain 81 species (see checklist in this paper), there remain only three groups which were not subject of a modern revision on the species level. These are the *Cardiocondyla emeryi* group, the *C. shuckardi* group and the *C. wroughtonii* group. Despite having received new investigation material since 2003, I was not motivated to publish revisions of the first two groups. This is because the taxonomic treatment of the *C. emeryi* group remained unchanged compared to Seifert (2003) and because the new analyses and too small sample size did not result in a stable clustering in some of the nine supposed species of the *C. shuckardi* group. As a consequence, there remains only the *C. wroughtonii* group in which some new and verifiable information can be published at the current stage and this is the purpose of this paper. The concept of the *C. wroughtonii* group presented here has to be considered as informal – i.e., it is directed on keying of the group based upon external morphology. I expect that the species with origin in Africa and the Arab Peninsula collected here provisionally in this group will be placed in another phylogenetic context once an analysis considering adequate markers of nuclear DNA on the basis of a broad sampling will be available.

2. Material

NUMOBAT data of the world-wide fauna were recorded in a total of 1300 samples with 2500 workers. The species considered in this paper comprise 126 numerically evaluated samples with 265 worker individuals. 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:

BMNH London – British Museum of Natural History London, England

MCZ Harvard – Museum of Comparative Zoology of the Harvard University, Cambridge, USA

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

MCZ Lausanne – Musée cantonal de zoologie, Lausanne, Switzerland

NHM Wien – Naturhistorisches Museum Wien, Wien, Austria

SIZ Kiev – Schmalhausen Institute of Zoology, Kiev, Ukraine

SMN Görlitz – Senckenberg Museum für Naturkunde, Görlitz, Germany

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

3. Methods

3.1 The species concept used

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, in the present paper, this ideal approach was only applicable to demonstrate heterospecificity of *C. wroughtonii* and *C. obscurior*. In the remaining nine species the sample size was too small (sometimes only a single type specimen!) to run exploratory or hypothesis driven analyses and subjective assessment of species status remained the only option. Unfortunately, there is so far no taxonomically informative investigation of nuclear DNA in *Cardiocondyla* and we are completely uninformed 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 the increased rate of intranidal mating and rarity of normal swarming flights with outcrossing. In the present material one sample was suspicuous to represent a hybrid.

3.2 Equipment and measurement procedures

A pin-holding stage, permitting full rotations around X, Y, and Z axes and a Leica M165C high-performance stereomicroscope equipped with a 2.0x planapochromatic objective (resolution 1050 lines/mm) was used for spatial adjustment of specimens at magnifications of 120–360x. The mean relative measuring error over all magnifications was 0.2 %. A Schott KL 1500 cold–light source equipped with two flexible, focally mounted light–cables, providing 30°–inclined light from variable directions, allowed sufficient illumination over the full magnification range and a clear visualization of silhouette lines. A Schott KL 2500 LCD cold–light source in combination with a Leica coaxial polarized–light illuminator provided optimal resolution of tiny structures and microsculpture at highest magnifications. Simultaneous or alternative use of the cold-light sources depending upon the required illumination regime was quickly provided by regulating voltage up and down. A Leica cross-scaled ocular micrometer with 120 graduation marks ranging over 52 % of the visual field was used. To avoid the parallax error, its measuring line was constantly kept vertical within the visual field. A mean measurement error of ± 0.6 µm was calculated for small and well-defined structures such as foveola width, but one of ± 2.0 µm for larger structures that are difficult to position such as cephalic length. Z-stack images of mounted specimens were produced with a KEYENCE VHX-7000 digital microscope using magnifications between 100 and 1000x. Depending on the object properties, illumination was varied between sectorial or full ring lighting, sectorial or complete coaxial lighting and multi-lighting as combination of ring and coaxial lighting.

3.3 The morphometric characters and terminology

Sixteen phenotypic standard characters were investigated and numerically recorded in worker ants. In bilaterally developed characters, arithmetic means of both body sides were calculated. All measurements were made on mounted and fully dried specimens.

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 found usually 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.

FL: maximum distance of the frontal carinae anterior of the FRS level. Accessory character, not thoroughly measured.

FL/FR: index of anterior divergence of frontal carinae. It is 1.0 when the frontal carinae are parallel and set to 1.0 when these diverge caudad on their whole length.

FR: minimum distance of the frontal carinae posterior of the FL level. Accessory character, not thoroughly measured.

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 straight line from the center of propodeal lobe (center of circus in Fig. 4) to the border point between anterior pronotal shield and propleuron.

MH: with mesosoma in lateral view and measured orthogonal to 'longitudinal mesosomal axis', MH is the longest measurable ***section*** line of mesosoma at mesopleural level (not height above all, Fig.4).

ML: mesosoma length from caudalmost point of propodeal lobe to transition point between anterior pronotal slope and anterior propodeal shield (Fig. 4; preferentially measured in lateral view; if the transition point is not well defined, use dorsal view and take the center of the dark-shaded borderline between pronotal slope and pronotal shield as anterior reference point).

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

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.

Pigmentation score: variation of pigmentation from light yellowish (score 4) to blackish brown (score 12) assessed by subjective comparison of a standard color table (Fig. 5 in Seifert 2023b) 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 7 measurements measured 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 mode of measuring 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 $PDG = BD^2 / PLG$.

3.4 NUMOBAT: Explorative and supervised data analyses, classification and statistical testing

If sample size was sufficient, formation of species hypotheses was done by running five different forms of exploratory data analyses (EDA) considering the morphological standard characters specified above. Four EDA methods using nest centroids as input data, named

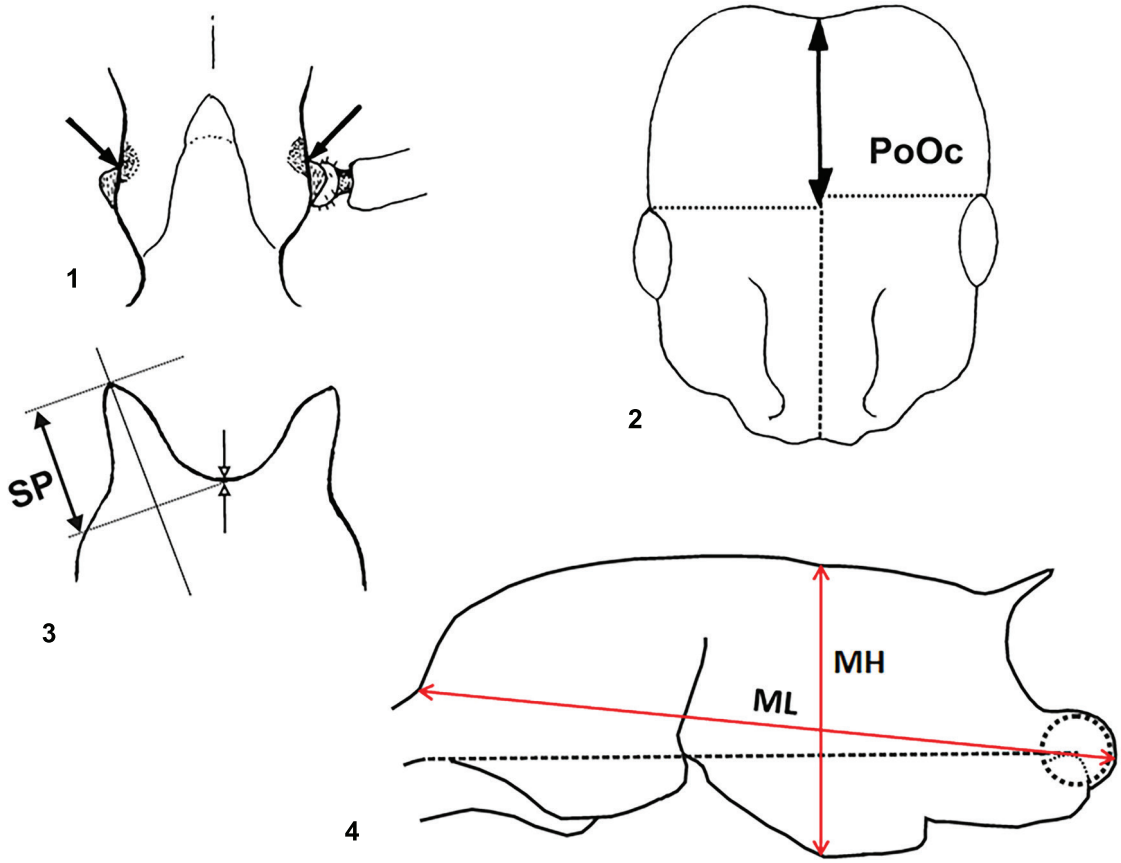


Figure 1–4. (**1**) Measuring FRS, the arrows mark the endpoints of the measure.(**2**) Bilateral measuring of postocular distance PoOc to correct for head asymmetries.(**3**) Measuring spine length in dorsofrontal view. (**4**) The dotted line marks the longitudinal axis of mesosoma in lateral view.

NC clustering, were applied. These were hierarchical NC-Ward clustering, the hierarchical method NC-part. hclust and the iterative vector-quantization method NC-part.kmeans – both implemented in partitioning algorithms based on recursive thresholding (for details see Csösz & Fisher 2015). As a fourth method, NC-NMDS.kmeans, a nonmetric multidimensional scaling combined with iterative vector-quantization (Seifert & al. 2013) was applied. All four methods of NC-clustering are excellent in formation of initial hypotheses but they tend to obscure intermediate morphologies possible generated by interspecific hybridization and introgression. Revealing such cases requires further analytical steps: checking the data sample by sample and analyzing them in the simple two-dimensional vectorial space. This was preferentially done by principle component analysis (PCA) with a maximum of three considered entities and often with character reduction. Alternatively, the position of suspicious samples was checked by wild-card runs in a LDA. Checking samples with controversial classifications was done by an interaction of NC clustering and a controlling linear discriminant analysis (LDA) in which these samples were run as wild-cards, following the rationale described in Seifert & al. (2013). The final classification ('final species hypothesis') was established by the LDA in an iterative procedure and there remained no undecided cases even if their posterior probabilities were close to 0.5. PCA, LDA, ANOVA and X^2 tests were run with the SPSS 15.0 software package.

4. Results

4.1 Delimitation of the *Cardiocondyla wroughtonii* group.

The bilobate shape of the postpetiolar sternite (see next paragraph) is considered here as a leading indicator of the *C. wroughtonii* group. However, when clustering attempts are made considering all 16 phenotypical characters, *Cardiocondyla yemeni* Collingwood & Agosti 1996, *C. yoruba* Rigato 2002, *C. weserka* and *C. neferka* Bolton 1982, which all show a bilobate

postpetiolar sternite, do not cluster with the remaining species of the *C. wroughtonii* group. In this context it should be noted that the six species from Africa and the Arabian Peninsula show diverging frontal carinae with FL/FR > 1.040 whereas the five species with Orientalic-Australasian origin have FL/FL < 1.040. Thus it seems that the *C. wroughtonii* group sensu stricto has to be reduced to the latter five species. Anyway, to clear up the relatedness of these species, we have to wait for an analysis of adequate nuDNA markers done on the basis of an extended sample size.

In the absence of better solutions and aiming at a simple keying in a worldwide context, I characterize here the *C. wroughtonii* group as follows: postpetiolar sternite anterolaterally with a rounded lobiform protrusion on each side which clearly elevates above the level of median surface of sternite; the surface of the sternite thus appearing deeply concave in frontal view. Mesosoma not stout (ratio ML/MH >2.2); dorsal mesomal profile not humpbacked, instead it is feebly convex with a metanotal depression, if the latter is nearly absent then dorsal profile rather linear; ratio SPBA/CS <0.314. The shape of postpetiolar sternite characteristic for the *wroughtonii* group is also seen in the following species restricted to the Orientalic-Australasian-Polynesian zoogeographical region: *C. argentea* Seifert 2023, *C. semiargentea* Seifert 2023, *C. argyrotricha* Seifert 2023, *C. latifrons* Seifert 2023, *C. micropila* Seifert 2023, *C. pirata* Seifert 2013. These species are easily separable, among other characters, by their stout, humpbacked mesosoma with a ratio ML/MH < 2.2 and broad spine bases with SPBA/CS > 0.314.

4.2 Key to the workers of the *Cardiocondyla wroughtonii* group

This key focusses on character combinations instead YES/NO decisions based on single characters and with the help of the figures a comparably feasible determination should be possible.

1a Postpetiolar sternite anterolaterally with a rounded lobiform protrusion on each side which clearly elevates above the level of median surface of sternite; the surface of the sternite thus appearing deeply concave in frontal view (Fig. 5). Mesosoma not stout (ratio ML/MH >2.2); dorsal mesomal profile not humpbacked, instead it is feebly convex with a metanotal depression – if the latter is absent, then dorsal profile rather linear; ratio SPBA/CS <0.314. *C. wroughtonii* group. **2**
1b Character combination different .... **remaining species of *Cardiocondyla***
2a Scape extremely short (SL/CL <0.68), metanotal depression shallow (MGR/CS <1.7%), Propodeal spines very short (SP/CS <0.140) (Figs 6–15). With all measurements in mm discriminant 50.34*SL -65.693*CL +109.51*SP+144.86*MGR +4.0 < 0 [error 0% in 9 specimens] **3**
2b Scape longer (SL/CL >0.68), metanotal depression distinct (MGR/CS >1.7%), Propodeal spines longer (SP/CS >0.140). Discriminant > 0 [error 0% in 249 specimens] **4**
3a Whole dorsum of gaster blackish brown, microsculpture on first gaster tergite stronger (Fig. 9). Africa: Ghana, Ivory Coast, Niger (Figs 6–10) .... ***yoruba***
3b All body parts yellowish or yellowish-brown, microsculpture on first gaster tergite weaker (Fig. 15). Arabian Penisula (Figs 11–15) ..... ***yemeni***
4a Frontal carinae not or only slightly diverging frontad (FL/FR 1.000-1.053), head shorter (CL/CW 1.069-1.174), pubescence on 1st gaster tergite more dilute. With sqPDG as square root µm and all other measurement in mm, discriminant 2.516*sqPDG+164.09*FRS+134.91*PeW -100.7*PPW-84.76*PeH -13.25 > 0 [error 0% in 256 workers]. Species with Orientalic-Australasian origin, but two are widely distributed as tramp species. **5**
4b Frontal carinae diverging frontad (FL/FR 1.050-1.106), head longer (CL/CW 1.145-1.253), pubescence on 1st gaster tergite more dilute. Discriminant < 0 [error 0% in 15 workers]. Species with African origin. **9**
5a Very small (CS 366 µm), Scape index larger (SL/CL 0.791). Paramedian and lateral areas of vertex with densely-arranged, deeply impressed, flat-bottomed and very large foveae of 19–23 µm diameter. The largest foveolae show a well-demarcated central ring of 8–9 µm diameter which is connected with the outer ring through 2–4 very fine microcarinulae in 90° cross-wire arrangement, such suggesting a four-leaf clover; in the smaller foveolae the number of microcarinulae may be reduced. Propodeal spines long and thin, rather steep, in profile deviating from longitudinal mesosomal axis by 43°. Petiole in profile with almost linear (only slightly concave) anterior face. Brunei (Figs 16–18). ..... ***nana***
5b Larger (CS 361-470), Scape index smaller (SL/CL 0.682-0.785). Paramedian and lateral vertex with more simple foveolae which are often smaller. Propodeal spines less erect. Concavity of anterior petiolar face deaper. **6**
6a Postpetiole massive (PpH/CS 0.348–0.361). Foveolae on paramedian vertex regular but not densely packed, the interspaces between foveolae delicately longitudinally striate (Fig. 22). With all

measurements in mm, discriminant 150.24*PpH -126.77*CW+167.57*FRS +9.0 > 0 [error 0% in 4 workers] Papua New Guinea (Figs 19–22). ..... ***allonivalis***

6b Postpetiole less massive (PpH/CS 0.268–0.341). Foveolae on paramedian vertex either densely packed and regular or difficult to discern, then more resembling smaller and larger meshes of reticular sculpture. Discriminant <0 [error 0% in 232 workers]. **7**

