A taxonomic revision of the *Cardiocondyla nuda* group (Hymenoptera: Formicidae)

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Abstract

A taxonomic revision of the *Cardiocondyla nuda* species group is presented based on methods of Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT) and supplemented by analysis of mtDNA. A total of 258 samples with 571 worker individuals were investigated by the hierarchical and non-hierarchical exploratory data analyses NC-Ward and NC-K-Means clustering considering 16 NUMOBAT characters. Two species are described as new, increasing the number of species in the group to eight. We separate the group into two main clades: the *C. mauritanica* species complex, which is of Oriental and Indo-Australian origin and contains the cryptic species *C. mauritanica* Forel 1890, *C. strigifrons* Viehmeyer 1922, *C. kagutsuchi* Terayama 1999, and *C. itsukii* sp. nov. and the Australasian and Polynesian *C. nuda* species complex with the cryptic species *C. nuda* (Mayr 1866), *C. atalanta* Forel 1915, *C. paranuda* Seifert 2003, and *C. compressa* sp. nov. The mean error of the two NC-clustering methods relative to the controlling linear discriminant analysis was 0.4% in *C. mauritanica*, 2.2% in *C. itsukii*, 0% in *C. strigifrons*, 0% in *C. kagutsuchi*, 1.5% in *C. nuda*, 3.2% in *C. atalanta* and 3.2% in *C. paranuda*—all these data are below the 4% threshold recommended by the Pragmatic Species Concept. The morphologically determined species clusters were confirmed by mtDNA data with a rather strong sequence divergence among the cryptic species of the *C. nuda* complex of 5.6–7.9%. The mean mismatch of two different mtDNA analyses with NUMOBAT clustering was 5.4% in 54 samples of seven species of the *C. nuda* group for which mtDNA data were available. The mismatch thus is smaller than in many other studies of Eumetazoa in general or ants in particular and is probably explained by low frequencies of ancient hybridization and/or incomplete lineage sorting. Comments on zoogeography, colony demography and behavior are given in the species sections and determination keys are provided.

Key words: numeric morphology-based alpha-taxonomy, nest centroid clustering, cryptic species, barcoding

1. Introduction

In his revision of several species groups of the ant genus *Cardiocondyla*, Seifert (2003) distinguished a *Cardiocondyla nuda* species group for which he proposed six species. Ants of this species group contain several tramp species and were the focus of investigations on male polymorphism, modes of reproduction and colony structure (Frohschammer & Heinze 2009, Heinze et al. 1993, 1998, 2005, 2013; Okita et al. 2013, 2016; Yamauchi & Kinomura 1993, Yamauchi et al. 2005). These investigations showed abundant morphological, social and ethological polymorphism, but whether specific combinations of traits could have taxonomic significance remained unclear. In the revision of Seifert (2003), two species, *C. atalanta* and *C. paranuda*, were based on single specimens, which left doubts on their taxonomic validity. *Cardiocondyla atalanta* was later confirmed as a distinct species on the basis of a much larger sample size (Seifert 2008a).

Okita et al. (2015) showed significant correlations between mtDNA phylogeny and worker morphology in the "*Cardiocondyla s.l. kagutsuchi*" species complex and they hypothesized the existence of cryptic lineages
potentially having species rank. Yet, their morphological investigation system considered only six characters, did not involve exploratory data analyses, and resulted in rather high ratios of disagreements with mtDNA phylogeny. These findings raised the question which of these lineages can be confirmed as taxonomically valid species by the application of high-resolution NC-clustering methods (Seifert et al. 2013). The recent development of this form of analysis and a considerable increase in material available for investigation resulted in an improved knowledge of the species composition in the C. nuda group.

In this paper, we present a taxonomic revision of the Cardiocondyla nuda species group that describes two species as new and increases the number of species in the group to eight. We separate the group into two main clades: the C. mauritanica species complex, which is of Oriental and Indo-Australian origin, and the Australasian and Polynesian C. nuda species complex. All but one species considered in this revision are truly cryptic. Such species have been defined by Seifert (2009) as follows: “...Cryptic species are two or more species which are not separable by primary visual or acoustic perception of an expert. This reflects the immediate sense of the word and restricts such species to truly cryptic cases—i.e., to species not safely separable by training of innate pathways of the human cognitive system. Rather, their reliable identification requires the application of elaborate methods such as numeric recording and analysis of phenotypic characters, DNA analysis, biochemistry or analysis of sound spectograms.”

2. Material

NUMOBAT data were recorded in a total of 258 samples and 571 worker individuals. 350 additional workers were investigated by subjective eye inspection only. Due to the difficulty of locating the hidden nest sites of Cardiocondyla ants, the majority of samples are collections of foragers, and a minority are clean nest samples taken by investigators particularly interested in the biology of these ants. The material came from all faunal regions of the world where ants of the C. nuda group are known to occur. In the individual species treatments, material examined is listed in following sequence and format: site, date in the format yyyy.mm.dd, sample number, (GenBank accession number), [latitude in decimal format, longitude in decimal format]. The accuracy of coordinates is proportional to the number of decimal points and "xx" in the sampling date sequence mean missing data. In some samples without any direct or derived information on date, the collector is given to allow an approximate conclusion on the time period of collection. Sample or field collection numbers are missing in many samples. The acronyms of depositories are as follows:

CAS California Academy of Sciences Collection, San Francisco, USA
FSAG Department of Zoology, Faculté universitaire des Sciences agronomiques, Gembloux, Belgium
LACM Los Angeles County Museum, Los Angeles, California, USA.
MNEHS Museum of Natural and Environmental History, Shizuoka, Japan
MNHAH Museum of Nature and Human Activities, Sanda, Hyogo, Japan
MHNG Muséum d'histoire naturelle de Genève, Genève, Switzerland
NHMW Naturhistorisches Museum, Wien, Austria
NHMB Naturhistorisches Museum, Basel, Switzerland
SMNG Senckenberg Museum für Naturkunde, Görlitz, Germany
ZMHB Zoologische Sammlungen am Museum für Naturkunde, Berlin, Germany

3. Methods

3.1. 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 petiole width, but one of ± 1.0 µm for larger structures that are difficult to position such as cephalic length.

3.2. The morphometric characters

Sixteen morphometric characters were investigated 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 mesh-like surface structures on vertex at about half way between the median line of head and the inner eye margin. These structures are in the *C. nuda* group meshes of a reticulum which usually have the base of a decumbent pubescence hair in their center. At least seven measurements at magnifications of 320x are averaged.

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

- **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).

- **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.

- **PLG:** mean length of pubescence hairs on dorsum of first gaster tergite as arithmetic mean of at least 7 measurements measured at magnifications of 320x.

- **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 that orthogonal to the long axis and 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 320x. 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 = BD² / PLG.

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

The species delimitation was done by an interaction of Nest-Centroid Clustering (NC clustering) and a controlling linear discriminant analysis (LDA). NC Clustering was run both as hierarchical NC-Ward clustering and non-hierarchical NC-K-means clustering. These methods were described in more detail by Seifert et. al. (2013), who also provided a script written in R and freely available under the GNU / GPL license from the following website: https://sourceforge.net/projects/agnesclustering/.

Among the hierarchical exploratory data analyses, NC-Ward clustering statistically proved to be more powerful than NC-UPGMA clustering in detection of cryptic species (Seifert et. al. 2013). NC-Ward presents species hypotheses more clearly than NC-UPGMA but it has the disadvantage of only rarely exposing outliers, usually not recognizing them and placing them within larger branches. This could result in a lumping tendency or a failure to discover real, but extremely cryptic species (as defined by Seifert 2009) when these are represented in the material by only a single or very few samples. Taking into account that NC-clustering results in the recognition of an uncomfortably high number of species, we consider this failure of NC-Ward as tolerable from a practical point of view—truly cryptic species should only be described if a sufficient sample size is available. As a consequence, we used NC-Ward as the leading system to indicate the putative number of K main clusters in the first step of analysis. In the second step, NC-K-means was performed with the setting of K classes suggested by NC-Ward. Classifications being coincident between the hierarchical and non-hierarchical clustering formed the hypothesis for the controlling LDA that was subsequently run. Samples with classifications disagreeing between NC-clustering

FIGURES 1–3. 1—measuring position for frontal carinae distance FRS; 2—measuring of postocular distance PoOc; 3—measuring of spine length SP.
methods were run in this LDA as wild-cards. The final classification (“final species hypothesis”) was established by the LDA in the iterative procedure described by Seifert et al. (2013). There remained no undecided cases even if their posterior probabilities were close to 0.5. The classification of particular samples and of the type specimens in general was checked by running them as wild-cards in a controlling LDA. This is basically a variant of the jackknife resampling technique. LDA, ANOVA and \(X^2\) tests were performed with the software package SPSS 15.0. Fisher’s two-tailed exact test was run with the software package R (R Development Core Team 2012).