7a Anterior pronotum in dorsal view with well-developed shoulders (Fig. 23B). Sculpture on head and mesoma very irregular, sculpture on head more resembling a reticulum with smaller and larger meshes, clear foveolae difficult to discern (Fig.27). India (Figs 24–27). ..... ***shagrinata***

7a Anterior pronotum in dorsal view rounded, without shoulders (Fig. 23B). Sculpture on head with clear and regular, densely packed foveolae(Figs 31, 35). **8**

8a With all measurements in mm, discriminant 152.2*PpW-63.79*PoOc-152.2*EYE+83.64*SL-65.39* FRS-100.37*SP-10.35 <0 [error 3.9% in 142 worker individuals and 0% in 51 nest samples with at least two workers]. Note: color type 1 of *wroughtonii*, with the whole ant entirely light yellowish except for a diffuse brown band in the posterior half of 1st gaster tergite is not known in *obscurior*, but color type 2 with entirely dark or blackish brown gaster tergite, typical for *obscurior*, also occurs in 24% of the *wroughtonii* samples. (Figs 28–31). Cosmopolitan tramp species. ..... ***wroughtonii***

8b Discriminant > 0 [error 3.9% in 91 worker individuals and 0% in 33 nest samples with at least two workers]. Color type 1 seems to be absent in this species (Figs 32–35). Cosmopolitan tramp species. ..... ***obscurior***

9a First gaster tergite with strongly developed microreticulum and dense pubescence (Fig. 40). Scape very short (SL/CS <0.737), postocular distance smaller (PoOC/CL <0.432), petiole wide (PeW/CS > 0.285). Sculpture on all body parts stronger. South Africa (Figs 36–40). ..... **sp. SPIT**

9b First gaster tergite with a very delicate microreticulum and less dense pubescence (Fig. 48). Scape longer (SL/CS >0.737), postocular distance larger (PoOC/CL >0.432), petiole narrower (PeW/CS < 0.285). Sculpture on all body parts weaker. **10**

10a Dorsal profile of mesosoma rather linear, metanotal depression very weak (Fig. 42). Distance of spine bases large (SPBA/CS 0.296). Cameroun (Figs 41–43). ..... ***weserka***

10b Dorsal profile of promesonotum and propodeum convex, metanotal depression distinct. Distance of spine bases smaller. **11**

11a Frontal carinae less strongly diverging FL/FR < 1.087. Spine base distance smaller (SPBA/CS <0.256). Ivory Coast (Figs 44–48). ..... ***heinzei* n.sp.**

11b Frontal carinae more strongly diverging FL/FR > 1.087. Spine base distance larger (SPBA/CS >0.256). Ghana (Figs 49–51). ..... **neferka**

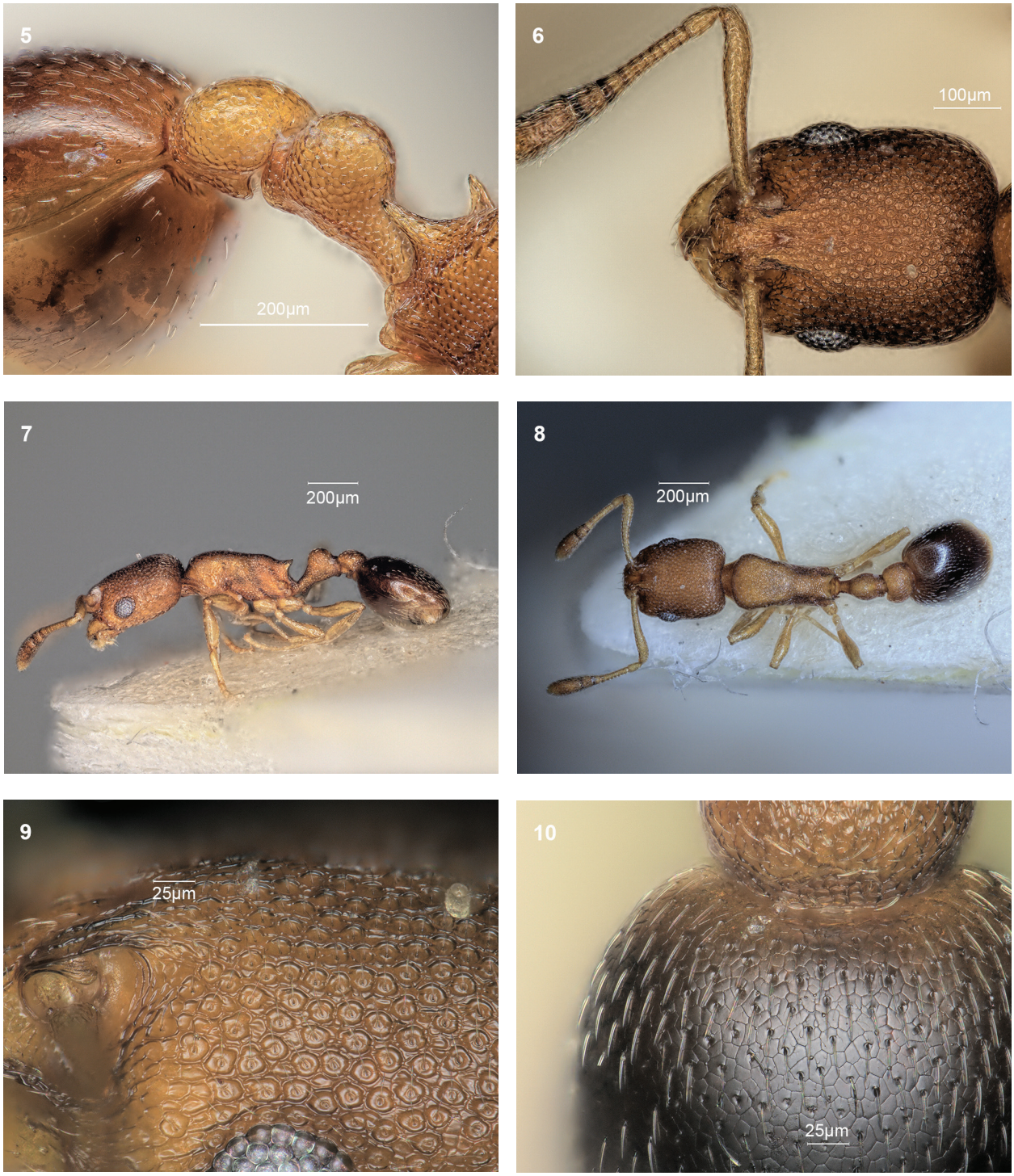


Figure 5. Waist segments of *Cardiocondyla obscurior* in frontolateral view showing the lateral lobe of postpetiolar sternite, Santa Cruz / Galapagos, 1—29 November 2012.

Figure 6–10. *Cardiocondyla yoruba,* Bondoukou / Ivory Coast, 2 April 2019. (**6**) head in dorsal view; (**7**) lateral view; (**8**) dorsal view; (**9**) head surface between inner eye margin and paramedian vertex. (**10**) anterior dorsum of 1st gaster tergite.

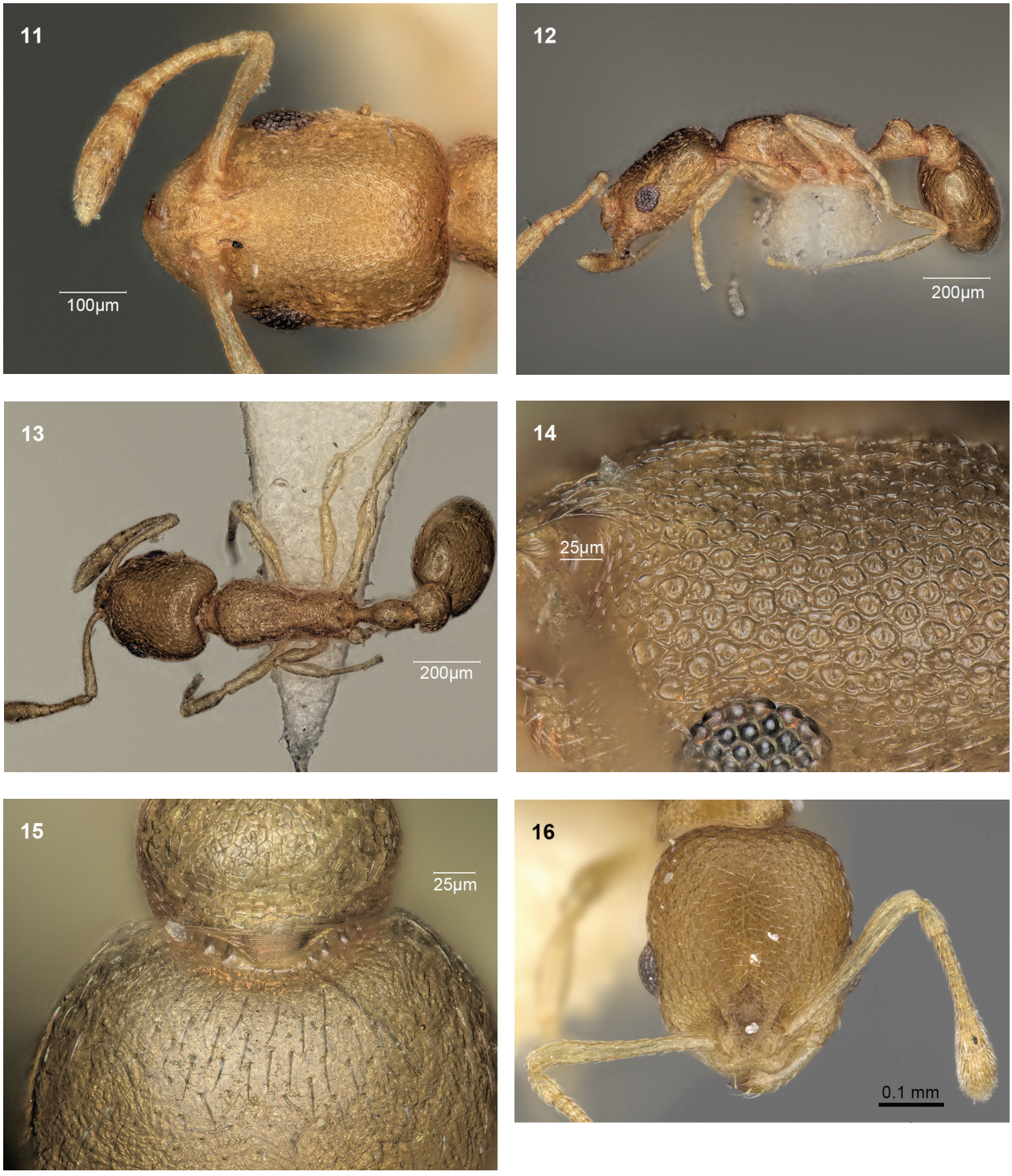


Figure 11–15. *Cardiocondyla yemeni*, type, Sanaa / Yemen, 5 March 1993. (**11**) head in dorsal view; (**12**) lateral view; (**13**) dorsal view; (**14**) head surface between inner eye margin and paramedian vertex. (**15**) anterior dorsum of 1st gaster tergite.

Figure 16. *Cardiocondyla nana*, holotype, Ulu Temburong / Brunei 22 February 1982; from www.antweb.org CASENT0901757, images by Ryan Perry.

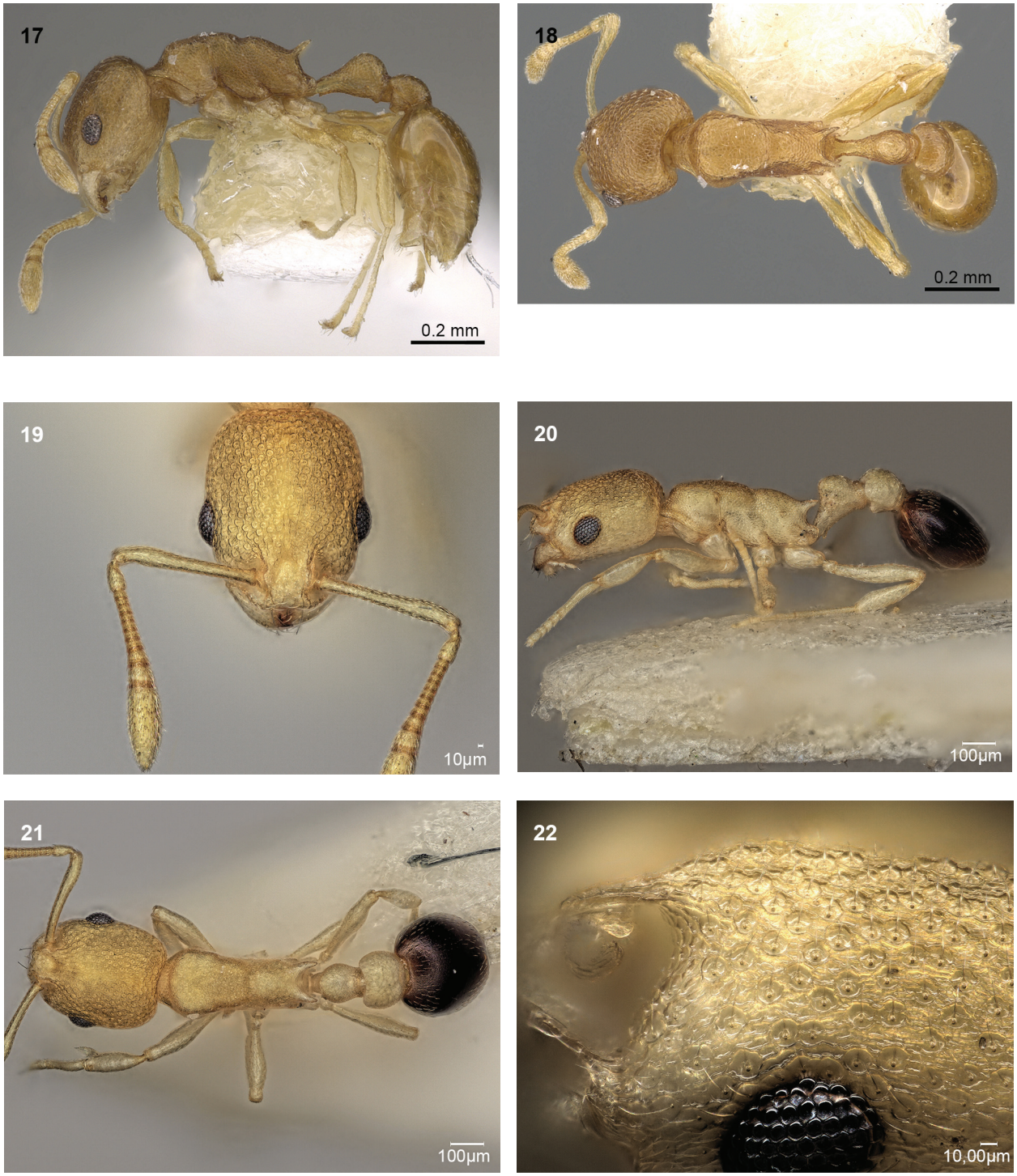


Figure 17–18. *Cardiocondyla nana*, holotype, Ulu Temburong / Brunei 22 February 1982; from www.antweb.org CASENT0901757, images by Ryan Perry. (**17**) lateral view; (**18**) dorsal view.

Figure 19–22. *Cardiocondyla allonivalis*, holotype, Wanang / Papua New guinea, 23 October 2007. (**19**) head in dorsal view; (**20**) lateral view; (**21**) dorsal view; (**22**) head surface between inner eye margin and paramedian vertex.

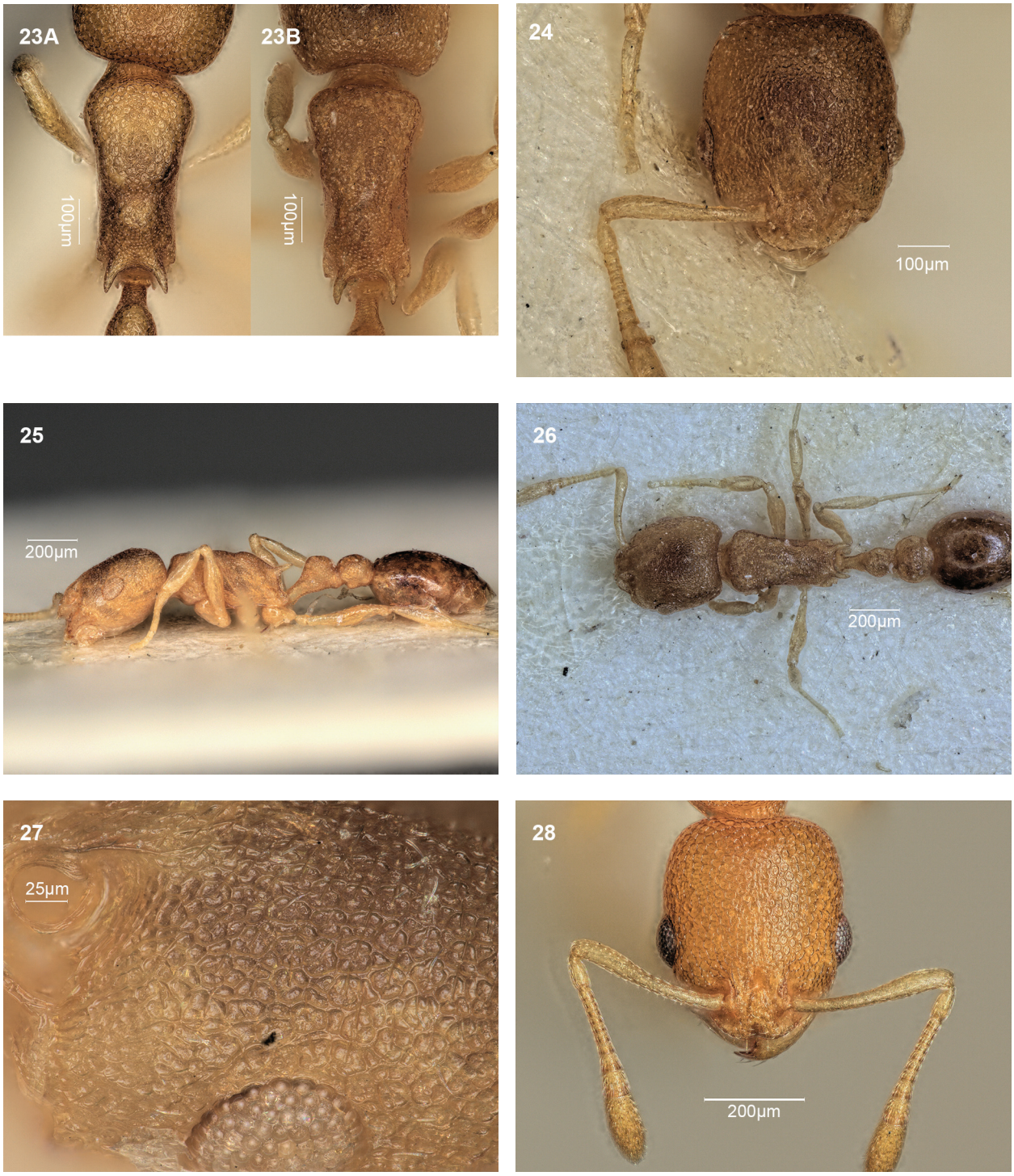


Figure 23. Mesosoma in dorsal view. (**A**) *Cardiocondyla obscurior*, neotype, Nago / Okinawa, 3 June 2003; (**B**) *Cardiocondyla shagrinata,* paratype, South Konkan / India.

Figure 24–27. *Cardiocondyla shagrinata*, paratype, South Konkan / India. (**24**) head in dorsal view; (**25**) lateral view; (**26**) dorsal view; (**27**) head surface between inner eye margin and paramedian vertex.

Figure 28. *Cardiocondyla wroughtonii*, Lundu / Malaysia, 27 May 2007. (**28**) head in dorsal view.

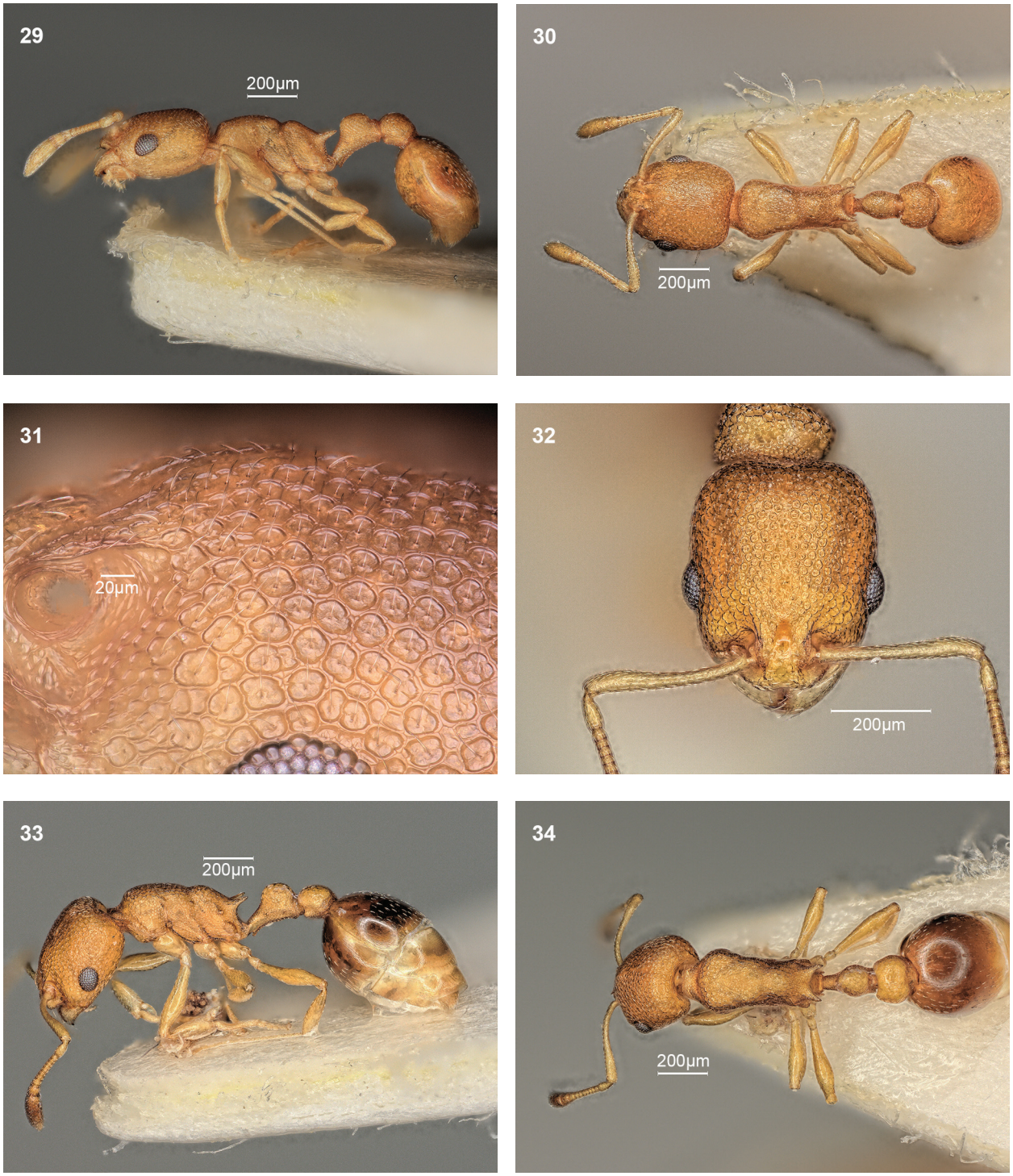


Figure 29–31. *Cardiocondyla wroughtonii*, Lundu / Malaysia, 27 May 2007. (**29**) lateral view; (**30**) dorsal view; (**31**) head surface between inner eye margin and paramedian vertex.

Figure 32–34. *Cardiocondyla obscurior*, neotype, Nago / Okinawa, 3 June 2003. (**32**) head in dorsal view; (**33**) lateral view; (**34**) dorsal view.

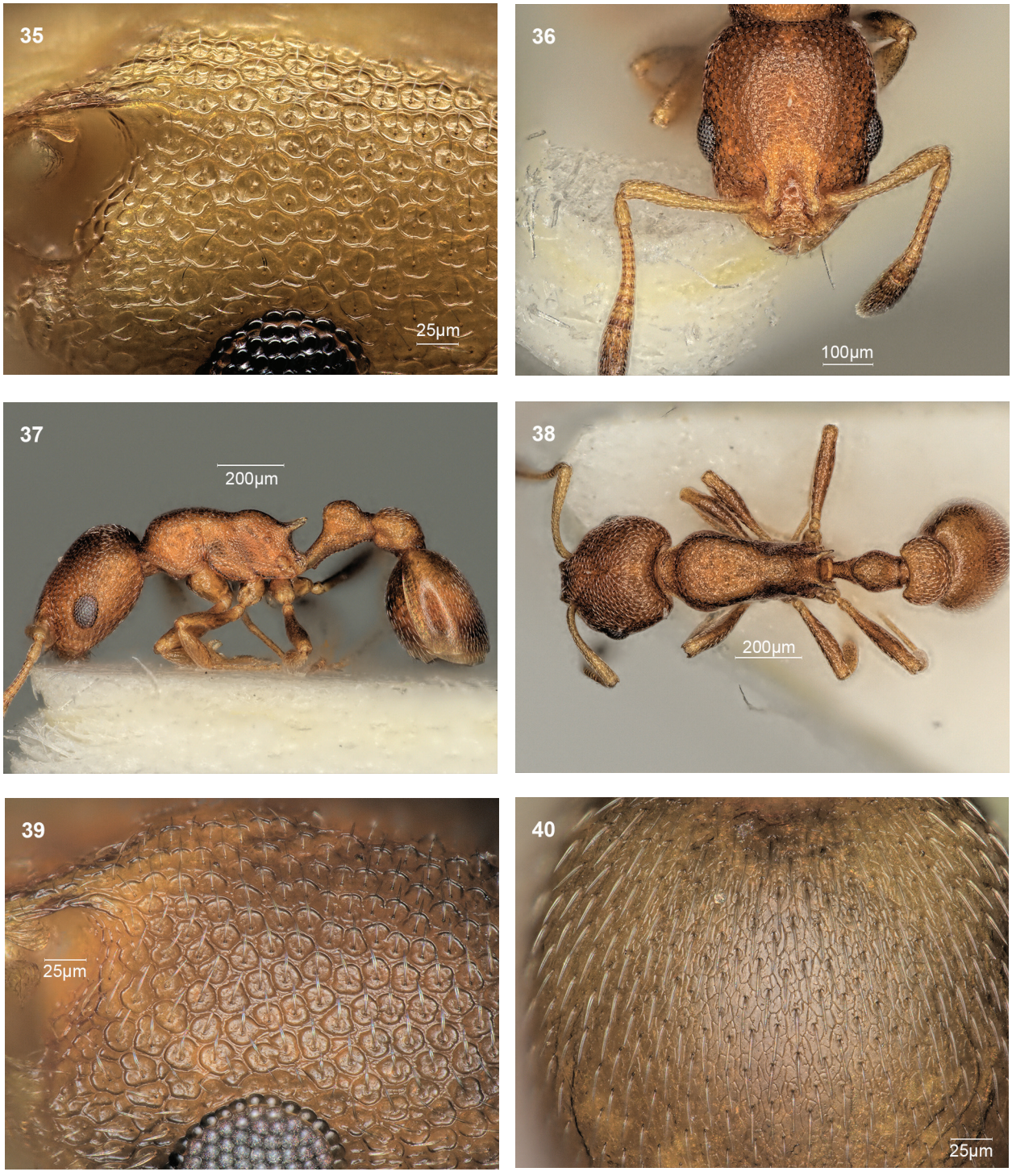
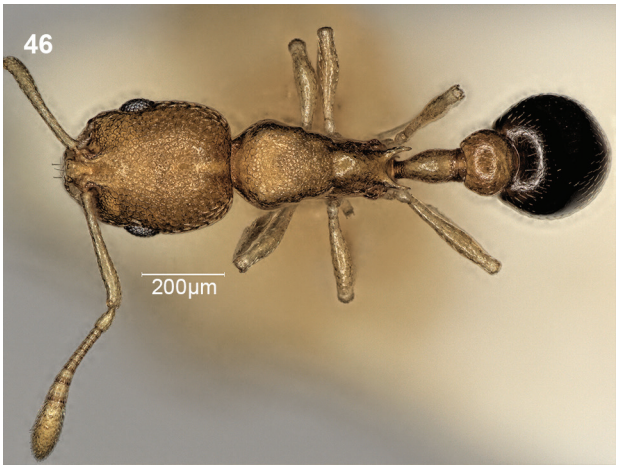


Figure 35. *Cardiocondyla obscurior*, neotype, Nago / Okinawa, 3 June 2003. (**35**) head surface between inner eye margin and paramedian vertex.

Figure 36–40: *Cardiocondyla* sp. SPIT, Spitskop / South Africa, 30 March 2009. (**36**) head in dorsal view; (**37**) lateral view; (**38**) dorsal view; (**39**) head surface between inner eye margin and paramedian vertex. (**40**) anterior dorsum of 1st gaster tergite.



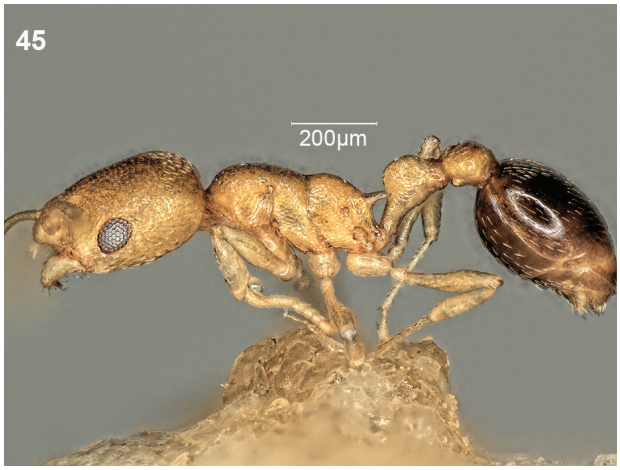
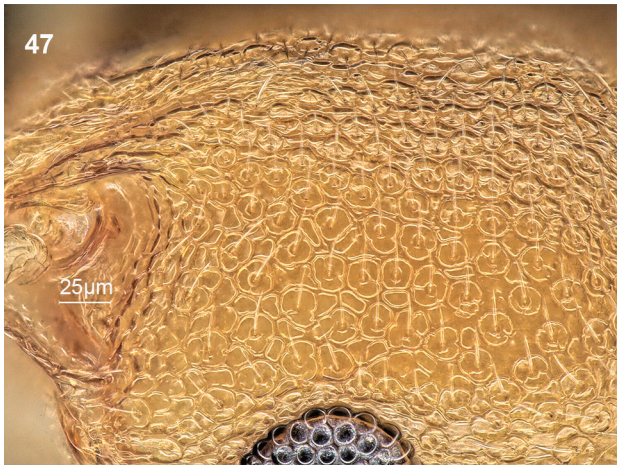
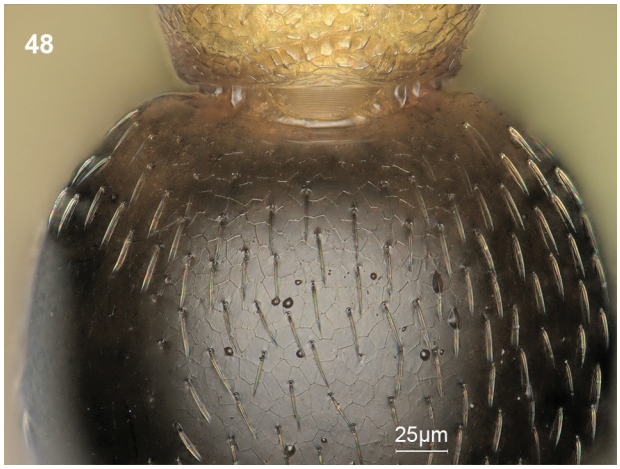


Figure 41–43: *Cardiocondyla weserka*, holotype, Nkoemvon / Kamerun, 1980; from www.antweb.org CASENT0901748, images by Ryan Perry. (**41**) head in dorsal view; (**42**) lateral view; (**43**) dorsal view.