The decision to recognize a cluster as a valid species was based on the criterion of the Pragmatic Species Concept (Seifert 2014) which requires that the mean error of the applied exploratory data analyses determined by the controlling LDA must be <4%. If more than two clusters are in a data set, clustering should be carried out in a stepwise, bifurcating procedure which becomes more important the more difficult species delimitation is. In the first step, EDA-LDA data analyses of all samples involved are run and the most clearly separable cluster is determined. The samples of this cluster are then excluded from the 2nd EDA-LDA run in which the next most clearly separable cluster is identified and excluded from the 3rd run. In theory, the analysis has to be terminated when no cluster previously separated can be further subdivided with an error rate < 4%. Compared to idiosyncratic approaches, which dominate in taxonomy, this threshold system provides a rigorous procedure and good remedy against over-splitting when the remaining sample size is sufficiently large. However, if the sample size becomes too small, say, if a cluster contains only eight samples and 25 worker individuals, there is some danger that combinations of accidental, taxonomically meaningless differences are ‘confirmed’. To handle such cases, Nilsen et al. (2013) introduced the stopping criterion of minimum cluster size which implies that clusters must have a minimum number of members to be considered valid. We generally considered the analysis of the extremely similar morphologies in the C. muda group problematic when the smallest cluster contained less than ten nest samples and/or when the number of individual workers in the smallest cluster is less than threefold of the number of characters considered by the controlling LDA. This 10-samples stopping threshold, of course, does not apply when the morphologies of the considered clusters are not extremely similar—Seifert & Galkowski (2016), for example, considered a cluster of six samples and 18 workers as a valid sister species. Even more, the description of a species on the basis of only a single sample may be justified under certain conditions. The latter applies when this sample is placed outside the 99.5% confidence range of variation of the next most similar species and when the sample is not suspected to represent a mutant or rare aberration—we separated C. compressa sp. nov. on the basis of this rationale.

A comment is necessary here why a stepwise, bifurcating procedure is preferred. In about 800 runs of NC-clustering in 10 ant genera, stepwise cluster exclusion clearly boosted the performance in separation of extremely similar species (Seifert, pers. obs.). This finding is supported by Nilsen et al. (2013). They have shown problems in identifying clusters by the usually applied horizontal cuts in dendrograms of datasets containing many entities. They emphasized that such global analyses of all samples/entities in a single step induce the risk that true or reasonable subclusters within major clusters are not correctly shown when some of the clusters are more dispersed than others, and when there are cases that do not fit in any clusters (outliers). Nilsen et al. (2013) and Nilsen & Lingjaerde (2013) presented as solution of the problem with a stepwise, fully automated procedure which optimizes the functions on each level, beginning with the demonstration of major clusters and ending with the smallest subclusters. Csősz and Fisher (2015) used this algorithm, named Partitioning Algorithm based on Recursive Thresholding (PART), for separation of eight non-cryptic species of Nesomyrmex. The performance of such fully automated procedures certainly has to be tested extensively in data sets with extremely similar, truly cryptic species before a final judgement on the value and pitfalls of this approach can be made. As this paper deals with extremely difficult species delimitations, we prefer a slower, supervised procedure in which the researcher examines the results at each step of the clustering process.

3.4. Analysis of mtDNA

The methodological details and results of the mtDNA analysis we used here for the C. mauritanica species complex are given in Okita et al. (2015). The sequence used was a 829-bp fragment of the COI/II regions deleting the tRNA leucine region between COI and COII. The phylogenetic tree of the C. muda species complex was estimated from a 871bp fragment of the same regions (see Heinze et al. 2005, 2016; Okita et al. 2013) using MrBayes version 3.2.2 with GTR+G+I as model for gene evolution. The default settings included three heated and one cold Markov chain and the heating parameter was set at 0.2. Each analysis was conducted with a Markov Chain Monte Carlo method with 3,000,000 generations and sampled every 1000 generations. The consensus tree was created discarding the first 25% of the sampled trees (the burn-in) and drawn using Fig Tree v1.4.3. Two
samples of Cardiocondyla elegans Emery 1869 were used as outgroup in the mtDNA tree. They came from France: Carennac-1.2 km SE, 2003.05.25, No CO1 (GenBank DQ023070) [44.91, 1.74] and Turkey: Edirne, 2002.06.04, No 61A (GenBank DQ023073) [41.67, 26.56].

4. Results and discussion

4.1. Diagnosis of the Cardiocondyla nuda group
The Cardiocondyla nuda group can be separated from other species of the genus by the following character combination:

Propodeal spines short, appearing in lateral view as smaller angles of 60–95° (in the C. shuckardi group forming blunt corners of 95–120°). Postpetiole in dorsal aspect frequently with angulate-convex sides—the outlines of postpetiole thus resembling a hexagon. Promesonotal and anterior propodeal profiles usually not forming evenly convex curvatures: as result, metanotum depression not as wide or completely absent (a difference to the C. shuckardi group). Eyes small (EYE/CS 0.231± 0.05), postocular index rather large (PoOc/CL 0.454±0.013) and postpetiole rather narrow (PPW/CS 0.487±0.030). Basic type of sculpture on paramedian vertex and mesosoma microreticulate, though varying in strength. The six known species of the C. minutior group are rather similar in shape of head, mesosoma and spines as well as in type of microsculpture but have significantly smaller absolute body size and a much lower absolute postpetiolar height PPH which is 111 ± 8 [92,130] µm in 207 workers of the C. minutior group but 153 ± 12 [123,188] µm in 577 workers of the C. nuda group.

4.2. The major subdivision of the C. nuda group into the C. nuda and C. mauritanica species complexes
Considering all 16 morphometric characters, the exploratory data analyses NC-Ward and NC-K-Means showed 100% agreement in subdividing the C. nuda group in two main clusters: the C. nuda species complex containing four species and 101 nest samples and the C. mauritanica species complex containing four species and 149 nest samples. There was also a 100% confirmation of these two clusters by the controlling linear discriminant analysis (data not shown) and a simplified separation of the two main clusters is given in the key (section 4.5.).

4.3. Stepwise subdivision of the C. mauritanica species complex into four species
NC-Ward showed two clearly separated clusters (Fig. 4) and disagreed with K-Means in one sample only. This sample was then run as wild-card in a controlling LDA which determined an error rate of 0.7% in NC-Ward and 0% in NC-K-Means. A mean error of 0.4% in two exploratory data analyses is clearly below the threshold of 4.0% of the Pragmatic Species Concept and confirms the status of C. mauritanica as a separate species. Attempts to further subdivide the C. mauritanica cluster clearly failed: the final error rates relative to the controlling LDA were 4.9% in NC-Ward and 16% in NC-K-Means.

The 61 samples of C. mauritanica were excluded from the next step of analysis which was run to subdivide two main clusters ABC and D in the remaining 88 samples of the C. mauritanica species complex. NC-Ward and K-Means disagreed in this analytical step in four samples, three of which were single specimens. These four samples were run as wild-cards in the controlling LDA which determined an error rate of 3.4% for NC-Ward and of 1.1% for NC-K-Means (Fig. 5). A mean error rate of 2.2% in two different exploratory data analyses is below the 4% threshold required by the PSC. This is a surprisingly good performance when considering that the two separated main clusters ABC and D show an extreme overlap in basically any character (Tab. 1), (b) that the samples came from a huge geographic range, extending over 17000 km from Reunion Island in the Indian Ocean to the Hawaii Islands in the Pacific Ocean, (c) that there is certainly a high degree of isolation between the many subpopulations scattered over this area and (d) that 21 of the 88 samples consisted of only a single specimen. The two main NUMOBAT clusters ABC and D are fully supported by mtDNA data. There was a complete agreement of phenotype clustering with the two main mtDNA clades A+B+C and D in Okita et al. (2015) for 30 samples where both a phenotyping and a COI/II mtDNA haplotyping was available (Fig. 5). A difference in adjusted sequence divergence (K2P distance) of > 3.5% between the main mtDNA clades (Okita et al. 2015) is a strong support for the heterospecificity of the two main NUMOBAT clusters.

The position of the type series within the NUMOBAT clusters ABC and D was checked by wild-card runs in the controlling LDA. According to this, the mean posterior probabilities of belonging to clusters ABC (first value) and D (second value) were 0.9647 and 0.0353 in four paratypes from the holotype nest of Cardiocondyla kagutsuchi, 0.0001 and 0.9999 for three paratypes from the holotype nest of Cardiocondyla itsuki sp. nov. and 0.7864 and 0.2136 for the type specimen of C. strigifrons from Java. The probability of 0.786 for the C. strigifrons type belonging to cluster ABC is not really convincing. Yet, this allocation is supported by several arguments the
FIGURE 4. NC-Ward clustering of 149 samples of the *Cardiocondyla mauritanica* species complex. The upper of the two main branches belongs to *C. mauritanica* Forel, the lower one to the remaining three species of the complex. The left column of bars indicates the final clustering hypothesis for K=2 (*C. mauritanica* vs. not *C. mauritanica*) determined by a controlling linear discriminant function (LDA), the right column of bars the classification by non-hierarchical NC-K-Means clustering. The classification errors in in NC-Ward and NC-K-Means are 0.7% and 0% respectively.
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FIGURE 5. NC-Ward clustering of 88 samples of the remaining species of the Cardiocondyla mauritanica species complex after exclusion of C. mauritanica. The upper of the two main branches belongs to C. itsukii sp. nov., the lower one to the other two species of the complex. The left column of bars indicates the two main branches of mtDNA haplotyping, the median column the final clustering hypothesis for K=2 (C. itsukii sp. nov. vs. not C. itsukii sp. nov.) determined by a controlling linear discriminant function (LDA), and the right column of bars the classification by non-hierarchical NC-K-Means clustering. The classification errors in in NC-Ward and NC-K-Means are 3.4% and 1.1% respectively. The agreement of mtDNA and all three NUMOAT analyses is 100% on the K=2 level.
FIGURE 6. NC-Ward clustering of 45 samples of the two remaining species of the Cardinalyta mauritanica species complex after exclusion of other species in the previous steps. The upper of the two main branches belongs to C. kagutsuchi Terayama, the lower one to C. strigifrons Viehmeyer. The left column of bars indicates the two sub-clusters of mtDNA haplotyping (cluster C red, cluster AB black), the median column the final clustering hypothesis for K=2 (C. kagutsuchi vs. C. strigifrons) determined by a controlling linear discriminant function (LDA), and the right column of bars the classification by non-hierarchical NC-K-Means clustering. The agreement between all three NUMOBAT methods is 100% whereas mtDNA haplotyping deviates from this classification in 12% of the samples.
first of which is a geographical one: within 33 samples from Malaysia, Singapore, Indonesia, the Philippines and Papua New Guinea, 90.9% belonged to cluster ABC and only 9.1% to cluster D. Subjective inspection of mesosomal and petiolar shape also favors an allocation of the *C. strigifrons* type to cluster ABC. Okita *et al.* (2015) have proposed that cluster D differs from ABC by the tips of spines being elevated significantly above the profile of the propodeum immediately anterior to the spines and by a steeper anterior face of the petiolar node (Figs. 6v, 6vi in Okita *et al.*). The picture of the *C. strigifrons* type in antweb.org (FOCOL 1611) shows a mesosomal shape indicating an allocation to cluster ABC (the petiolar profile may also favor this placement but is not fully visible). The spine and petiole shape argument, though perhaps statistically true, is also not compelling because the variability of cluster D in these shape characters is quite large—several individuals within some 108 studied workers of cluster D in the collection of SMN Görlitz approached the ABC condition. However, a fourth and convincing argument for allocation of the *C. strigifrons* type to cluster ABC is the CL/CW value of 1.229: the largest value within 108 investigated workers of cluster D was 1.215 (Tab. 1). Because CL/CW is normally distributed in cluster D with mean ± standard deviation being 1.1686 ± 0.0183, the probability in this cluster for achieving a value of 1.229 or larger is calculated as $p=0.0005$. These four congruent lines of argumentation justify placing *C. strigifrons* in cluster ABC. With both the *C. strigifrons* and *C. kagutsuchi* types placed in cluster ABC, cluster D represents the new species *C. itsukii*.

In the next step, the 45 samples in NUMOBAT cluster ABC were checked for substructuring. Assuming two main branches, the classifications of NC-Ward and NC-K-Means agreed by 100%. The NC-Ward dendrogram (Fig. 6) showed a cluster C with 29 samples that included the type series of *C. kagutsuchi* and another cluster AB consisting of 16 samples that included the type of *C. strigifrons*. If the types are run as wild-cards in a controlling LDA, the type series of *C. kagutsuchi* is allocated with $p=0.9890$ to cluster C and the type of *C. strigifrons* with $p=0.9999$ to the cluster AB. The classification agreed in 97.2% of the 141 individual workers with the classification on the nest sample level. All these data provide strong evidence for heterospecificity of *C. kagutsuchi* and *C. strigifrons*. The NC-Ward clustering (Fig. 6) also shows geographic structuring of populations. All Japanese samples of *C. strigifrons* are grouped within the same subcluster and all but one sample of *C. strigifrons* from outside Japan form the other subcluster. Within the *C. kagutsuchi* cluster, all samples from Japan, the Philippines, Thailand and the Mariana Islands are grouped within the same subcluster whereas 76% of the samples from Indonesia and Malaysia are placed in the other subcluster. The full agreement of NUMOBAT clustering with mtDNA haplotyping as seen in the two main clusters ABC and D was not repeated here. Two *C. kagutsuchi* samples from Malaysia: Kuala Lumpur University-2002.12.17-M13 and Malaysia: Ulu-Gombak-2002.12.24-M14 showed mtDNA haplotypes typically found in *C. strigifrons*. 12% mtDNA paraphyly in a total of 17 samples represent a normal situation in Eumetazoa in general (reviewed by Funk & Omland 2003) and in ants in particular (e.g., Shoemaker *et al.* 2006, Fisher & Smith 2008, Goropashnaya *et al.* 2004, Heinze *et al.* 2005, Kaden *et al.* 2005, Seifert 2009, Seifert *et al.* 2017, Seifert & Goropashnaya 2004, Wild 2008). It remains unclear if this mismatch is due to ancient hybridization, incomplete lineage sorting or other causes.

Attempts to further subdivide the *C. strigifrons*, *C. kagutsuchi* and *C. itsukii* sp. nov. clusters resulted in disagreements between NC-Ward and NC-K-Means of 12.5%, 40% and 9% respectively and it was not possible to achieve better results by running a controlling LDA with character reduction.

4.4. Stepwise subdivision of the *C. nuda* species complex into four species

This analysis was done in the first step with 14 characters only because SPBA and FRS data were not measured in 45% of the *Cardiocondyla nuda* samples. NC-Ward showed two clearly separated clusters of the 101 samples (Fig. 7) and disagreed with NC-K-Means in 3.0% of the samples. These samples were then run as wild-cards in a controlling LDA which determined the error of NC-Ward as 1.0% and that of NC-K-Means as 2.0%. A mean error of 1.5% in two different forms of exploratory data analyses is clearly below the threshold of 4% required by the PSC and the subdivision of the two main clusters E and F (upper and lower cluster in Fig. 7) is of strong taxonomic significance. If run as wild-cards in a controlling LDA, the type specimen of *C. nuda* is allocated with $p=0.9903$ and 0.9946 respectively.