Figure 44–46. *Cardiocondyla heinzei* n.sp., holotype, Comoe / Ivory Coast, 4 April 2019. (**44**) head in dorsal view; (**45**) lateral view; (**46**) dorsal view.





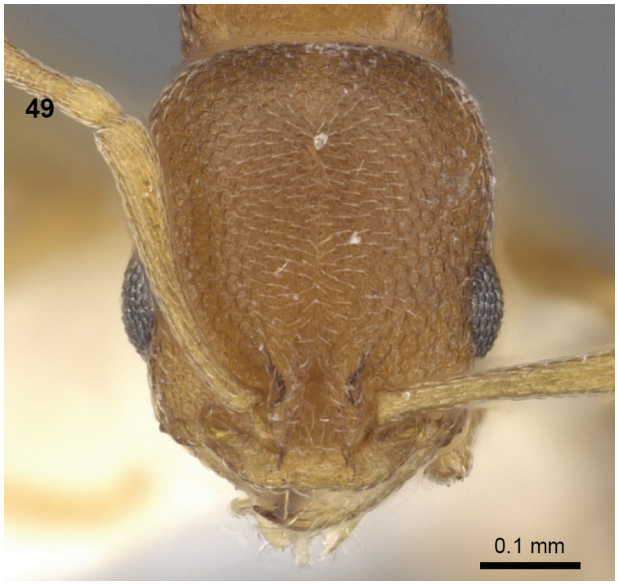


Figure 47–48. *Cardiocondyla heinzei* n.sp., holotype, Comoe / Ivory Coast, 4 April 2019. (**47**) head surface between inner eye margin and paramedian vertex. (**48**) anterior dorsum of 1st gaster tergite.

Figure 49–51: *Cardiocondyla neferka*, holotype, Mampong / Ghana, 10 February 1970; from www.antweb.org CASENT0901747, images by Ryan Perry. (**49**) head in dorsal view; (**50**) lateral view; (**51**) dorsal view.

4.3 Treatment by species

Cardiocondyla wroughtonii (Forel 1890)

Emeryia wroughtonii Forel 1890 [type investigation]

The species has been described from Pune (Poona)/ India. Investigated were the holotype (ergatoid male) and 3 worker paratypes labelled by Forel 'Poona, Wroughton, s^{r} feuiles Eugenia jambolana, B_4', NHM Basel and one worker paratype, labelled by Forel himself 'Wroughtonii Forel, Poona, Wroughton' and by G.Mayr 'Wroughtonii, Forel, Type', NHM Wien. In his original description of *wroughtonii*, Forel erroneously considered the extremely deviating ergatoid male of this species as worker of a separate genus *Emeryia* that he believed to be a social parasite of *Cardiocondyla*. This ergatoid male was found together with workers and females of a *Cardiocondyla* species nesting in the space between the two layers of leaves of *Eugenia jambolana* in Poona /India (Forel 1890). Later Forel corrected his mistake (Forel 1892). Formally, the above-mentioned workers have no paratype status since the original description of *Emeryia wroughtonii* did not directly refer to them. However, their undoubted conspecifity with the holotype and their strong genetic relatedness give them a high taxonomic significance. This worker sample is allocated to the *C. wroughtonii* cluster with p =1.000 if run as wild-card in a LDA (for details see below).

***Cardiocondyla wroughtonii* var. *hawaiensis* Forel 1899 [type investigated]**

This taxon has been described from the island Molokai / Hawaii Archipelago. Investigated was 1 worker type labelled 'C.wroughtonii For. r. hawaiensis Forel type, Iles Sandwich' and 'Molockai Mts., 3000 ft. Perkins IX 1893', MHN Genève. The type specimen is allocated to the *C. wroughtonii* cluster with p = 0.9999 if run as wild-card in a LDA (for details see below).

***Cardiocondyla wroughtonii* subsp. *quadraticeps* Forel 1912 [types investigated]**

This taxon has been described from Singapore. Investigated were 2 gyne and 3 worker syntypes labelled 'Singapore H.Overbeck' and 'Cardiocondyla wroughtonii For quadraticeps For', ZM Berlin. The type workers are allocated to the *C. wroughtonii* cluster with p = 0.9995 if run as wild-card in a LDA (for details see below).

***Cardiocondyla wroughtonii* var. *bimaculata* Wheeler 1929 [types investigated]**

This taxon has been described from Taiwan. Investigated were 5 worker and 1 gyne syntype labelled 'Karashisho Silvestri \ Wm.M.Wheeler \ Cotypes var. bimaculata Wheeler \ M.C.Z.Cotype 1-3 20746', MCZ Cambridge. The type workers are allocated to the *C. wroughtonii* cluster with p = 0.9986 if run as wild-card in a LDA (for details see below).

***Cardiocondyla emeryi* subsp. *chlorotica* Menozzi 1930 [supposed synonymy]**

This taxon has been described in workers and a gyne based on material from Somalia: Ducca Abruzzi, leg. G. Paoli & A. Chiaromonte, October 1926. Types were not investigated. The synonymization supposed here follows Bolton (1982) who, however, had no safe key character at hand to separate *C. wroughtonii* from *C. obscurior*. Hence, this taxon is a junior synonym of either species.

***Cardiocondyla longispina* Karavajev 1935 [types investigated]**

This taxon has been described from Java. Investigated were 5 worker syntypes labelled 'Tjibodas, Java Karavaiev\ 5377. Coll. Karavaievi \ Cardiocondyla longispina Karav. Typus'; IZ Kiev. The type workers are allocated to the *C. wroughtonii* cluster with p = 0.9997 if run as wild-card in a LDA (for details see below).

***Cardiocondyla yamauchii* Terayama 1999 [types investigated]**

Okinawa /Japan 3 worker paratypes from the same sample as holotype: 'Ada, Okinawa-jima Okinawa Pref. 12.VI.1991 K.Yamauchi leg.' and 'Cardiocondyla yamauchii Terayama, 1999, Paratype', SMN Goerlitz. The type workers are allocated to the *C. wroughtonii* cluster with p = 0.9958 if run as wild-card in a LDA (for details see below).

All material examined. Numeric phenotypical data were available in 64 samples (51 nest samples and 17 single-specimen stray samples) with 140 workers. For details see supplementary information SI1, SI2. Excluding single-specimen samples with unclear separation from *C. obscurior*, this material originated from Australia (10 samples), Brunei (1), the Comores (1), Egypt (1), Hawaii (4), India (1), Indonesia (7), Japan (3), Kenia (1), Malaysia (13), Mauritius (3), Nepal (1), Philippines (5), Papua New Guinea (2), Singapore (1), Sri Lanka (1), Taiwan (1), Tanzania (1), Tailand (4), USA (5).

Geographic range. As a tramp species of putatively Southeast Asian origin this species is widely distributed over the tropical regions of the world. However, it has not been confirmed so far for South and Central America where *C. obscurior* is found. Occurrence in buildings in the temperate zone is so far not verified by voucher specimens.

Diagnosis: --Worker (Tab. 1, Figs 28–31, key). Very small and slightly smaller than *obscurior*, CS 410

µm. Head short, CL/CW 1.120. Anterocentral clypeal margin straight or slightly notched; central occipital margin usually straight or with a very weak concavity. Postocular distance large, PoOc/CL 0.440. Frons broad (FRS/CS 0.272), frontal carinae caudal of FRS level parallel (FL/FR 1.008). Eye medium-sized, EYE/CS 0.233. Scape slightly shorter than in *obscurior*, SL/CS 0.772. Promesonotal plane in dorsal view without 'shoulders' due to a strongly convex frontal margin and rather straight lateral margins (Fig. 23A). Metanotal groove in lateral view deep (MGr/CS 3.65 %) and usually with steep anterior and posterior slopes. Propodeal spines longer than in *obscurior* (SP/CS 0.193) and their bases more approached (SPBA/CS 0.278). Petiole narrower and slightly lower than in *obscurior* (PeW/CS 0.277, PeH/CS 0.328), Axis of petiolar peduncle in lateral aspect deviating by 30° from the longitudinal axis of the petiole node. Postpetiole narrower and lower than in *obscurior* (PpW/CS 0.437, PpH/CS 0.303), the sternite anterolaterally with a rounded lobiform protrusion on each side which clearly elevates above the level of median surface of sternite; the surface of the sternite thus appearing deeply concave in frontal view. Whole head and mesosoma without any notable rugosity. Paramedian and lateral vertex with deep (sometimes shallower) foveolae of 17–21 µm diameter which are frequently arranged in dense honey-comb arrangement and show an inner elevation around the hair bases of 6–9 µm diameter (Fig. 31); median vertex with slightly smaller and weaker foveolae, occasionally weakly foveolate-carinulate. Whole surface of mesosoma and waist densely foveolate-reticulate, the meshes with lower diameters than on vertex (Figs 29, 30). Pubescence on first gaster tergite moderately long and dilute (PLG/CS 6.3 %, sqPDG 5.05). Color dimorphism. Light morph (76 % of samples): whole ant entirely light yellowish except for a diffuse brown band in the posterior half of 1st gaster tergite; this band may be interrupted in the centre to form 2 separated lateral patches (as seen in Wheeler´s var. *bimaculata*), PigG1 9.5 ± 8.2 [0, 45] % n= 108. Dark morph (24 % of samples): Head, mesosoma, waist, and appendages light yellowish brown; funicular club blackish brown; 1st gaster tergite and sternite dark brown, the following segments substantially lighter, PigG1 86.8 ± 19.1 [55, 100] %, n=34.

Taxonomic comments and clustering results. *C. wroughtonii* is extremely similar to *C. obscurior* and the occurrence of a dark morph in *wroughtonii* restricts the use of pigmentation for species separation. Species hypotheses were formed in 84 samples of both species with 205 worker individuals under exclusion of single-specimen samples. In the first step of analysis, the 15 characters CS, CL/CW, PoOc/CL, SL/CS, EYE/CS, FRS/CS, SPBA/CS, SP/CS, PeW/CS, PeH/CS, PPW/CS, PpH/CS, MGr/CS, sqPDG and PLG/CS were run in the exploratory data analyses NC-Ward, NC-NMDS.kmeans and PCA. Hypotheses were fixed in the controlling LDA when the classifications in the three exploratory data analyses coincided whereas samples with controversial classification were run as wild-cards. In the next run of the LDA the corrected classifications were accepted but now the type samples were run as wild-cards. The posterior probabilities for allocation to the *C. wroughtonii* cluster were 1.0000 in the types of *wroughtonii*, 0.9999 in the type of *hawaiensis*, 0.9997 in the types of *longispina*, 0.9995 in the types of *quadraticeps*, 0.9984 in the types of *bimaculata* and 0.9958 in the types of *yamauchii*. The posterior probabilities for allocation to the *C. obscurior* cluster were 0.9993 in the neotype series of *obscurior* and 0.9992 in the types of *bicolor*. As a third step, a stepwise character reduction to CS, CL/CW, SL/CS, EYE/CS, FRS/CS, SP/CS and PPW/CS was performed. This increased the agreement of the exploratory data analyses with the final species hypothesis determined by the controlling LDA to 96.4 % in NC-Ward, 98.8 % in NC-NMDS.kmeans, 98.8 % in NC-part.kmeans (Fig. 52) and to 98.8 % and in the PCA (Fig.53). This is a mean error in four forms of analysis of only 1.8 %. In laboratory experiments, males of *C. obscurior* and gynes of *C. wroughtonii* produced hybrids but the opposite mating combination so far not (K. Yamauchi pers. comm. 2000). Hybridisation is supposed to be rare or absent under natural conditions as concluded from the strong separation of the clusters. However, the available sample size, in particular the low number of 2.4 workers per sample, makes assessment of hybridization frequency difficult. There is so far only one suggestion on a possible hybridization: the only sample of *obscurior* with a gaster pigmentation corresponding to light morph of *wroughtonii* (SaNo 1072 Singapore) was allocated to the *obscurior* cluster with p=0.9456 if run as a wild-card in a LDA of the reduced 7-characters data set and was placed by the PCA in a marginal position (Fig. 53). It was found under the bark of a tree in 1.50 m height which supports the determination by the LDA.

Biology. In contrast to its sibling species *C. obscurior*, it was reported to nest near to or on the ground; it was found in hollow stems of dead *Eulalia* grasses (Okinawa), in a dead twig on the ground (New Orleans/USA), between layers of *Eugenia jambolana* leaves (India), in litter (Sulawesi), and 'under leaves in a silk patch' (Tanzania). Nest populations are polygynous and adopt alien queens. There is polyphenism showing winged and wingless (ergatoid) males. The wingless males have sickle-shaped mandibles used to kill male callows or pupae whereas they besmear adult rivals with a secretion that elicits worker aggression.

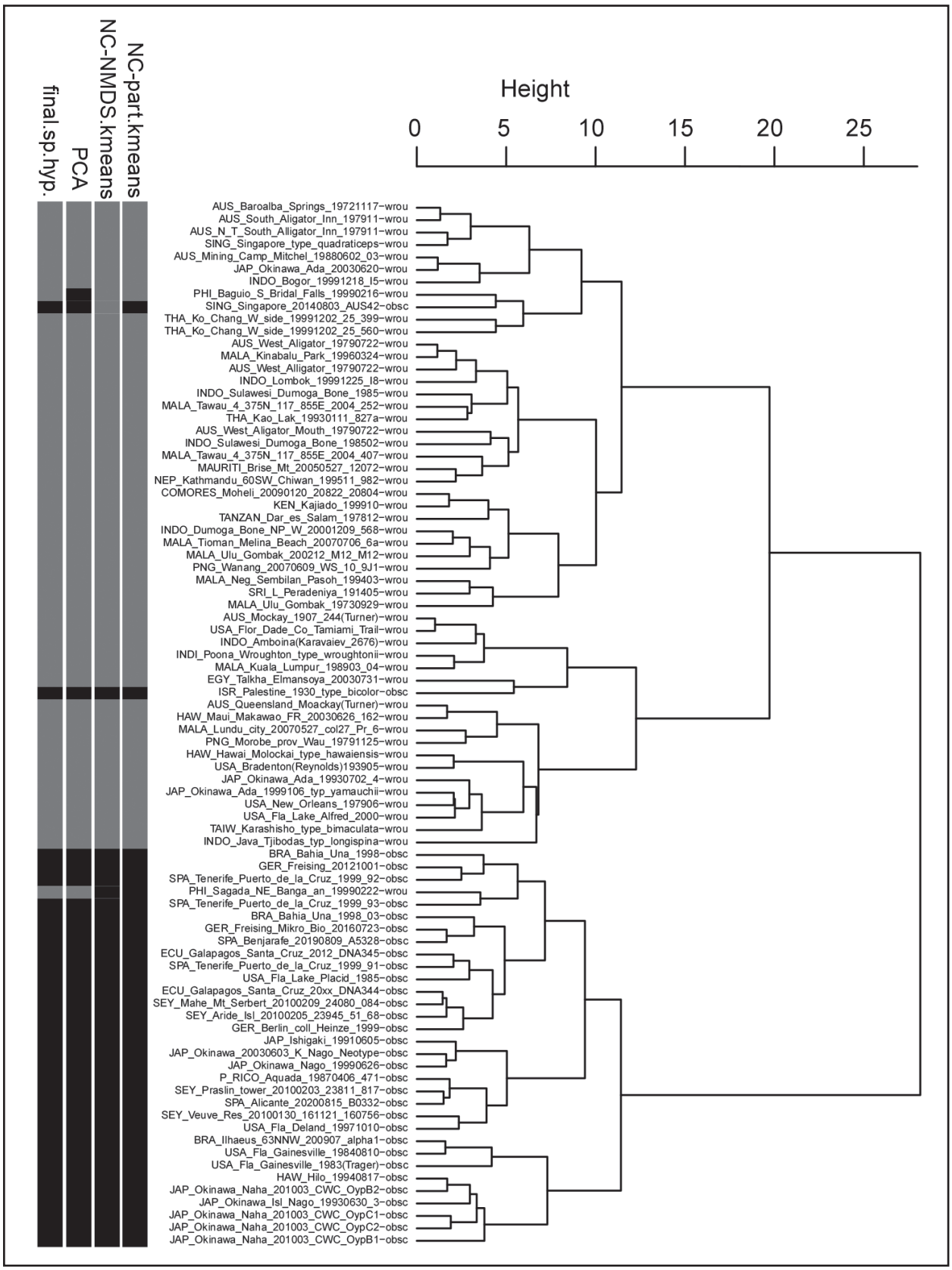


Figure 52. Classification of 84 nest samples of *Cardiocondyla wroughtonii* and *C. obscurior* by the exploratory data analyses NC-Ward (hierarchical), NC-part.kmeans, NC-NMDS.kmeans and PCA based on 7 morphometric characters taken in 205 worker individuals. The mean error of the four exploratory data analyses relative to the controlling LDA (final.sp.hyp) is 1.8%.

Cardiocondyla obscurior Wheeler 1929

***Cardiocondyla wroughtonii* var. *obscurior* Wheeler 1929 [neotype fixed]**

The species has been described from Taiwan (Formosa). The three gynes from the MCZ collection, investigated by Seifert (2003) and labelled by Wheeler 'Kagi, Formosa 11.1.1927 R.Takahashi Wm.M.Wheeler\ Cotypes\ var. obscurior Wheeler' cannot be considered as genuine type material. These gynes were the basis of a second description, published 7 March 1930 (Wheeler 1930). Wheeler's first description, published 22 October 1929, was based upon one worker and a headless dealate queen collected at Eisei/ Formosa (Wheeler 1929). These specimens were not available from MCZ Cambridge and are believed to be lost. Seifert (2003) used Wheeler's statements on the extent of dark gaster pigmentation to conclude on the identity of *obscurior*. However the material gathered since then showed that the extent of pigmentation typical for *obscurior* (PigG1 > 75%) also occurs in 17% of the *wroughtonii* workers. It is therefore not advisable to use of pigmentation for species discrimination and/or interpretation of original descriptions. After Seifert (2003) provided measures for separation of the two species, a lot of publications recognizing the heterospecificity were released (Schrempf & Heinze 2006; Cremer et al. 2012, Bressan et al. 2015, Schrader et al. 2015, Klein et al. 2016a, Klein et al. 2016b, Heinze 2017, Oettler et al. 2018, Ün et al. 2021, Schultner et al. 2023). As we have a tradition for the correct use of the name *obscurior* and in order to safe a stable nomenclature, a neotype fixation is reasonable. Accordingly, a neotype was fixed in the top specimen of a pin with three workers labelled 'JAP: 26.59°N, 127.98°E Okinawa Isl. Nago leg. Yamauchi 2003.06.03-K-Nago'. Depository: SMN Görlitz. The neotype sample is allocated to the *C. obscurior* cluster with p =0.9993 if run as wild-card in a LDA (see above).

***Cardiocondyla bicolor* Donisthorpe 1930 [types investigated]**

This taxon was described from Israel. Investigated was the worker holotype labelled 'Palestine: Drs. D.Scheinkin & J.Carmin B.M.1930-163\ On Ficus sycamore\ bicolor Donisthorpe\ Type « and one worker paratype labelled 'Palestine: Drs. D.Scheinkin & J.Carmin B.M.1930-163\ On Ficus sycamore\ bicolor Donis.\ Cotype'. Depository: BMNH London. The type sample is allocated to the *C. obscurior* cluster with p =0.9992 if run as wild-card in a LDA (see above).

All material examined. Numeric phenotypical data were available in 43 samples (35 nest samples and 9 single-specimen stray samples) with 93 workers. For details see supplementary information SI1, SI2. Excluding single-specimen samples with unclear separation from *C. wroughtonii*, this material originated from Brasil (3

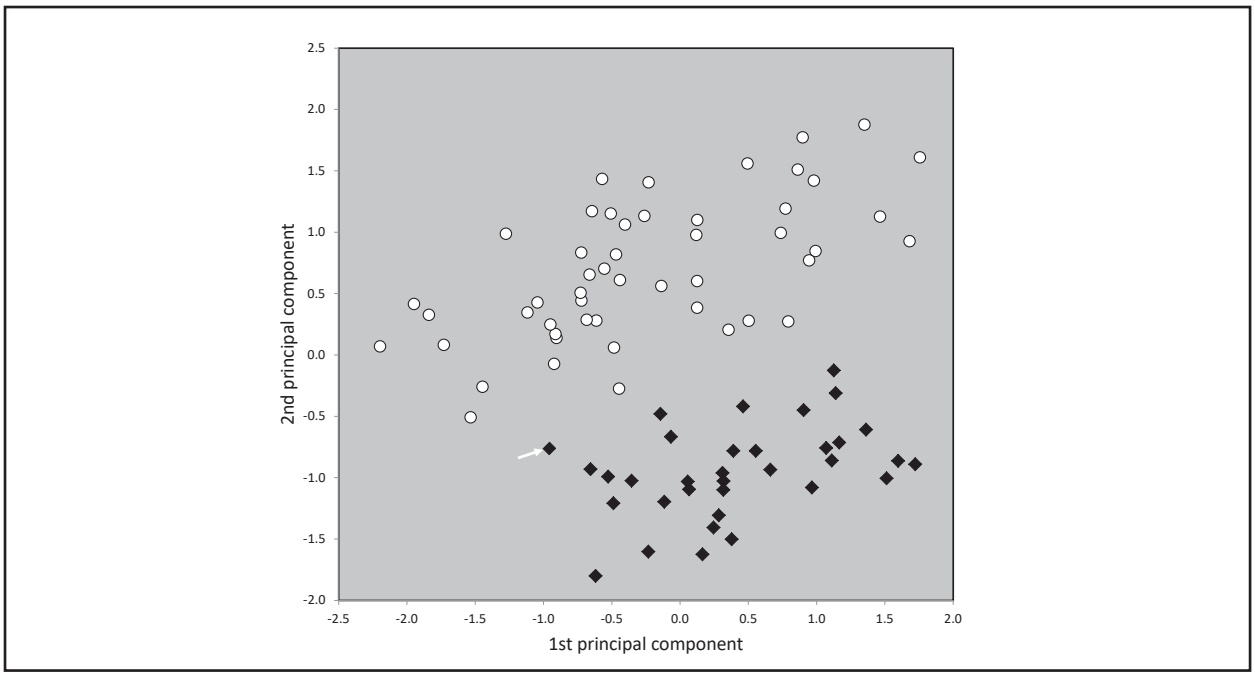


Figure 53. Principal component analysis of 84 nest samples of *Cardiocondyla wroughtonii* and *C. obscurior* based on 7 morphometric characters taken in 205 worker individuals. The arrow points to the sample determined as *C. obscurior* by a wild-card LDA with p = 0.9456 which, however, showed a pigmentation typical for *C. wroughtonii*. The mean error of the four exploratory data analyses relative to the controlling LDA (final.sp.hyp) is 1.8%.

samples), Bermuda (1), Ecuador (2), Germany (3), Hawaii (2), India (1), Israel (1), Japan (10), Micronesia (1), Puerto Rico (2), Seychelles (5) Singapore (1), Spain (5), USA (4)

Geographic range. As a tramp species of putatively Southeast Asian origin this species is, like *wroughtonii*, widely distributed over the tropical regions of the Old and New World. However, with exception of a finding from Singapore, there are no verified vouchers from the Indo-Malayan and Australasian regions where *C. wroughtonii* is dominant. It has also been found in buildings in the temperate zone (Germany).

Diagnosis: --Worker (Tab. 1, Figs 32–35, key). Very small and slightly larger than *wroughtonii*, CS 430 µm. Head short, CL/CW 1.111. Anterocentral clypeal margin straight or slightly notched; central occipital margin usually straight or with a very weak concavity. Postocular distance large, PoOc/CL 0.435. Frons broad (FRS/CS 0.268), frontal carinae caudal of FRS level parallel (FL/FR 1.011). Eye medium-sized, EYE/CS 0.229. Scape short and slightly longer than in *wroughtonii*, SL/CS 0.772. Metanotal groove in lateral view deep (MGr/CS 3.65%) and usually with steep anterior and posterior slopes. Promesonotal plane in dorsal view without 'shoulders' due to a strongly convex frontal margin and rather straight lateral margins (Fig. 34). Propodeal spines shorter than in *wroughtonii* (SP/CS 0.185) and their bases less approached (SPBA/CS 0.292). Petiole wider and slightly higher than in *wroughtonii* (PeW/CS 0.292, PeH/CS 0.338), axis of petiolar peduncle in lateral aspect deviating by 30° from the longitudinal axis of the petiole node. Postpetiole wider and higher than in *wroughtonii* (PpW/CS 0.459, PpH/CS 0.314), the sternite anterolaterally with a rounded lobiform protrusion on each side which clearly elevates above the level of median surface of sternite; the surface of the sternite thus appearing deeply concave in frontal view. Sculpture on head, mesosoma and waist similar to *wroughtonii* . Pubescence on first gaster tergite moderately long and dilute (PLG/CS 6.2%, sqPDG 5.13). The dark color morph, which resembles the dark color morp of *wroughtonii*, is found in 98% of the samples – one sample, possibly hybrids, showed a pattern similar to the light color morph of *wroughtonii*.

Taxonomic comments. The morphological separation from *C. wroughtonii* is described above.

Biology. In contrast to *C. wroughtonii*, *C. obscurior* was reported to nest in cavities of bushes and trees 2–5 m above the ground level; it was found in dead twigs of trees such as *Erythrina variegata* (Okinawa), in dwarf coconuts (Brazil), galls of *Acacia* trees (Brazil), between crippled-curled leaves of a Citrus tree (Brasil), in a dead twig on a tree (Florida), on a *Ficus* tree (Israel), in the gall of a *Tamarix* bush (Israel), below the bark of strong trees (Tenerife) and in the cavity of a coconut high in the tree (Zanzibar). Demography and behavior of nest populations as well as male polyphenism and behavior are the same as in *C. wroughtoni* (Heinze 2017). Errbii et al. (2021) have shown that populations of *Cardiocondyla obscurior* belong to two distinct lineages, a lineage so far only found in Latin America and a more cosmopolitan Old World lineage. A strong genetic differentiation of these lineages began latest 40,000 generations ago but introgression from the Old World lineage is a dominant source of genetic diversity in the Latin America lineage and is likely to contribute to the adaptive potential of the Latin America lineage. The lineages are infected by different *Wolbachia* strains, one causing cytoplasmic incompatibility (Ün et al. 2021).

Cardiocondyla shagrinata Seifert 2003

***Cardiocondyla shagrinata* Seifert 2003**
[type investigation]

This taxon has been described from India. Investigated was the holotype worker labelled by Forel '*C.Wroughtonii Forel € South Konkan (Wroughton)* I/10', MZ Lausanne; and two 2 paratype workers with the same labelling; SMN Görlitz.

All material examined. Only the type series is known.

Geographic range. The type locality is situated at 16.42°N, 73.390°E and 100 m a.s.l.

Diagnosis: --Worker (Tab. 1, Figs 23–27, key). Very small, CS 426 µm. Head very short, CL/CW 1.099. Anteromedian clypeal margin notched, median occipital margin in 2 of 3 specimens gently excavated. Postocular distance large, PoOc/CL 0.427. Frons broad (FRS/CS 0.282), frontal carinae immediately behind the FRS level slightly diverging caudad. Eye small, EYE/CS 0.222. Scape short, SL/CS 0.760. Promesonotal plane in dorsal view with a rather straight frontal margin and more concave lateral margins resulting in pronounced pronotal 'shoulders' (Fig. 23B) – in *wroughtonii* and *obscurior*, no 'shoulders' are developed due to a strongly convex frontal margin and rather straight lateral margins. Metanotal groove in lateral view deep (MGr/CS 3.21%) and with steep anterior and posterior slopes. Propodeal spines moderately long (SP/CS 0.184) and acute, slightly diverging and incurved in dorsal view and with large basal distance (SPBA/CS 0.292). Petiole rather narrow and moderately high (PeW/CS 0.279, PeH/CS 0.333). Axis of petiolar peduncle in lateral aspect deviating by 30° from the longitudinal axis of the petiole node. Postpetiole moderately wide and high (PpW/CS 0.446, PpH/CS 0.308), with a bilateral pair of anteroventral corners (but weaker than usually seen in *wroughtonii* and *obscurior*); in dorsal view, the strongly

convex sides meet with the concave anterior margin in a blunt corner and converge significantly more than in *wroughtonii*. Sculpture on head and mesosoma compared to *wroughtonii* and *obscurior* very irregular and with smaller meshes of reticular sculpture (Fig. 27), without the regularly arranged, large and clearly demarcated foveolae seen in the former species. Lateral mesosoma and waist with dense reticulum the meshes of which have an inner diameter of 4–5 µm. Pubescence on first gaster tergite moderately long and dilute (PLG/CS 6.2%, sqPDG 4.87). Head, mesosoma, waist, and appendages more dirty yellowish brown compared to *wroughtonii* and *obscurior*.

Taxonomic comments. Using the 16 standard morphometric characters shown in Tab. 1, *C. shagrinata* is almost inseparable from *wroughtonii* and *obscurior* and is apparently closely related. An easy separation from these species is given by the strong differences in sculpture of head and mesosoma and the pronounced pronotal shoulders.

Biology. Unknown.

Cardiocondyla nana Seifert 2003

***Cardiocondyla nana* Seifert 2003 [type investigation]**

This taxon has been described from Brunei. Investigated was the holotype worker labelled 'BRUNEI: Ulu Temburong L.P.-283.m.T. 22.ii.82.MC.Day', depository BMNH London.

All material examined. Only the type specimen is known.

Geographic range. The type locality is situated at 1.47°S, 123.559°E and 12 m a.s.l.

Diagnosis: --Worker (Tab. 1, Figs 16–18, key). Extremely small, CS 366 µm. Head extremely short, CL/CW 1.069. Median third of anterior clypeal margin deeply, median third of occipital margin slightly concave. Postocular distance large, PoOc/CL 0.464. Frons moderately broad (FRS/CS 0.266), frontal carinae diverging caudad. Eye without any microsetae and small, EYE/CS 0.220. Scape rather long, SL/CS 0.818. Metanotal groove in lateral view relatively deep (MGr/CS 2.50%). Propodeal spines long and thin, rather steep, in profile deviating from longitudinal mesosomal axis by 43° (SP/CS 0.192), in dorsal view strongly diverging and their bases moderately wide (SPBA/CS 0.277). Petiole rather narrow and moderately high (PeW/CS 0.264, PeH/CS 0.336); in profile with almost linear (only slightly concave) anterior face and semicircular dorsum; in dorsal view with rather slender peduncle and almost globular node, which is slightly longer than wide. Postpetiole moderately wide and low (PpW/CS 0.426, PpH/CS 0.289); the sternite anterolaterally with a rounded lobiform protrusion on each side which clearly elevates above the level of median surface of sternite; the surface of the sternite thus appearing deeply concave in frontal view. Postpetiole in dorsal view with a concave anterior margin and convex sides. Anterior clypeus smooth, not shining. Frontal laminae and anteromedian vertex with weak microsculpture, consisting of an irregular mixture of corrugated, foveolate, and carinulate elements. Paramedian and lateral areas of vertex with a unique sculpture: densely-arranged, deeply impressed, flat-bottomed and very large foveae of 19–23 µm diameter. The largest foveolae show a well-demarcated central ring of 8–9 µm diameter which is connected with the outer ring through 2–4 very fine microcarinulae in 90° cross-wire arrangement, such suggesting a four-leaf clover; in the smaller foveolae the number of microcarinulae may be reduced. Whole lateral area of mesosoma, anterior area of pronotum, and dorsal area of propodeum strongly microreticulate; dorsal area of promesonotum similarly foveate as paramedian vertex. Longitudinal sculpture on whole mesosoma, including metapleural gland bulla, completely absent. Petiole strongly microreticulate, postpetiole shining, very finely microreticulate. Pubescence on first gaster tergite moderately long and very dilute (PLG/CS 6.29%, sqPDG 5.60). All body parts light-yellowish.