The *C. nuda* samples were removed from the analysis which considered now the remaining 63 samples and 15 characters—SPBA/CS and FRS/CS were included and dFov was excluded because of measurement inconsistencies. The disagreement of NC-Ward and NC-K-Means was 6.3%. After running the mismatching samples as wild-cards in a controlling LDA, the error rates were determined as 0% in NC-Ward (Fig. 8) and 6.3% in NC-K-Means, which is, as mean of both analyses, below the critical threshold. If run as wild-cards in a LDA
FIGURE 7. NC-Ward clustering of 100 samples of the Cardiocondyla nuda species complex. The lower of the two main branches belongs to *C. nuda* (Mayr), the upper one to the three remaining species of the complex. The left column of bars indicates the final clustering hypothesis for $K=2$ (*C. nuda* vs. not *C. nuda*) determined by a controlling linear discriminant function (LDA), and the right column of bars the classification by non-hierarchical NC-K-Means clustering. The classification errors in NC-Ward and NC-K-Means are 1.0% and 2.0% respectively.
FIGURE 8. NC-Ward clustering of 61 samples of the two remaining Cardiocondyla nuda species complex after C. nuda has been removed from analysis. The lower of the two main branches belongs to C. atalanta Forel, the upper one to C. paranuda. The left column of bars indicates the final clustering hypothesis for K=2 (C. atalanta vs. C. paranuda) determined by a controlling linear discriminant function (LDA), and the right column of bars the classification by non-hierarchical NC-K-Means clustering. The classification errors in NC-Ward and NC-K-Means are both 3.3%.
FIGURE 9. Phylogenetic tree estimated from a 871bp fragment of CO I / CO using MrBayes version 3.2.2 with GTR+G+I as model for gene evolution. Bayesian posterior probabilities given as percentages at the nodes. Using two samples of the Cardiocondyla elegans species complex as outgroup, mtDNA shows a strong separation of the C. nuda species group into two major clades containing four species of the C. mauritanica species complex and three species of the C. nuda species complex. The disagreement between the species identification based on morphology and the mtDNA tree is here 3.8%.

considering all 15 characters, the type specimen of C. paranuda was allocated to the upper cluster in Fig. 8 with \( p = 0.9148 \) and the type specimen of C. atalanta to the lower one with \( p = 0.9859 \). Wild-card runs in a stepwise, character-reduced LDA using the seven characters CS, PLG/CS, MpGr/CS, SL/CS, sqPDG, FRS/CS, and PoOc/CL increased the posterior probabilities to 0.9916 the type specimen of C. paranuda and to 0.9984 in the type specimen of C. atalanta. The classification error in 115 worker individuals was 0% in the LDA considering 15
characters and 1.7% in the character-reduced LDA. Heterospecificity of *C. atalanta* and *C. paranuda* is also supported by a clear ecological separation (see below) and coincident mtDNA phylogeny (Fig. 9). The sequence divergence of *C. atalanta* and *C. paranuda* was 7.0–7.9 % within a 871bp fragment of COI/CO. Considering the same fragment, *C. nuda* differs from *C. atalanta* by 5.6–5.9% and from *C. paranuda* sp. nov. by 7.0–7.4%. No attempts were made to further subdivide the *C. atalanta* and *C. paranuda* clusters because the sample size in the subclusters was too small for reliably running a controlling LDA. There is no indication that the *C. atalanta* and *C. paranuda* clusters could represent an intraspecific dimorphism: within 38 samples of both species from the sympatric area in Australia with at least two specimens per sample, there was one sample with one worker of each *C. atalanta* and *C. paranuda* on the same pin. This sample represents a forager collection and the two workers are not known to come from the same nest. If this pin is considered a mixed nest sample and related to a total of 16 pure *C. paranuda* samples and 21 pure *C. atalanta* samples, the DIMORPH test of Seifert (2016) rejects intraspecific dimorphism with p=0.014 whereas heterospecificity of non-parasitic species is confirmed with p=1.000 (Fisher's exact test). The corresponding data in the $X^2$ test are $F_{1,2} = 9.01$, p=0.011 and $F_{1,2} = 0.714$, p=0.224.

Above we separated seven species in the *C. nuda* group based on a sufficient sample size and objective operational criteria. However, one species is described here on the basis of only a single sample. We present here a brief justification. The types of *Cardiocondyla compressa* are two workers collected from Hammond Island in the Torres Strait between Australia and Papua New Guinea. The two specimens are morphometrically close to *C. atalanta* (Tab. 2) but the head size (CS) and petiole width (PEW/CS) are below the lower extremes known in *C. atalanta*. A head size of 410 µm or lower, as found in both *C. compressa* sp. nov. workers, has a probability of 0.0018 to occur in *C. atalanta*. The two values of PEW/CS, 0.246 and 0.255, have probabilities of 0 and 0.0007 respectively. After RA V-correction within the allometric space (Seifert 2008b), the probabilities for PEW/CS increase to 0.0007 and 0.0061 respectively but these are still very low values.

4.5. Synoptic list of the species of the *C. nuda* group and key to the workers

*Cardiocondyla atalanta* Forel 1915  
*Cardiocondyla compressa* sp. nov.  
*Cardiocondyla itsukii* sp. nov.  
*Cardiocondyla kagutsuchi* Terayama 1999  
*Cardiocondyla mauritanica* Forel 1890  
*Cardiocondyla nuda* (Mayr 1866)  
*Cardiocondyla paranuda* Seifert 2003  
*Cardiocondyla strigifrons* Viehmeyer 1922

There is no doubt that species separation in the *C. nuda* group is difficult. It requires careful consideration of character definitions and the use high-resolution optical and measurement systems. This presents a significant challenge for practitioners of biodiversity research who have to process thousands of ant samples in their usual business. The key presented here considers 13 out of 16 recorded characters (excluding dFov, PoOc and sqPDG) and it achieves an acceptable error rate when 4–6 numeric characters are used in almost each step of the determination procedure. Considering this, the best (and in the end more time-saving) procedure is to measure all these 13 characters for a specimen and run the specimen as a wild-card in a LDA against a large body of reference data of determined specimens. In order to allow a user such an approach, the senior author is willing to provide this reference system with primary data of all eight species.

A dichotomous key it is presented below. The key has the advantage that the two tramp species with the largest geographic ranges are keyed out first and with low error rates. All characters are given as absolute measurements in mm. The geographic information included in the key has to be taken with caution as some species of the group have tramp species properties and could be found outside the range currently known.

1a Discriminant 176.328 PPH -49.049 CW +51.521 SP -59.844 PPW +6.61 < 0  
1b Discriminant 176.328 PPH -49.049 CW +51.521 SP -59.844 PPW +6.61 > 0  
2a Discriminant 214.193 PLG -88.759 SP +57.676 SL -106.17 PEH -10.465 < 0  
2b Discriminant 214.193 PLG -88.759 SP +57.676 SL -106.17 PEH -10.465 > 0
Discriminant 319.279 PLG -49.672 PPW +133.938 FRS -177.726 EYE +91.370 CW -63.848 SL -12.955 >0

Leptothorax caparica

Cardiocondyla ectopia

data but their determination was clear by geographic indication alone.

3b Discriminant 319.279 PLG -49.672 PPW +133.938 FRS -177.726 EYE +91.370 CW -63.848 SL -12.955 <0

Morocco

3a Discriminant 319.279 PLG -49.672 PPW +133.938 FRS -177.726 EYE +91.370 CW -63.848 SL -12.955 >0


4b Discriminant 75.783 PPH -157.227 SP +62.967 PPW -117.467 SPBA +101.708 EYE -17.387 > 0

6a Discriminant 538.753 PLG -72.321 CL +174.434 MpGr +46.778 SL +4.27 < 0

7b Petiole not very narrow, discriminant 124.351 PEW -1.129 CW -13.561 > 0; Australia without the inner parts of the continent, Papua New Guinea

1985.11.10, [30.66, 35.24]; Tal Yeroham, 1966.03.27, [31.00, 34.91].