Taxonomic comments. This species is not to confuse due to extremely small size, the extremely low CL/CW and the large characteristic foveolae on vertex.

Biology. Unknown.

Cardiocondyla allonivalis Seifert 2023.

***Cardiocondyla allonivalis* Seifert 2023**
[type investigation]

This taxon has been described from Papua New Guinea. Investigated was the Holotype and one paratype worker on separate pins, both labelled 'PNG: 5.25°S, 145.267°N, Wanang, Sogeram riv. 95 m, Bait trap – ground – D4, coll. Janda 2007.10.23'; depository SMN Görlitz.

All material examined. Examined were four samples with five workers from Papua New Guinea – three samples through direct stereomicroscopic evaluation and one sample through photo evaluation of the specimen CASENT0914964 in www.antweb.org . For details see supplementary information SI1, SI2.

Geographic range. The species is so far only known from sea level up to 350 m in four sites in Papua New Guinea: Cape Wom (3.533°S, 143.583°E); Wanang (5.250°S, 145.267°E), Goldie River (9.30°S, 147.42°E) and Popondetta (8.77°S, 148.24°E).

Diagnosis: --Worker (Figs 19–22, Tab. 1, pictures CASENT0914964 in ww.antweb.org): Very small size,

CS 380. Head moderately long (CL/CW 1.137); with maximum CL and CW in visual plane, its posterior margin straight or very slightly concave and anterior clypeal margin slightly concave. Postocular distance rather large, PoOc/CL 0.440. Scape rather long, SL/CS 0.808. Eye relatively large, EYE/CS 0.242. Frons rather narrow with short and almost parallel frontal carinae, FRS/CS 0.299, FL/FR 1.017. Mesosoma slender; dorsal profile of promesonotum and propodeum slightly convex but with a notable metanotal depression. Anterior pronotum in dorsal view rounded, without pronounced corners. Propodeal spines short (SP/CS 0.185), in dorsal view slightly diverging, in lateral view nearly straight and their axis deviating 26–28° from longitudinal axis of mesosoma. Petiole wide and high (PeW/CS 0.319, PeH/CS 0.363), in lateral view with a short peduncle, a concave anterior margin, a weakly convex dorsum of node that more or less linearly slopes down to caudal cylinder; petiole in dorsal view with a semiglobular node which is slightly wider than long. Postpetiole moderately wide and very high (PpW/CS 0.470, PpH/CS 0.356), in dorsal view much wider than long and with a concave anterior and slightly convex posterior margin when these margins are adjusted to the same focal level; the sternite anterolaterally with a rounded lobiform protrusion on each side which clearly elevates above the level of median surface of sternite; the surface of the sternite thus appearing deeply concave in frontal view. Whole surface of dorsal head with circular foveolae that show a flat central tubercle, mean dFov 15.5 µm; the interspaces between foveolae on vertex smaller than foveolar diameter and delicately longitudinally striate (Fig. 22). Microsculpture on dorsum of mesosoma weaker than on vertex, microreticulate-corrugated and without foveolae; lateral mesosoma microreticulate. Petiole laterally finely microreticulate, dorsally more microcorrugated. Postpetiole finely microcorrugated and in overall appearance matt. Basal part of 1st gaster tergite very finely microreticulate and appearing rather shiny at lower magnifications. Pubescence on 1st gaster tergite of medium length and rather dilute (PLG/CS 6.44%, sqPDG 4.36]. Gaster jet black and all remaining body parts excluding the eyes very pale yellowish brown.

Taxonomic comments. As a combination of high and wide postpetiole, long scape and (probably) diagnostic coloration, *C. allonivalis* is not to confuse.

Biology. One nest was found by P.S. Ward in soil of a semi-dry littoral forest.

Cardiocondyla heinzei n.sp.

Etymology: the name is given in honor of Jürgen Heinze wo has done and supervised outstanding research on the fascinating biology of *Cardiocondyla* ants over three decades.

Type material:

Holotype worker labelled 'IVO: 8.7703°N,3.7897°W, Comoé Res. Station, 191m, foragers on path halfway between station and river, Heinze 2019.04.04 –CI 18', 'SMNG20240630' [unique specimen identifier]; three worker paratypes with same labelling on another pin; three worker paratypes labelled 'IVO: 8.84028°N, 3.77111°W, Comoé Park, Iringo River 202 m, Heinze 2019.04.06 –CI 45'; two worker paratypes labelled 'IVO: 8.7703°N, 3.7897°W, Comoé Res. Station, 191m, foragers on path halfway, between station and river, Heinze 2019.04.07 –CI 55'; depository SMN Görlitz.

All material examined. Only the three type samples from Ivory Coast were available.

Geographic range. Only known from the two type localities in Ivory Coast.

Diagnosis: --Worker (Tab. 2, Figs 44–48, key). Extremely small, CS 377 µm. Head elongated, CL/CW 1.189. Median third of anterior clypeal margin slightly concave, median third of occipital margin straight. Postocular distance large, PoOc/CL 0.457. Frons very narrow (FRS/CS 0.219), widening frontad (FL/FR 1.063), caudal of FRS level parallel. Eye without any microsetae and rather smalll, EYE/CS 0.232. Scape moderately long, SL/CS 0.786. Metanotal groove in profile in absolute terms rather deep (MGr/CS 3.25%) but with shallow slopes to mesonotum and propodeum. Prododeal spines long (SP/CS 0.201), thin and acute; in profile deviating from longitudinal mesosomal axis by only 25°, in dorsal view slightly diverging and and slightly incurved; their bases narrow (SPBA/CS 0.240). Petiole very narrow and moderately high (PeW/CS 0.234, PeH/CS 0.333); in lateral view with a concave anterior face and a long weakly convex dorsal profile; petiole in dorsal view very slender, its node 1.5 fold as long as wide and narrowing frontad. Postpetiole rather wide and low (PpW/CS 0.454, PpH/CS 0.276); the sternite anterolaterally with a rounded lobiform protrusion on each side which clearly elevates above the level of median surface of sternite; the surface of the sternite thus appearing deeply concave in frontal view. Postpetiole in dorsal view with a concave anterior margin and convex sides. Anterior clypeus with fine transverse rugulae. Vertex with densely-arranged, flat-bottomed and moderately large foveolae (dFov 16.7). The largest foveolae show a flat tubercle around the hair base of 6–8 µm diameter which is sometimes connected with the outer ring through 1–2 fine microcarinulae (Fig. 47). Whole lateral area of mesosoma microreticulate, promesontum foveolate-reticulate. Petiole microreticulate, postpetiole more shiny. First gaster tergite with a rather long and dense

pubescence (PLG/CS 7.12 %, sqPDG 4.14) and a weak microreticulum (Fig. 48). All body parts yellowish with exception of the blackish brown gaster.

Taxonomic comments. As a combination of large CL/CW and small PeW/CS and FRS/CS not confuse with other members of the *wroughtonii* group.

Biology. The workers foraged on ground in both open and woody situations.

Cardiocondyla sp. SPIT

This species of the *Cardiocondyla wroughtonii* group is intended to be validly described by Peter Hawkes (pers. com. 2024) based on a larger sample size. I describe it here the morphological characters under a taxonomically invalid code designation.

All material examined. Only one sample labelled 'S AFRICA Limpopo Province, Spitskop 333 portion 12, 811 m 24.80525 S 30.14368 E, P. Hawkes, J. Fisher, 30. iii.2009 P3-SS-25', 'Bushveld, Net sweeping' and 'Cardiocondyla AFRC-LIM-01', depository SMN Görlitz.

Geographic range. Only known to me from the a single locality (24.80525°S, 30.14368°E, 811 m) in South Africa.

Diagnosis: --Worker (Tab. 2, Figs 36–39, key). Small, CS 409 µm. Head elongated, CL/CW 1.162. Median third of anterior clypeal margin slightly concave, median third of occipital margin straight or very feebly concave. Postocular distance small, PoOc/CL 0.415. Frons very wide (FRS/CS 0.277), widening frontad (FL/FR 1.097). Eye moderately large, EYE/CS 0.244 and with microsetae of 4–6 µm length. Scape shorter than in any species of the *wroughtonii* group, SL/CS 0.694. Metanotal groove in profile in absolute terms rather deep (MGr/CS 3.29 %) but with shallow slopes to mesonotum and propodeum. Prododeal spines rather long (SP/CS 0.189), thin and acute; in profile deviating from longitudinal mesosomal axis by only 25°, in dorsal view slightly diverging; their bases rather narrow (SPBA/CS 0.257). Petiole wide and high (PeW/CS 0.304, PeH/CS 0.369); in lateral view with a concave anterior face and a conspicuous node with a convex dorsal profile; petiole node in dorsal view as long as wide and slightly narrowing frontad. Postpetiole very wide and high (PpW/CS 0.510, PpH/CS 0.337); the sternite anterolaterally with a rounded lobiform protrusion on each side which clearly elevates above the level of median surface of sternite; the surface of the sternite thus appearing deeply concave in frontal view. Postpetiole in dorsal view with a concave anterior margin and convex sides. Anterior clypeus deeply foveloate-microrugulose. Vertex with densely-arranged, flat-bottomed but very deep and moderately large foveolae (dFov 17.0). The largest foveolae show a flat tubercle around the hair base having 5–7 µm diameter (Fig. 39). Dorsum of promesonotum deeply and densely-packed foveolate. Propodeum and whole lateral area of mesosoma deeply microreticulate. Waist segments deeply microreticulate-foveolate. First gaster tergite with a strongly developed microreticum, with the hair bases placed in microfoveolae of 5–6 µm diameter (Fig. 40) and with long and very dense pubescence (PLG/CS 6.68 %, sqPDG 3.49). As result, the surface appears rather matt at low magnification. Whole ant homogenously orange brown.

Taxonomic comments. As a combination of very short scape, very dense pubescence on first gaster tergite, wide waist segments, and the more pronounced microsculpture on all body parts not to confuse with any known species of the *wroughtonii* group.

Biology. Unknown.

Cardiocondyla yemeni Collingwood & Agosti 1996

***Cardiocondyla yemeni* Collingwood & Agosti 1996 [type investigation]**

This taxon has been described from Yemen. Investigated was one type worker labelled in Collingwoods handwriting 'YEMEN: SANAA (sandy path) 05 03 1993', 'Typus' and 'Cardiocondyla yemeni'; one topotypical worker, without postpetiole and gaster, labelled '*YEMEN Sana'a 17 III 93*' (day not clearly legible, other possible reading *'27 III 93'*) and 'Cardiocondyla yemeni n.sp. Collingwood & Agosti 1996'; depository SMN Görlitz.

All material examined. Morphometrically investigated were only the type samples.

Geographic range. Known so far only from the Arabian Peninsula: Yemen and Oman (by image evaluation of CASENT0922296 in www.antweb.org).

Diagnosis: --Worker (Tab. 2, Figs 11–15, key). Very small, CS 377 µm. Head very long, CL/CW 1.260. Median third of anterior clypeal margin straight, median third of occipital margin slightly concave. Postocular distance large, PoOc/CL 0.453. Frons relatively narrow (FRS/CS 0.242); frontal carinae slightly diverging frontal of FRS level (FL/FR 1.063), caudal of FRS level parallel or slightly converging. Eye rather small, EYE/CS 0.238. Scape very short, SL/CS 0.724. Metanotal depression nearly absent (MGr/CS 0.55 %). Propodeal spines short (SP/CS 0.103) and almost triangular in lateral view, their axis in profile deviating from longitudinal mesosomal axis by 25°, in dorsal view not diverging and their bases relatively narrow (SPBA/CS 0.266).

Petiole rather narrow and moderately high (PeW/CS 0.276, PeH/CS 0.336); in profile with a concave anterior face and a semicircular dorsum; in dorsal view with an almost globular node, which is only slightly longer than wide. Postpetiole narrow and low (PpW/CS 0.430, PpH/CS 0.268); postpetiolar sternite anterolaterally with a rounded lobiform protrusion on each side which clearly elevates above the level of median surface of sternite; the surface of the sternite thus appearing deeply concave in frontal view. Postpetiole in dorsal view with a straight to slightly concave anterior margin and convex sides. Lateral parts of clypeus each with 2–3 rugulae, central part slightly carinulate-reticulate. Frontal laminae with weak microsculpture, consisting of an irregular mixture of microrugulate, foveolate and microreticulate elements. Whole vertex foveolate, mediad of the eyes with densely-arranged, flat-bottomed foveolae of 14–16 µm diameter. The largest foveolae show a well-demarcated but flat central tubercule of 6–8 µm diameter around the hair bases (Fig. 14). Whole surface of mesosoma foveolate-microreticulate; petiole and postpetiolar tergite microreticulate. First gaster tergite with moderately long and dense pubescence (PLG/CS 6.78 %, sqPDG 3.76) and a weakly developed microreticulum, with the hair bases placed in microfoveolae of 4–6 µm diameter. All body parts yellowish or yellowish-brown.

Taxonomic comments. For separation from closely related *Cardiocondyla yoruba* see there.

Biology. As habitat was reported a sandy path in Saana / Yemen.

Cardiocondyla yoruba Rigato 2002

***Cardiocondyla yoruba* Rigato 2002**
[type investigation]

This taxon has been described from Niger. Investigated were three paratype workers on the same pin with the site equal to the holotype (see CASENT0901752 in www.antweb.org), labelled 'NIGERIA Ibadan, IITA.xi.87, T.Noyes' (handwritten), 'Cardiocondyla yoruba n.sp. PARATYPI, det. F.Rigato 2002' (handwritten), BMNH London.

All material examined. Morphometrically investigated were two samples with seven workers: the type sample plus a sample of four workers from Bondoukou /Ivory Coast.

Geographic range. Known so far only from West Africa: Ghana (by image evaluation of CASENT0901752), Ivory Coast and Niger.

Diagnosis: --Worker (Tab. 2, Figs 6–10, key). Very small, CS 380 µm. Head very long, CL/CW 1.247. Median third of anterior clypeal margin straight, median third of occipital margin slightly concave. Postocular distance large, PoOc/CL 0.459. Frons relatively narrow (FRS/CS 0.245); frontal carinae slightly diverging frontal of FRS level (FL/FR 1.063), caudal of FRS level parallel or slightly converging. Eye rather small, EYE/CS 0.240 and with scattered microsetae of 6–7 µm length. Scape very short, SL/CS 0.724. Metanotal depression shallow (MGr/CS 1.27 %). Propodeal spines short (SP/CS 0.120) and almost triangular in lateral view, their axis in profile deviating from longitudinal mesosomal axis by 25°, in dorsal view not diverging and their bases moderately wide (SPBA/CS 0.275). Petiole rather narrow and moderately high (PeW/CS 0.274, PeH/CS 0.334); in profile with a concave anterior face and semicircular dorsum; in dorsal view with an almost globular node, which is only slightly longer than wide. Postpetiole narrow and low (PpW/CS 0.427, PpH/CS 0.288); postpetiolar sternite anterolaterally with a rounded lobiform protrusion on each side which clearly elevates above the level of median surface of sternite; the surface of the sternite thus appearing deeply concave in frontal view. Postpetiole in dorsal view with a straight to slightly concave anterior margin and convex sides. Lateral parts of clypeus each with 2–3 rugulae, central part slightly carinulate-reticulate. Frontal laminae with weak microsculpture, consisting of an irregular mixture of microrugulate, foveolate and microreticulate elements. Whole vertex foveolate, mediad of the eyes with densely-arranged, flat-bottomed foveolae of 14–16 µm diameter. The largest foveolae show a well-demarcated but flat central tubercule of 6–8 µm diameter around the hair bases (Fig. 9). Whole surface of mesosoma foveolate-microreticulate; petiole strongly and postpetiolar tergite less strongly microreticulate. First gaster tergite with moderately long and dense pubescence (PLG/CS 6.89 %, sqPDG 3.86) and a more strongly developed microreticum, with the hair bases placed in microfoveolae of 4–6 µm diameter (Fig. 10). The microreticulum is an optical illusion in perpendicular view on the surface that is produced by the margins of roof-tile-like surface structures. Color: whole dorsum of gaster blackish brown and all remaining body parts yellowish or yellowish-brown.