Jordan: Ein Yahaf, 1985.11.10, [30.66, 35.24]; Tal Yeroham, 1966.03.27, [31.00, 34.91]. Hammam Matin, 1996.11.01, [31.60, 35.61]; Rum, 1996.11.07, [29.57, 35.42].

4.6. Treatment by species

Cardiocondyla mauritanica Forel 1890

Tab. 1


All material examined. A total of 71 nest samples with 147 workers were subject to NUMOBAT investigation. Four samples marked with "***" were not included in the multivariate exploratory data analyses of NUMOBAT data but their determination was clear by geographic indication alone.

Afghanistan: Kandahar: Kunar, 1953.01.22, [34.820, 71.104]; Kandahar: Kunar, 1953.01.18, [34.820, 71.104].

Egypt: Assuan, pre 1940 (Karavajev), [24.09, 32.90]; EGY: Hurghada Gifthun, 1992.09.12, [27.19, 33.82]; South Sinai: Mafareq, 1998.03.08, [29.0, 34.0].


India: Himachal Pradesh: Kullu-20 km E, 1996.10.03, No 494, No xx, [32.00, 77.20]; Himachal Pradesh: Kullu-10 km N, 1996.10.xx, [32.00, 77.10]; Panjab: Chandigarh, 1978.08.21, [30.70, 76.80].


Iraq: Mesopotamia, 1918.10.18, [32.00, 46.0].

Iran: Basest, 1974.05.25, [30.36, 51.16]; Shiraz-10 km SSW, 1997.09.14, [29.50, 52.49]; Shiraz-16 km ESE, 1997.09.16, [29.52, 52.71]; Shiraz-7 km NE, 1997.09.18, No 17, [29.63, 52.63].

Israel: Ein Yahaf, 1985.11.10, [30.66, 35.24]; Tal Yeroham, 1966.03.27, [31.00, 34.91].

Jordan: Hammam Matin, 1996.11.01, [31.60, 35.61]; Rum, 1996.11.07, [29.57, 35.42].

Libya: Tripolis, Dernah, 1906.08.xx, [32.87, 13.19].


Morocco: Qued Draa-24 km E, 1991.05.09, [30.80, -5.55]; Ait Ourir-8 km E, 1995.05.09, [31.55, -7.58]; Zagora-11 km S, 1998.05.29, [30.24, -5.82].

Oman: Kayma Desert, 1993.05.03, [21.0, 57.0]; Wahiba Sands, 1989.12.15,
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Pakistan: Swat: Madyan, 1974.06.22, [35.14, 72.54].


Saudi Arabia: Qarina valley farm, 2009.11.05, No A5, [25.13, 46.16]; Salboukh farm, 2009.11.05, No A8, [25.08, 46.35].


Tunisia: Gabes, pre 1890.xx.xx (Forel), type Cardiocondyla nuda, [33.88, 10.09]; Hammamet-80 km S, 1993.03.02, [36.41, 10.59]; Kairouan, pre 1940 (coll. Santschi), [35.68, 10.10].

Turkey: Inkuma, 1984.06.12, [39.00, 36.00]; Incesu-2 km N, 1997.05.xx, [38.44, 35.58]; Mersin: Silifke-15 km SE, 1993.05.29, [36.30, 34.04].


Geographic range. For details, see Material examined. If the distributional centre is indicative, its native range is supposed to extend from India over Pakistan west to the Middle East and the Mediterranean. The populations in the Canaries, the Nearctic and Indonesia were most probably founded by anthropogenous introduction. Partial sympatry with Cardiocondyla itsukii sp. nov. is observed in the Oriental region but Cardiocondyla mauritanica apparently has difficulties penetrating the Indo-Malayan ranges occupied by the other species of the group and it seems to be fully absent from the Australasian and Polynesian faunal regions.

Diagnosis. See key.

Biology. Cardiocondyla mauritanica is mainly a species of semi-deserts and other xerothermic habitats and the most widely distributed tramp species of the Cardiocondyla nuda group. Mating is strictly intranidal and colonies are polygynous (Heinze et al. 1993), traits considered preadaptations for the tramp species strategy. Winged males are unknown, wingless ergatoid males use their shear-shaped mandibles to crush the cuticle and to cut off the legs and antennae of other freshly emerged males (Heinze et al. 1993).

Comments. The synonymies stated above are very clear. The five paratype workers of Cardiocondyla mauritanica, three paratype workers of Cardiocondyla ectopia and the holotype of Leptothorax caparica are allocated to the Cardiocondyla mauritanica cluster with p=1.0000, 1.0000 and 0.9999 respectively when run as wild-cards in a LDA considering all 16 characters.

Cardiocondyla itsukii sp. nov.

Tab. 1, Figs. 10–12

Etymology. The species is dedicated to Itsuki Okita, the son of the junior author.

Type material. The holotype plus 8 paratypes (4 workers, 2 gynes and 2 males) are on three pins labelled "JAP: 34.72297 N, 137.83881 E / Shizuoka Pref. Iwata-shi, 12 m / street margin in rural land/ leg. I. Okita 2010.09.05-81". The pin with the holotype carries a red type label "Holotype (top specimen) / & Paratypes / Cardiocondyla itsukii / Seifert & Okita" and the two pins with paratypes have labels "Paratypes / Cardiocondyla itsukii / Seifert & Okita". These are deposited at SMNG. Five additional paratype workers are deposited at CAS. Furthermore, 120 workers, 86 gynes, and 1 ergatoid male are stored in ethanol at MNEHS.

All material examined. A total of 45 nest samples with 108 workers were subject to NUMOBAT investigation.
**FIGURE 10.** Head of holotype of *Cardiocondyla itsukii* sp. nov. in dorsal aspect.

FIGURE 11. Lateral aspect of holotype of *Cardiocondyla itsukii* sp. nov.

**Description of worker caste.** Worker (Tab. 1, Figs. 10–12): Head less elongated than in all other members of the *C. nuda* group, CL/CW 1.169. Postocular distance moderately large, PoOc/CL 0.444. Eyes relatively small, EYE 0.228. Frontal carinae immediately caudal of the FRS level parallel or very slightly converging (Fig. 10). Foveolae on vertex without interspaces, deeply impressed, with 15–22 µm diameter, and with an inner corona (a flat tubercle) of 7–9 µm diameter having the base of a decumbent pubescence hair in its center. This type of sculpture can also be described as a strongly sculptured microreticulum. Longitudinal sculpture on vertex reduced; only frontal laminae, clypeus, and a narrow area on anteromedian vertex finely longitudinally carinulate; a weak semicircular rugosity is found around the antennal fossae. Lateral mesosoma on whole surface regularly and strongly microreticulate; longitudinal sculpture except for 4–6 weak and short carinulae on metapleuron entirely absent (Fig. 11); dorsal promesonotum with more irregular reticulum the meshes of which have twice the diameter than on lateral mesosoma. Whole surface of petiole and postpetiole more shining, with a very fine microreticulum. The strength of sculpture on mesosoma and waist in particular shows considerable variation within the huge
distributional range, without showing regional trends. Cuticular surface of first gaster tergite smooth and shining, a
very delicate microreticulum with wide meshes becomes visible at higher microscopic resolution. Pubescence hair
length on gaster tergites is the largest within the C. nuda group, PLG/CS 7.12% (Fig. 12). Metanotal groove
distinct but rather flat, MGr/CS 2.16%. Propodeal spines reduced to short dents. Petiolar profile in many specimens
with a steeper frontal face compared to C. strigifrons and C. kagutsuchi. Petiole node slightly longer than wide.
Postpetiole narrower than in C. mauritanica; in dorsal view with clearly angulate sides and straight anterior margin
that is clearly shorter than posterior margin (Fig. 12); postpetiolar sternite flat, without any protrusions. Color most
variable over the huge distributional range: most frequent are morphs with a medium brown mesosoma and waist,
a dark brown head and a dark to blackish brown gaster but much lighter or darker color morphs are not rare. For
morphometric data of 108 workers see Tab. 1.