Taxonomic comments. *C. yoruba* is inseparable in a PCA from *C. yemeni* considering all 16 NUMOBAT characters: the type samples of *yemeni* and *yoruba* and the non-type sample of *yoruba* from Ivory coast form a coherent cluster in a PCA (Fig. 54). However, I stood back from synonymization of *yoruba* because of the very remote allopatric ranges, the blackish brown gaster not observed so far in the *yemeni* samples from Yemen and Oman and because of the stronger microsculpture of *yoruba* in particular on first gaster tergite. We have to

wait if *yoruba* might be more convingly demonstrated as a separate cryptic species when plenty of samples were analyzed morphometrically or genetically.

Biology. The species is seems to follow other *Cardiocondyla* species by living in anthropogenously disturbed areas. As habitats were reported a grassy patch adjacent to a paved road in the urban center of Accra / Ghana and a path in the suburban area of Bondoukou / Ivory coast.

Cardiocondyla weserka Bolton 1982

***Cardiocondyla weserka* Bolton 1982**
[investigation of type]

This taxon has been described from Cameroun. Investigated was the holotype worker labelled 'Cameroun Nkoemvon 1980. M D.Jackson' and 'Cardiocondyla weserka Bolton det. B.Bolton, 1981', BMNH London.

All material examined. Morphometrically investigated was only the type specimen.

Geographic range. Known so far only from Cameroun.

Diagnosis: --Worker (Tab.2, Figs 41–43, key). Small, CS 404 µm. Head very long, CL/CW 1.232. Median third of anterior clypeal margin slightly concave, median third of occipital margin straight. Postocular distance rather low, PoOc/CL 0.440. Frons relatively narrow (FRS/CS 0.230); frontal carinae slightly diverging frontad (FL/FR 1.050). Eye rather small, EYE/CS 0.247 and without microsetae. Scape rather long, SL/CS 0.790. Dorsal mesosoma profile from pronotum caudad to propodeum at spiracular level rather linear, convex curvatures only suggested. Metanotal depression shallow (MGr/CS 1.79%). Pronotal shoulders rather developed but rounded, not angulate**.** Propodeal spiracle very small, its inner diameter only 5 µm. Propodeal spines long (SP/CS 0.213) and rather thin, their axis in profile deviating from longitudinal mesosomal axis by only 21°, in dorsal view incurved and their bases widely distant (SPBA/CS 0.296). Petiole narrow but very high (PeW/CS 0.265, PeH/CS 0.356); its node clearly longer than wide, with a narrow dorsal plane; node in lateral view massive, petiolar peduncle moderately long. Postpetiole moderately wide and high (PpW/CS 0.455, PpH/CS 0.290), in dorsal view wider than long with angulate-convex sides and concave anterior margin; postpetiolar sternite anterolaterally with a rounded lobiform protrusion on each side which clearly elevates above the level of median surface of sternite; the surface of the sternite thus appearing deeply concave in frontal view. Clypeus with two carinae running to the lateral margins of the anterior concavity. Frontal laminae and clypeus foveolate. Whole head and mesosoma without longitudinal sculpture, except for small patches with weak carinulae mentioned below.

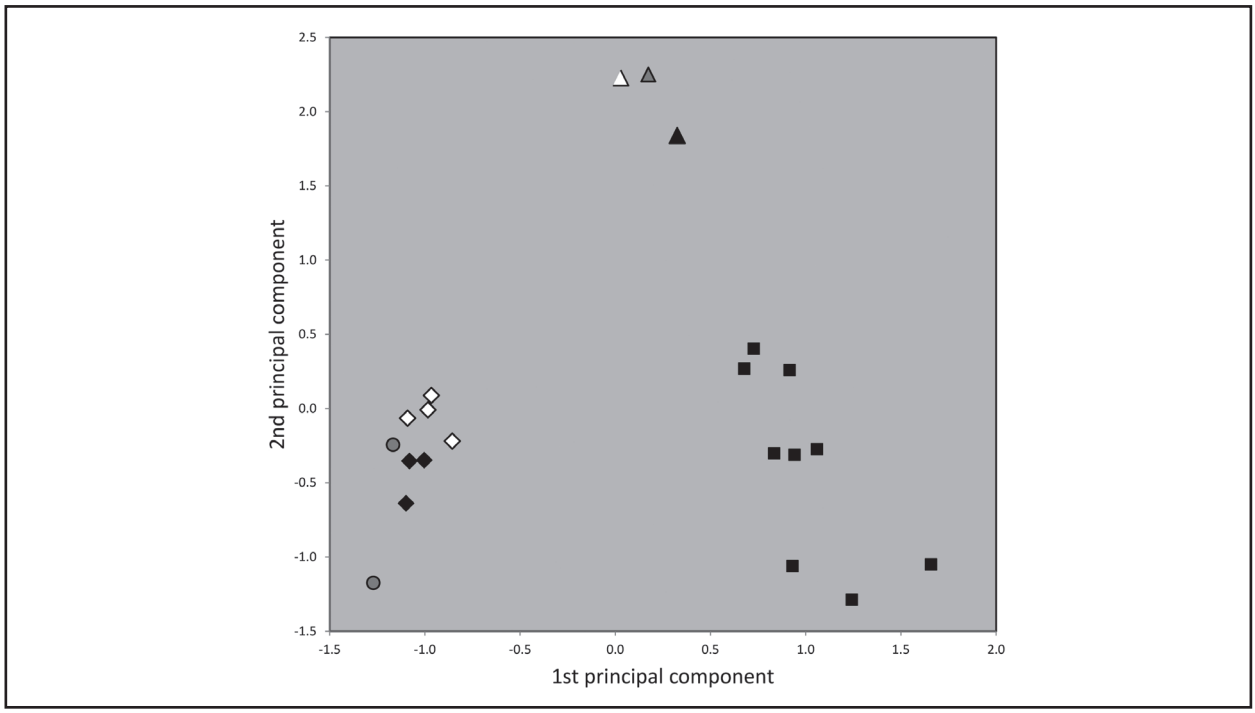


Figure 54. Principal component analysis of worker individuals considering all 16 morphometric characters. Triangles: *Cardiocondyla weserka* (grey: type of *weserka*, black: type of *neferka*, white: no type). Grey discs: syntypes of *Cardiocondyla yemeni* (Black rhombs: types of *Cardiocondyla yoruba*. White rhombs: *C. yoruba* sample from Comoe / Ivory coast). Black squares: Holotype and eight paratypes of *Cardiocondyla heinzei* n.sp. from Comoe / Ivory coast.

Vertex with deeply impressed, flat-bottomed foveolae of 16–18 µm diameter in a densely-packed honey-comb arrangement; foveolae showing an inner corona (tubercle) of 8–10 µm diameter; median vertex posterior of the frontal triangle with 2–3 very short longitudinal carinulae. Dorsal promesonotum irregularly reticulate, width of meshes 5–7 µm, scattered foveolae are present. Dorsal propodeum irregularly reticulate-foveolate; whole lateral mesosoma strongly microreticulate. Petiole except for its more smooth and finely microreticulate dorsum with a well-pronounced and dense microreticulum. Postpetiole, rather smooth, finely microreticulate. First gaster tergite with a rather long and rather dilute pubescence (PLG/CS 7.62 %, sqPDG 4.07). Head, mesosoma, waist, and gaster dark brown; lateral pronotum and appendages lighter.

Taxonomic comments. *C.weserka* is most similar to *neferka* in surface structures, shape of head and waist segments, and morphometry. The only significant difference seems to exist in mesosomal shape. The dorsal propodeal profile is much less convex in *weserka* which gives the whole dorsal mesosoma profile a more linear appearance (Fig. 42) though this difference is less expressed than suggested by the figures in Bolton (1982). Furthermore the pronotum of the *weserka* type shows less developed anterolateral pronotal corners as it is seen in *neferka*. I have doubts if these differences between both taxa suggested by the poor sample size can be confirmed in larger material but I recommend to maintain the heterospecific status until more information is available.

Biology. Unknown.

Cardiocondyla neferka Bolton 1982

***Cardiocondyla neferka* Bolton 1982**
[investigation of type]

This taxon has been described from Ghana. Investigated was the holotype worker labelled 'Mampong GHANA 10.2.70 P.Room' and 'Cardiocondyla neferka Bolton det. B.Bolton, 1981', BMNH London.

Geographic range. Known so far only in two single specimens from Ghana: Mampong, 1970.02.10 and Nigeria: Gambari, 1969.06.10.

Diagnosis: -- Worker (Tab. 2, Figs 49–51, key): Small, CS 408 µm. Head very long, CL/CW 1.224. Median third of anterior clypeal margin suggestedly concave, hind margin of vertex slightly convex. Postocular distance rather large, PoOc/CL 0.462. Frons narrow (FRS/CS 0.226); frontal carinae diverging frontad (FL/FR 1.115). Eye rather small, EYE/CS 0.243 and without microsetae. Scape moderately long, SL/CS 0.770. Dorsal promesonotal profile slightly convex, dorsal propodeal profile with stronger convexity. Metanotal depression well-developed (MGR/CS 3.54 %), in profile with shallow (30°) anterior and posterior slopes. Pronotal shoulders more developed than in *weserka*, each forming a rounded angle of 120°. Propodeal spiracle very small, its inner diameter only 6 µm. Propodeal spines long (SP/CS 0.204) and rather thin, their axis in profile deviating from longitudinal mesosomal axis by 26°, in dorsal view slightly incurved and their bases less widely distant than in *weserka* (SPBA/CS 0.271). Petiole narrow but high (PeW/CS 0.264, PeH/CS 0.349); its node longer than wide, lateral view massive and with a relatively short peduncle. Postpetiole rather wide and high (PpW/CS 0.478, PpH/CS 0.294); in dorsal view a little wider than long, with a clearly concave anterior margin and angulate-convex sides; postpetiolar sternite anterolaterally with a rounded lobiform protrusion on each side which clearly elevates above the level of median surface of sternite; the surface of the sternite thus appearing deeply concave in frontal view. Clypeus with two carinae running to the lateral margins of the concavity. Frontal laminae and clypeus with scattered smaller foveolae. Whole head and mesosoma without longitudinal sculpture. Vertex with deeply impressed, flat-bottomed foveolae of 15–18 µm diameter in a densely-packed arrangement; foveolae showing an inner corona (tubercle) of 8–9 µm diameter. Dorsal promesonotum irregularly microreticulate-corrugated, frontal pronotum in the transitional zone from dorsal plane to declivity foveolate. Dorsomedian propodeum rather shiny, finely microreticulate. Whole lateral mesosoma strongly microreticulate. Dorsal plane of petiole rather smooth, only microreticulate, the node in lateral view strongly microreticulate. Postpetiolar node shiny but finely microreticulate. First gaster tergite with a rather long and rather dilute pubescence (PLG/CS 7.52 %, sqPDG 3.78) and a very fine, widely-meshed microreticulum. Type worker: whole body light yellowish brown. Gambari worker: head, mesosoma, and petiole light yellowish brown, postpetiole a little darker, antennal club dark brown, gaster blackish brown.

Comments. See the statements under *C. weserka*.

Biology. Unknown.

4.4 Morphometric tables

Data for *C. wroughtonii* group workers are presented in two tables: (Tab. 1) for Oriental and Australasian workers with a mean FL/FR ratio < 1.040, and (Tab. 2) for African and Arabian Peninsula workers with a mean FL/FR ratio > 1.040. Each table includes arithmetic mean ± standard deviation, along with minimum and maximum values.

Table 1. Workers of the *C. wroughtonii* group of Orientalic-Australasian origin with mean FL/FR < 1.040. Sequence of data: arithmetic mean ± standard deviation [minimum, maximum].

	allonivalis (n=4)	***shagrinata*** (n=3)	***wroughtonii*** (n=138)	***obscurior*** (n=86)	***nana*** (n=1)
CS [µm]	380 ± 17 [361,402]	426 ± 8 [418,433]	410 ± 19 [363,458]	430 ± 19 [379,470]	366
CL/CW	1.137 ± 0.016 [1.115,1.148]	1.099 ± 0.009 [1.090,1.107]	1.120 ± 0.023 [1.064,1.174]	1.111 ± 0.017 [1.073,1.148]	1.069
SL/CS	0.808 ± 0.019 [0.787,0.824]	0.760 ± 0.005 [0.754,0.763]	0.772 ± 0.021 [0.729,0.825]	0.788 ± 0.013 [0.738,0.814]	0.818
PoOc/ CL	0.440 ± 0.005 [0.434,0.444]	0.427 ± 0.004 [0.424,0.431]	0.440 ± 0.011 [0.413,0.496]	0.435 ± 0.008 [0.410,0.452]	0.464
EYE	0.242 ± 0.002 [0.240,0.244]	0.222 ± 0.005 [0.219,0.227]	0.233 ± 0.007 [0.212,0.248]	0.229 ± 0.005 [0.217,0.242]	0.220
dFOV	15.5± 0.8 [14.8,16.5]	13.5 ± 0.1 [13.4,13.6]	19.0 ± 1.2 [16.4,22.0]	19.7 ± 1.2 [17.0,22.6]	21.0
FRS/CS	0.299 ± 0.010 [0.290,0.314]	0.282 ± 0.003 [0.280,0.285]	0.272 ± 0.008 [0.254,0.294]	0.268 ± 0.006 [0.252,0.284]	0.266
FL/FR	1.017 ± 0.021 [1.000,1.046]	1.004 ± 0.008 [1.000,1.013]	1.008 ± 0.011 [1.000,1.049]	1.011 ± 0.012 [1.000,1.053]	1.000
SPBA/CS	0.309 ± 0.005 [0.306,0.316]	0.292 ± 0.010 [0.281,0.301]	0.279 ± 0.012 [0.251,0.305]	0.292 ± 0.012 [0.271,0.325]	0.277
SP/CS	0.185 ± 0.009 [0.178,0.197]	0.184 ± 0.007 [0.179,0.192]	0.193 ± 0.015 [0.149,0.249]	0.185 ± 0.014 [0.143,0.214]	0.192
PeW/CS	0.319 ± 0.011 [0.304,0.329]	0.279 ± 0.008 [0.270,0.284]	0.277 ± 0.013 [0.249,0.323]	0.292 ± 0.012 [0.262,0.319]	0.264
PPW/CS	0.470 ± 0.013 [0.452,0.482]	0.446 ± 0.006 [0.441,0.450]	0.437 ± 0.012 [0.408,0.462]	0.459 ± 0.010 [0.438,0.485]	0.426
PeH/CS	0.363 ± 0.012 [0.352,0.374]	0.333 ± 0.003 [0.330,0.335]	0.328 ± 0.011 [0.296,0.358]	0.338 ± 0.009 [0.317,0.369]	0.336
PpH/CS	0.356 ± 0.006 [0.348,0.361]	0.308 ± 0.006 [0.304,0.312]	0.303 ± 0.012 [0.268,0.332]	0.314 ± 0.010 [0.292,0.341]	0.289
sqrtPDG	4.36 ± 0.55 [3.91,5.08]	4.87 ± 0.04 [4.84,4.90]	5.05 ± 0.26 [4.47,5.79]	5.13 ± 0.24 [4.60,5.79]	5.60
PLG/CS [%]	6.44 ± 0.66 [5.79,7.23]	6.22 ± 0.34 [5.98,6.47]	6.30 ± 0.40 [5.55,7.29]	6.23 ± 0.31 [5.68,7.01]	6.29
MGr/CS [%]	2.15 ± 0.40 [1.56,2.40]	3.21 ± 0.58 [2.5,3.6]	3.65 ± 0.96 [1.4,6.0]	3.65 ± 0.89 [1.0,5.7]	2.50

Table 2. Workers of the *C. wroughtonii* group with mean FL/FR > 1.040 and originating from Africa and the Arabian Peninsula. Sequence of data: arithmetic mean ± standard deviation [minimum, maximum].