**TABLE 1.** Morphometric data of workers of C. mauritanica species complex in the sequence arithmetic mean ± standard
deviation [minimum, maximum], n = number of measured individuals.

<table>
<thead>
<tr>
<th></th>
<th>mauritanica (n=147)</th>
<th>strigifrons (n=44)</th>
<th>kagutsuchi (n=97)</th>
<th>itsukii (n=108)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CS [µm]</td>
<td>514 ± 21</td>
<td>530 ± 28</td>
<td>516 ± 24</td>
<td>531 ± 20</td>
</tr>
<tr>
<td></td>
<td>[460,568]</td>
<td>[475,591]</td>
<td>[455,565]</td>
<td>[477,574]</td>
</tr>
<tr>
<td>CL/CW</td>
<td>1.182 ± 0.020</td>
<td>1.202 ± 0.024</td>
<td>1.198 ± 0.024</td>
<td>1.169 ± 0.018</td>
</tr>
<tr>
<td></td>
<td>[1.126,1.224]</td>
<td>[1.159,1.256]</td>
<td>[1.144,1.263]</td>
<td>[1.125,1.215]</td>
</tr>
<tr>
<td>SL/CS</td>
<td>0.813 ± 0.012</td>
<td>0.840 ± 0.013</td>
<td>0.833 ± 0.013</td>
<td>0.826 ± 0.012</td>
</tr>
<tr>
<td></td>
<td>[0.787,0.849]</td>
<td>[0.816,0.872]</td>
<td>[0.802,0.862]</td>
<td>[0.801,0.856]</td>
</tr>
<tr>
<td>PoOc/CL</td>
<td>0.447 ± 0.008</td>
<td>0.446 ± 0.007</td>
<td>0.457 ± 0.009</td>
<td>0.444 ± 0.008</td>
</tr>
<tr>
<td></td>
<td>[0.426,0.467]</td>
<td>[0.435,0.464]</td>
<td>[0.433,0.484]</td>
<td>[0.428,0.469]</td>
</tr>
<tr>
<td>EYE</td>
<td>0.232 ± 0.005</td>
<td>0.234 ± 0.006</td>
<td>0.231 ± 0.005</td>
<td>0.228 ± 0.005</td>
</tr>
<tr>
<td></td>
<td>[0.222,0.246]</td>
<td>[0.219,0.245]</td>
<td>[0.218,0.245]</td>
<td>[0.218,0.239]</td>
</tr>
<tr>
<td>dFOV [µm]</td>
<td>17.7 ± 1.2</td>
<td>17.7 ± 1.1</td>
<td>16.7 ± 1.4</td>
<td>18.1 ± 1.6</td>
</tr>
<tr>
<td></td>
<td>[15.0,20.0]</td>
<td>[15.7,20.5]</td>
<td>[14.3,21.0]</td>
<td>[15.0,21.7]</td>
</tr>
<tr>
<td>FRS/CS</td>
<td>0.265 ± 0.007</td>
<td>0.265 ± 0.007</td>
<td>0.261 ± 0.007</td>
<td>0.270 ± 0.009</td>
</tr>
<tr>
<td></td>
<td>[0.248,0.286]</td>
<td>[0.252,0.285]</td>
<td>[0.246,0.273]</td>
<td>[0.250,0.290]</td>
</tr>
<tr>
<td>SPBA/CS</td>
<td>0.268 ± 0.010</td>
<td>0.252 ± 0.011</td>
<td>0.261 ± 0.012</td>
<td>0.257 ± 0.013</td>
</tr>
<tr>
<td></td>
<td>[0.239,0.296]</td>
<td>[0.230,0.280]</td>
<td>[0.227,0.301]</td>
<td>[0.208,0.283]</td>
</tr>
<tr>
<td>SP/CS</td>
<td>0.090 ± 0.013</td>
<td>0.061 ± 0.009</td>
<td>0.075 ± 0.011</td>
<td>0.072 ± 0.011</td>
</tr>
<tr>
<td></td>
<td>[0.047,0.119]</td>
<td>[0.042,0.079]</td>
<td>[0.050,0.102]</td>
<td>[0.042,0.096]</td>
</tr>
<tr>
<td>PEW/CS</td>
<td>0.265 ± 0.013</td>
<td>0.278 ± 0.012</td>
<td>0.268 ± 0.013</td>
<td>0.271 ± 0.011</td>
</tr>
<tr>
<td></td>
<td>[0.233,0.298]</td>
<td>[0.260,0.318]</td>
<td>[0.236,0.335]</td>
<td>[0.247,0.301]</td>
</tr>
<tr>
<td>PPW/CS</td>
<td>0.485 ± 0.013</td>
<td>0.475 ± 0.021</td>
<td>0.466 ± 0.020</td>
<td>0.455 ± 0.012</td>
</tr>
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<td></td>
<td>[0.449,0.533]</td>
<td>[0.442,0.527]</td>
<td>[0.431,0.524]</td>
<td>[0.430,0.487]</td>
</tr>
<tr>
<td>PEH/CS</td>
<td>0.329 ± 0.009</td>
<td>0.313 ± 0.009</td>
<td>0.311 ± 0.013</td>
<td>0.314 ± 0.009</td>
</tr>
<tr>
<td></td>
<td>[0.309,0.339]</td>
<td>[0.293,0.336]</td>
<td>[0.283,0.367]</td>
<td>[0.296,0.338]</td>
</tr>
<tr>
<td>PPH/CS</td>
<td>0.287 ± 0.008</td>
<td>0.285 ± 0.010</td>
<td>0.280 ± 0.013</td>
<td>0.282 ± 0.009</td>
</tr>
<tr>
<td></td>
<td>[0.270,0.318]</td>
<td>[0.257,0.303]</td>
<td>[0.250,0.326]</td>
<td>[0.258,0.307]</td>
</tr>
<tr>
<td>sqrtPDG</td>
<td>3.72 ± 0.28</td>
<td>3.44 ± 0.16</td>
<td>3.53 ± 0.19</td>
<td>3.54 ± 0.20</td>
</tr>
<tr>
<td></td>
<td>[3.15,4.64]</td>
<td>[3.13,4.03]</td>
<td>[3.11,4.00]</td>
<td>[3.10,4.15]</td>
</tr>
<tr>
<td>PLG/CS [%]</td>
<td>6.38 ± 0.41</td>
<td>6.76 ± 0.42</td>
<td>6.72 ± 0.37</td>
<td>7.12 ± 0.36</td>
</tr>
<tr>
<td></td>
<td>[5.43,7.73]</td>
<td>[5.90,7.54]</td>
<td>[5.51,7.91]</td>
<td>[6.02,7.98]</td>
</tr>
<tr>
<td>MGr/CS [%]</td>
<td>2.14 ± 0.52</td>
<td>1.71 ± 0.46</td>
<td>1.84 ± 0.51</td>
<td>2.16 ± 0.54</td>
</tr>
<tr>
<td></td>
<td>[1.1,3.5]</td>
<td>[0.8,2.7]</td>
<td>[0.8,3.8]</td>
<td>[0.8,3.3]</td>
</tr>
</tbody>
</table>
A TAXONOMIC REVISION OF THE CARDIOCONDYLÀ NUDA GROUP

A TAXONOMIC REVISION OF THE CARDIOCONDYLÀ NUDA GROUP

FIGURE 12. Waist and gaster of holotype of Cardiocondyla itsukii sp. nov. in dorsal aspect.

Geographic range. C. itsukii shows a huge range extending over 17000 km from the Island Reunion in the Indian Ocean, over East India, Indochina, Japan and diverse Pacific Islands east to Hawaii. The most marginal, isolated populations on Island Reunion and Hawaii most probably have been founded by anthropogenous introduction. Despite showing tramp species properties C. itsukii is rare in the Indo-Malayan Archipelago where C. kagutsuchi and strigifrons dominate.

Diagnosis. See key.

Biology. On Hawaii it is one of the very few ants occurring in high densities in primary rain forests with Metrosideros sp. trees and Cibotium ferns and is found also at higher elevations on Mauna Kea volcano (Krushelnycky et. al. 2005, Wetterer et. al. 1998). Biological traits of C. itsukii were studied by Frohschammer & Heinze (2009), Heinze et. al. (2013) and Okita et. al. (2015). Winged males are not known in C. itsukii but only wingless ergatoid males with more than one male usually being present in a colony. The males are in reproductive competition and use the strong shear-shaped mandibles to attack freshly eclosed rivals by crushing their heads or cutting-off appendages but males do not fight when in adult stage. As in C. mauritanica, the strictly intranidal mating and polygyny is considered as a preadaptation for a successful tramp species strategy. The total number of sexual offspring of queens is positively associated with their life-span. More fecund queens live longer than less fecund queens and early onset of sexual production does not negatively affect the queen’s life-span. The number of
eggs present in colonies increased with queen’s age until shortly before death, indicating negligible reproductive senescence. Several queens produced only males late in their lives, suggesting the occurrence of sperm depletion.

**Cardiocondyla strigifrons Viehmeyer 1922**

Tab. 1

**Cardiocondyla nuda** ssp. *strigifrons* Viehmeyer 1922: 211. Lectotype worker (by present designation), Indonesia, Java, Malang (labels "Java", "Cardiocondyla nuda Mayr strigifrons Viehm." and "GBIF-D/FoCol 1611 specimen + label data documented") [ZMHB, antweb.org images of specimen FOCOL1611] (examined). Raised to species: Seifert 2003: 255.

**All material examined.** A total of 16 nest samples with 44 workers were subject to NUMOBAT investigation.

**Indonesia:** Java: Malang, type *C. strigifrons*, pre 1922 (coll. Viehmeyer), [-7.97, 112.63]. **Japan:** Iriomote, 2013.09.18, No 198, (GenBank LC199020), [24.424, 124.083]; Ishigaki, 2013.09.20, No 211, (GenBank LC199022), [24.342, 124.197]; Iwata, 2013.07.17, No 162, (GenBank LC199023), [34.740, 137.888]; Nago 2013.09.17, No 191 (GenBank LC199024), [26.513, 128.013]; Shimonomoseki, 2013.08.26, No 172 (GenBank LC199025), [33.990, 130.996]. **Malaysia:** Lundu, 2007.05.31, No 60/1, [1.683, 109.850]; Sarawak: Gunung Mulu National Park, 1978.03, [4.07, 114.90]; Tioman, 2007.06.08, No 141, [2.779, 104.203]; Ulu Gombak, 2002.12.24, No M3, (GenBank DQ023080), No M51, [3.30, 101.78]. **Philippines:** Luzon: Baguio-W, 1999.02.17, No 11, [16.39, 120.54]. **Papua New Guinea:** Malai Island, [-5.896, 147.943]. **Singapore:** Singapore, pre 1920 (coll. H. Overbeck), [1.31, 103.83].

**Geographic range.** The known range of *C. strigifrons* extends over 6100 km and goes from Thailand over the Indomalayan Archipelago to Papua New Guinea and north to the south Japanese islands. The absence of very isolated populations suggests that it has a lower tramp species potential.

**Diagnosis.** The basic morphology is similar to the condition described for *C. itsukii* sp. nov. There are no subjectively perceivable characters known allowing a reliable separation of this species from the next related species *C. kagutsuchi*. The reduction of dorsal mesosomal sculpture proposed by Seifert (2003) as a character on the basis of a much smaller sample size is also found in other species and is only a statistical difference. Therefore, we omit a lengthy verbal description and refer to combinations of NUMOBAT characters presented in the key or in Tab.1.

**Biology.** The only known social type is a combination of several ergatoid males, intranidal mating and polygyny (observations in the laboratory of J. Heinze).

**Cardiocondyla kagutsuchi** Terayama 1999

Tab. 1


**All material examined.** A total of 29 nest samples with 97 workers was subject to NUMOBAT investigation.

Geographic range. The species is certainly of Indo-Malayan origin and, according to the close morphological proximity and mtDNA phylogeny, its closest relative is *C. strigifrons*. The distributional areas of *C. kagutsuchi* and *C. strigifrons* overlap considerably and no large differences in distribution are apparent.

Diagnosis. The basic morphology is similar to the condition described for *C. itsukii* sp. nov. from which it differs by a more elongated head. The morphological similarity to *C. strigifrons* is extreme in basically any character (Tab.1) and there is no other option for reliable species separation than multivariate analyses using nearly all NUMOBAT characters (section 4.3). Reducing the number of considered characters to four as performed in the simplified key results in an error of 4.4% on the sample level. We omit a lengthy verbal description, which would not provide any help in species delimitation.

Biology. In contrast to its sister species *C. strigifrons*, nest populations of *C. kagutsuchi* show both winged and ergatoid males (Yamauchi et al. 2005). Clonal production of both male and female sexuals and sexual production of workers is very likely for one mtDNA lineage of *C. kagutsuchi* in Japan (Okita et al. 2016).

**Cardiocondyla nuda** (Mayr 1866)

Tab. 2


All material examined. A total of 38 nest samples with 62 workers were subject to NUMOBAT investigation.

**Australia**: New South Wales: Bulli, 1915.05.xx, [-34.31, 150.93]; Northern Territory: Gove, 1982.07.xx, [-11.30, 132.30]; Queensland: Cairns: Esplanade Park, 2014.07.12, No AUSS (GenBank LT718195), No AUSS6 (GenBank LT718196), No AUS7 (GenBank LT718197), No AUS15 (GenBank LT718201), No AUS17 (GenBank LT718202), [-16.910, 145.767]; Queensland: Giru, 1981.xx.xx, [-19.51, 147.13]; Queensland: Kuranda, 1950.11.01, [-16.820, 145.630]; **Fiji Islands**: Ovalau, pre 1866.xx.xx (leg. Godeff), No 2768, type *Cardiocondyla nuda*, [-17.68, 178.79]; Saiaro, pre 1960 (leg. W.M. Mann), [-17.90, 178.00]; Viti Levu, 1976.04.17, [-17.83, 177.94].


**New Hebrides (= Vanuatu)**: Aneityum, 1930.09.xx, [-16.50, 167.60].


**Tonga**: Tonga Tapu, pre 1866.xx.xx (leg. Godeff), [-21.18, -175.22].


Geographic range. The distributional range of *C. nuda* extends over 6000 km in an east-west direction and includes the coast line of North and East Australia, Papua New Guinea and probably all Polynesian islands east to Samoa. The presence of populations in very isolated Polynesian islands (Fiji and Samoa) as early as the mid 19th century suggests that there was some natural way of dispersal over a huge Pacific area before modern ship traffic and goods transport developed.

Diagnosis. see key. The clear cluster allocation of the lectotype is discussed in section 4.4.

Biology. Three of six colonies excavated in 2014 in Cairns contained multiple fertile queens. Males are ergatoid, kill callow males and fight with adult males. Slightly larger, ergatoid males with stubby wings may occasionally occur (observations in the laboratory of J. Heinze).
**TABLE 2.** Morphometric data of workers of *C. muda* species complex in the sequence arithmetic mean ± standard deviation [minimum, maximum], *n* = number of measured individuals. Data with reduced number of measured individuals in *C. muda* are given in italics.