	sp. SPIT. (n=3)	***weserka*** (n=1)	***neferka*** (n=2)	***yemeni*** (n=2)	***yoruba*** (n=7)	***heinzei n.sp*** (n=9)
CS [µm]	409 ± 6 [405,415]	404	408 ± 11 [401,416]	377 ± 3 [368,385]	380 ± 6 [368,385]	377 ± 9 [364,391]
CL/CW	1.162 ± 0.016 [1.145,1.177]	1.232	1.224 ± 0.041 [1.195,1.253]	1.260 ± 0.019 [1.246,1.273]	1.247 ± 0.016 [1.227,1.273]	1.189 ± 0.017 [1.154,1.212]
SL/CS	0.694 ± 0.012 [0.682,0.705]	0.790	0.770 ± 0.001 [0.769,0.771]	0.724 ± 0.005 [0.720,0.727]	0.724 ± 0.012 [0.708,0.738]	0.786 ± 0.012 [0.769,0.808]
PoOc/CL	0.415 ± 0.004 [0.410,0.418]	0.440	0.462 ± 0.021 [0.447,0.477]	0.453 ± 0.004 [0.450,0.456]	0.459 ± 0.006 [0.450,0.469]	0.457 ± 0.007 [0.449,0.470]
EYE	0.246 ± 0.002 [0.244,0.248]	0.247	0.243 ± 0.001 [0.242,0.244]	0.238 ± 0.001 [0.237,0.238]	0.240 ± 0.004 [0.235,0.245]	0.232 ± 0.004 [0.227,0.239]
dFOV	17.0± 1.2 [15.8,18.1]	17.0	16.5 ± 0.7 [16.0,17.0]	14.5± 0.7 [14.0,15.0]	15.1± 0.6 [14.5,16.2]	16.7± 0.8 [15.9,18.2]

Table 2 continued.

	sp. SPIT. (n=3)	***weserka*** (n=1)	***neferka*** (n=2)	***yemeni*** (n=2)	***yoruba*** (n=7)	***heinzei n.sp*** (n=9)
FRS/CS	0.277 ± 0.005 [0.272,0.281]	0.230	0.226 ± 0.003 [0.224,0.228]	0.242 ± 0.009 [0.235,0.248]	0.245 ± 0.011 [0.236,0.259]	0.219 ± 0.008 [0.211,0.234]
FL/FR	1.097 ± 0.012 [1.083,1.106]	1.050	1.115	1.063 ± 0.002 [1.061,1.065]	1.063 ± 0.021 [1.039,1.052]	1.063 ± 0.017 [1.024,1.079]
SPBA /CS	0.257 ± 0.013 [0.246,0.271]	0.296	0.271 ± 0.011 [0.263,0.279]	0.266 ± 0.004 [0.264,0.269]	0.277 ± 0.006 [0.267,0.288]	0.240 ± 0.008 [0.229,0.250]
SP/CS	0.189 ± 0.013 [0.292,0.317]	0.213	0.204 ± 0.003 [0.202,0.207]	0.103 ± 0.025 [0.085,0.121]	0.120 ± 0.009 [0.108,0.132]	0.201 ± 0.009 [0.188,0.215]
PeW/CS	0.304 ± 0.013 [0.292,0.317]	0.265	0.264 ± 0.004 [0.262,0.267]	0.276 ± 0.005 [0.272,0.279]	0.274 ± 0.008 [0.264,0.288]	0.234 ± 0.012 [0.214,0.252]
PPW/CS	0.510 ± 0.012 [0.497,0.517]	0.455	0.478 ± 0.001 [0.478,0.479]	0.430 ± 0.001 [0.429,0.431]	0.427 ± 0.006 [0.418,0.435]	0.454 ± 0.009 [0.439,0.466]
PeH/CS	0.369 ± 0.002 [0.367,0.371]	0.356	0.349 ± 0.010 [0.342,0.356]	0.336 ± 0.016 [0.325,0.348]	0.334 ± 0.005 [0.328,0.340]	0.333 ± 0.009 [0.317,0.345]
PpH/CS	0.337 ± 0.006 [0.332,0.344]	0.290	0.294 ± 0.006 [0.289,0.298]	0.268 ± 0.006 [0.264,0.272]	0.288 ± 0.013 [0.273,0.304]	0.276 ± 0.012 [0.251,0.289]
sqrtPDG	3.49 ± 0.10 [3.37,3.57]	4.07	3.78 ± 0.29 [3.57,3.98]	3.76 ± 0.28 [3.56,3.96]	3.86 ± 0.07 [3.79,3.95]	4.14 ± 0.10 [4.01,4.27]
PLG/CS [%]	6.68 ± 0.26 [6.39,6.90]	7.62	7.52 ± 0.35 [7.28,7.77]	6.78 ± 0.06 [6.73,6.82]	6.89 ± 0.40 [6.42,7.53]	7.12 ± 0.27 [6.83,7.51]
MGr/CS [%]	3.29 ± 0.26 [3.00,3.51]	1.79	3.54 ± 0.96 [2.9,4.2]	0.55 ± 0.21 [0.40,0.70]	1.27 ± 0.24 [0.89,1.55]	3.25 ± 0.58 [2.43,3.86]

4.5 Checklist of the *Cardiocondyla* species of the world

The underrecording of these tiny ants which have hidden nests with small populations resulted in describing many species only by a single sample or even single specimen. This makes objective or testable species separation impossible when very similar species are considered. In such cases I was forced to decide by gut instinct. Including *Cardiocondyla heinzei* n.sp., the checklist considers 128 names. These names divide into 81 recognized species, 34 junior synonyms and 12 incertae sedis and one homonym. The category incertae sedis refers to taxa not assignable to species level because of insufficient descriptions or images and missing or heavily damaged type specimens. Including the undescribed *Cardiocondyla* sp. SPIT, I can now separate 82 species but, considering the number of species still to be discovered, the real number worldwide will clearly exceed 100. The listing is in alphabetical order with the valid species given in heavy type (Tab. 3).

Table 3. The abbreviations mean B = bona species, S = junior synonym, I = incertae sedis, H = homonym, U = unavailable name. Sequences such as '*bimaculata* Wheeler 1929, *wroughtonii* var.' have to be understood as '*wroughtonii* var. *bimaculata* Wheeler 1929'.

status	**taxon**	**species group**
B	***allonivalis* Seifert 2023**	*wroughtonii* group
B	***argentea* Seifert 2023**	*argentea* group
B	***argyrotricha* Seifert 2023**	*argentea* group
B	***atalanta* Forel 1915**	*nuda* group
S	*badonei* Arnold 1926	syn. of *venustula*; *shuckardi* group
B	***batesii* Forel 1894**	*batesii* group
S	*bicolor* Donisthorpe 1930	syn. of *obscurior*; *wroughtonii* group
S	*bicoronata* Seifert 2003	syn. of *nigra*; *batesii* group
S	*bimaculata* Wheeler1929, *wroughtonii* var.	syn. of *wroughtonii*; *wroughtonii* group
S	*bogdanovi* Ruzsky 1905	syn. of *stambuloffii; stambuloffii* group
B	***brachyceps* Seifert 2003**	*elegans* group
S	*breviscapa* Seifert 2003	syn. of *minutior; minutior* group

Table 3 continued.

status	taxon	species group
S	*brevispinosa* (Donisthorpe 1947)	syn. of *paradoxa*, *thoracica* group
H, I	*brevispinosa* Weber 1952	*shuckardi* group, jun. secondary homonym; holotype worker AMNH New York, presumed lost]
B	***britteni* Crawley 1920**	*minutior* group
B	***bulgarica* Forel 1892**	*ulianini* group
S	*caparica* (Henin, Paiva & Collingwood 2002); *Leptothorax*	syn. of *mauritanica*; *nuda group*
B	***carbonaria* Forel 1907**	*minutior* group
B	***caspiense* Seifert 2023**	*ulianini* group
S	*chlorotica* Menozzi 1930, *emeryi* subsp	syn. of *emeryi*; *emeryi* group
I	*christatum* Santschi 1912	type lost from mount in NHM Basel. Drawing in original description excludes *Cardiocondyla*. It is either a *Monomorium* or *Solenopsis*.
B	***compressa* Seifert et al. 2017**	*nuda* group
B	***dalmatica* Soudek 1925**	*elegans* group
B	***dalmaticoides* Seifert 2023**	*elegans* group
S	*ectopia* Snelling 1974	syn. of *mauritanica; nuda group*
B	***elegans* Emery 1869;**	*elegans* group
S	*eleonorae* Forel 1911, *elegans* var.	synonym of *bulgarica*; *ulianini* group
B	***emeryi* Forel 1881**	*emeryi* group
B	***excavata* Seifert 2023**	*wheeleri* group
B	***fajumensis* Forel 1913**	*shuckardi* group
I	*fezzanensis* Bernard 1948; *emeryi* ssp.	*Cardiocondyla*, but to no species group assignable
I	*fusca* Weber 1952	*shuckardi* group, holotype not AMNH New York, presumed lost
S	*gallagheri* Collingwood & Agosti 1996	syn. or *mauritanica; nuda group*
S	*gallica* (Bernard 1957); *Xenometra*	syn. of *elegans; elegans* group
B	***gallilaeica* Seifert 2003**	*ulianini* group
B	***gibbosa* Kuznetzov-Ugamsky 1927**	*stambuloffii* group
B	***globinodis* Stitz 1923**	syn. *venustula; shuckardi* group
B	***goa* Seifert 2003**	*minutior* group
B	***goroka* Seifert 2023**	*wheeleri* group
B	***hashemi* Sharaf 2024**	*batesii* group
S	*hawaiensis* Forel 1899	syn. of *wroughtonii; wroughtonii* group
B	***heinzei* Seifert 2024**	*wroughtonii* group
I	*insutura* Zhou 2001	*minutior* group
B	***israelica* Seifert 2003**	*ulianini* group
B	***itsukii* Seifert et al. 2017**	*nuda* group
I	*jacquemini* Bernard 1953	probably *batesii* group
B	***kagutsuchi* Terayama 1999**	*nuda* group
I	*kazanensis* Terayama 2013	to no group assignable
B	***koshewnikovi* Ruzsky 1902**	*stambuloffii* group
B	***kushanica* Pisarski 1967**	*batesii* group
B	***latifrons* Seifert 2023**	*argentea* group
B	***littoralis* Seifert 2003**	*ulianini* group
B	***longiceps* Seifert 2003**	syn. *melana*?; *shuckardi* group
B	***longinoda* Rigato 2002**	monotypical
S	*longispina* Karavajev 1935	syn. *wroughtonii; wroughtonii* group
S	*luciae* Rigato 2002	syn. of *mauritanica*, *nuda group*
S	*mahdii* Karavaiev 1911	syn. of *emeryi; emeryi* group
B	***mauritanica* Forel 1890**	*nuda* group

Table 3 continued.

status	taxon	species group
S	*mauritia* Donisthorpe 1946	syn. of *emeryi; emeryi* group
B	***melana* Seifert 2003**	*shuckardi* group
B	***micropila* Seifert 2023**	*argentea* group
B	***minutior* Forel 1899**	*minutior* group
B	***monardi* Santschi 1930;** (*Loncyda*)	monotypical
S	*monilicornis* (Emery 1917); *Xenometra*	syn. of *venustula*; *shuckardi* group
S	*montandoni* Santschi 1912	syn. of *stambuloffii; stambuloffii* group
B	***nana* Seifert 2003**	*wroughtonii* group; Borneo: Brunei
B	***neferka* Bolton 1982**	*wroughtonii* group;
S	*nereis* W.M.Wheeler 1927	syn. of *emeryi*; *emeryi* group
B	***nigra* Forel 1905**	*batesii* group
B	***nigrocerea* Karavajev** 1935	*wheeleri* group
S	*nilotica* Weber 1952	syn. of *fajumensis*; *shuckardi* group
I	*nitida* Bernard 1948; *emeryi* ssp.	*batesii* group
B	***nivalis* Mann 1919**	monotypical
B	***nuda* (Mayr 1866)**; *Leptothorax*	*nuda* group
B	***obscurior* Wheeler 1929**	*wroughtonii* group
B	***opaca* Seifert 2003**	*minutior* group
B	***opisthopsis* Seifert 2003**	*batesii* group
B	***papuana* (Reiskind 1965);** *Prosopidris*	*sima* group
B	***paradoxa* Emery 1897**	*thoracica* group
B	***paranuda* Seifert 2003**	*nuda* group
B	***parvinoda* Forel 1902**	*minutio*r group (Oettler et al. 2010) but body size much larger than in other members of the group
B	***persiana* Seifert 2003**	*ulianini* group
B	***pirata* Seifert et al. 2013**	*argentea* group
S	*provincialis* Bernard 1956	syn. of *elegans; elegans* group
S	*quadraticeps* Forel 1912; *wroughtonii* subsp.	syn. of *wroughtonii; wroughtonii* group
S	*rasalamae* Forel 1891	syn. of *emeryi*; *emeryi* group
B	***rolandi* Seifert 2023**	*stambuloffii* group
B	***rugulosa* Seifert 2003**	*batesii* group
S U	*sabulosa* Arnoldi 1928; *stambulovi* ssp. *taurica* morpha *sabulosa*	syn. of *stambuloffii* or *koshewnikovi*; *stambuloffii* group
B	***sahlbergi* Forel 1913**	*ulianini* group
S U	*salina* Arnoldi 1928; *stambulovi* ssp. *taurica* morpha *salina*	syn. of *stambuloffii* or *koshewnikovi*; *stambuloffii* group
S	*santschii* Forel 1905	syn. of *elegans; elegans* group
S	*schatzmayri* Finzi 1936	syn. of *fajumensis; shuckardi* group
I	*schkaffi* Arnoldi 1933; *elegans* subsp.	probably *elegans* group
B	***schulzi* Seifert 2023**	*minutior* group
I	*sculptinodis* Santschi 1913; *shuckardi* st.	*shuckardi* group, type gyne in NHM Basel without head;
I	*sculptior* Santschi 1926; *wasmanni* var.	*shuckardi* group, holotype NHM Basel [missing from mount]
B	***semiargentea* Seifert 2023**	*argentea* group
B	***semirubra* Seifert 2003**	*batesii* group
B	***sekhemka* Bolton 1982**	*shuckardi* group;
B	***shagrinata* Seifert 2003**	*wroughtonii* group
B	***shuckardi* Forel 1891**	*shuckardi* group
S	*shuckardoides* Forel 1895	syn. of *shuckardi; shuckardi* group
B	***sima* Wheeler 1935**	*sima* group

Table 3 continued.

status	taxon	species group
B	***stambuloffii* Forel 1892**	*stambuloffii*group
B	***strigifrons* Viehmeyer 1922; *nuda* ssp.**	*nuda* group
B	***subspina* Seifert 2023**	*thoracica* group
B	***sulcata* Seifert 2023**	monotypical
S	*taurica* Karavajev 1927; *stambuloffii* ssp.	syn. of *stambuloffii; stambuloffii* group
B	***tenuifrons* Seifert 2003**	*batesii* group
B	***thoracica* (F.Smith 1859);** *Myrmica*	*thoracica* group
B	***tibetana* Seifert 2003**	*stambuloffii* group
I	*tiwarii* Gosh, Sheela & Kundu 2005	not assignable to a species group
B	***tjibodana* Karavajev 1935**	*minutior* group
S	*torretassoi* Finzi 1936	syn. of *nigra; batesii* group
S	*tsukuyomi* Terayama 1999	syn. of *minutior; minutior* group
B	***ulianini* Emery 1889;**	*ulianini* group;
B	***unicalis* Seifert 2003**	*shuckardi* group
B	***venustula* Wheeler 1908**	*shuckardi* group
B	***verdensis* Seifert 2023**	*batesii* group
I	*wassmanni* Santschi 1921	type specimen in NHM Basel without head; *shuckardi* group
B	***weserka* Bolton 1982**	*wroughtonii* group
B	***wheeleri* Viehmeyer 1914**	*wheeleri* group
B	***wroughtonii* (Forel 1890)**	*wroughtonii* group
S	*yamauchii* Terayama 1999	syn. of *wroughtonii; wroughtonii* group
B	***yemeni* Collingwood & Agosti 1996**	*wroughtonii* group
B	***yoruba* Rigato 2002**	*wroughtonii* group
B	***zoserka* Bolton 1982**	described on a single male; *shuckardi* group;

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