<table>
<thead>
<tr>
<th></th>
<th><strong>nuda</strong> (n=62,43)</th>
<th><strong>paranuda</strong> (n=52)</th>
<th><strong>atalanta</strong> (n=63)</th>
<th><strong>compressa</strong> (n=2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CS [µm]</td>
<td>472 ± 24</td>
<td>473 ± 26</td>
<td>455 ± 15</td>
<td>410 ± 0</td>
</tr>
<tr>
<td></td>
<td>[429,526]</td>
<td>[413,549]</td>
<td>[422,484]</td>
<td>[410,410]</td>
</tr>
<tr>
<td>CL/CW</td>
<td>1.228 ± 0.021</td>
<td>1.214 ± 0.019</td>
<td>1.209 ± 0.019</td>
<td>1.200 ± 0.001</td>
</tr>
<tr>
<td></td>
<td>[1.184,1.307]</td>
<td>[1.178,1.256]</td>
<td>[1.157,1.247]</td>
<td>[1.199,1.200]</td>
</tr>
<tr>
<td>SL/CS</td>
<td>0.812 ± 0.012</td>
<td>0.777 ± 0.018</td>
<td>0.788 ± 0.018</td>
<td>0.794 ± 0.007</td>
</tr>
<tr>
<td></td>
<td>[0.783,0.839]</td>
<td>[0.745,0.829]</td>
<td>[0.757,0.834]</td>
<td>[0.789,0.799]</td>
</tr>
<tr>
<td>PoOc/CL</td>
<td>0.469 ± 0.008</td>
<td>0.464 ± 0.006</td>
<td>0.470 ± 0.008</td>
<td>0.476 ± 0.004</td>
</tr>
<tr>
<td></td>
<td>[0.456,0.498]</td>
<td>[0.452,0.478]</td>
<td>[0.453,0.488]</td>
<td>[0.473,0.478]</td>
</tr>
<tr>
<td>EYE</td>
<td>0.231 ± 0.005</td>
<td>0.233 ± 0.006</td>
<td>0.232 ± 0.005</td>
<td>0.225 ± 0.003</td>
</tr>
<tr>
<td></td>
<td>[0.221,0.244]</td>
<td>[0.218,0.246]</td>
<td>[0.223,0.247]</td>
<td>[0.223,0.227]</td>
</tr>
<tr>
<td>dFOV [µm]</td>
<td>16.3 ± 1.2</td>
<td>15.5 ± 1.5</td>
<td>16.3 ± 1.0</td>
<td>16.2 ± 0.5</td>
</tr>
<tr>
<td></td>
<td>[14.3,19.1]</td>
<td>[13.2,18.6]</td>
<td>[13.1,18.4]</td>
<td>[15.8,16.5]</td>
</tr>
<tr>
<td>FRS/CS</td>
<td>0.264 ± 0.006</td>
<td>0.267 ± 0.008</td>
<td>0.270 ± 0.008</td>
<td>0.262 ± 0.011</td>
</tr>
<tr>
<td></td>
<td>[0.250,0.278]</td>
<td>[0.250,0.283]</td>
<td>[0.253,0.286]</td>
<td>[0.255,0.270]</td>
</tr>
<tr>
<td>SPBA/CS</td>
<td>0.286 ± 0.016</td>
<td>0.289 ± 0.013</td>
<td>0.300 ± 0.015</td>
<td>0.274 ± 0.002</td>
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<td></td>
<td>[0.249,0.330]</td>
<td>[0.264,0.322]</td>
<td>[0.265,0.329]</td>
<td>[0.273,0.276]</td>
</tr>
<tr>
<td>SP/CS</td>
<td>0.118 ± 0.012</td>
<td>0.120 ± 0.009</td>
<td>0.133 ± 0.013</td>
<td>0.124 ± 0.008</td>
</tr>
<tr>
<td></td>
<td>[0.095,0.148]</td>
<td>[0.099,0.142]</td>
<td>[0.096,0.157]</td>
<td>[0.119,0.130]</td>
</tr>
<tr>
<td>PEW/CS</td>
<td>0.287 ± 0.014</td>
<td>0.296 ± 0.015</td>
<td>0.295 ± 0.012</td>
<td>0.250 ± 0.006</td>
</tr>
<tr>
<td></td>
<td>[0.254,0.320]</td>
<td>[0.259,0.338]</td>
<td>[0.272,0.327]</td>
<td>[0.246,0.255]</td>
</tr>
<tr>
<td>PPW/CS</td>
<td>0.501 ± 0.016</td>
<td>0.524 ± 0.018</td>
<td>0.532 ± 0.017</td>
<td>0.510 ± 0.000</td>
</tr>
<tr>
<td></td>
<td>[0.474,0.533]</td>
<td>[0.471,0.560]</td>
<td>[0.492,0.576]</td>
<td>[0.510,0.510]</td>
</tr>
<tr>
<td>PEH/CS</td>
<td>0.344 ± 0.011</td>
<td>0.352 ± 0.016</td>
<td>0.364 ± 0.014</td>
<td>0.350 ± 0.006</td>
</tr>
<tr>
<td></td>
<td>[0.321,0.372]</td>
<td>[0.322,0.388]</td>
<td>[0.333,0.398]</td>
<td>[0.346,0.354]</td>
</tr>
<tr>
<td>PPH/CS</td>
<td>0.341 ± 0.013</td>
<td>0.354 ± 0.014</td>
<td>0.363 ± 0.013</td>
<td>0.327 ± 0.000</td>
</tr>
<tr>
<td></td>
<td>[0.315,0.374]</td>
<td>[0.329,0.381]</td>
<td>[0.321,0.395]</td>
<td>[0.327,0.327]</td>
</tr>
<tr>
<td>sqrtPDG</td>
<td>3.68 ± 0.20</td>
<td>4.24 ± 0.27</td>
<td>3.90 ± 0.20</td>
<td>3.93 ± 0.00</td>
</tr>
<tr>
<td></td>
<td>[3.25,4.29]</td>
<td>[3.73,4.81]</td>
<td>[3.30,4.42]</td>
<td>[3.93,3.93]</td>
</tr>
<tr>
<td>PLG/CS [%]</td>
<td>6.39 ± 0.37</td>
<td>5.04 ± 0.38</td>
<td>6.12 ± 0.39</td>
<td>5.88 ± 0.00</td>
</tr>
<tr>
<td></td>
<td>[5.61,7.31]</td>
<td>[4.34,5.75]</td>
<td>[5.36,6.96]</td>
<td>[5.88,5.88]</td>
</tr>
<tr>
<td>MGr/CS [%]</td>
<td>1.51 ± 0.52</td>
<td>1.27 ± 0.59</td>
<td>1.36 ± 0.40</td>
<td>1.10 ± 0.25</td>
</tr>
<tr>
<td></td>
<td>[0.2,2.7]</td>
<td>[0.2,2.9]</td>
<td>[0.2,2.4]</td>
<td>[0.9,1.3]</td>
</tr>
</tbody>
</table>

*Cardiocondyla paranuda* Seifert 2003

Tab. 2, Figs. 14–16


**Material examined** A total of 30 nest samples with 52 workers were subject to NUMOBAT investigation.
A TAXONOMIC REVISION OF THE CARDIOCONDYL A NUDA GROUP

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Redescription of worker caste. Worker (Tab. 2, Figs. 14–16): Head elongated, CL/CW 1.214. Postocular distance rather large, PoOc/CL 0.463. Eyes relatively small, EYE 0.234. Frontal carinae immediately caudal of the FRS level parallel or very slightly converging. Foveolae on vertex without interspaces, deeply impressed, with 13–19 µm diameter, and with an inner corona (a flat tubercle) of 7–9 µm diameter having the base of a decumbent pubescence hair in its center. This type of sculpture can also be described as a strongly sculptured microreticulum. Longitudinal sculpture on vertex often completely absent (Fig. 15). Weak semicircular rugae are found around the antennal fossae. Lateral mesosoma on whole surface regularly and strongly microreticulate-foveolate; longitudinal sculpture except for 4–6 weak and short carinulae on metapleuron completely absent (Fig. 16); dorsal mesosoma irregularly reticulate-foveolate-shagrinata. Sides of petiole with a deeply sculptured microreticulum, dorsal petiole and postpetiole with a weak and shallowly sculptured microreticulum. Cuticular surface of first gaster tergite rather smooth and shining but on its whole surface with a well-developed microreticulum (Fig. 14). The pubescence hairs on gaster tergites are the shortest within the C. nuda group, PLG/CS is only 5.06%. Metanotal depression very shallow, MGr/CS 1.28%. Propodeal spines short but clearly longer than in the C. mauritanica species complex. Dorsal propodeum sloping down to base of spines under an angle of 20°. Petiole node slightly longer than wide. Postpetiole in dorsal view with only suggestedly angulate sides and straight anterior margin that is slightly shorter than posterior margin; postpetiolar sternite bulging, without any protrusions but on each side with a suggested paramedian, longitudinal carina. Head, mesosoma, waist and appendages often amber-colored, gaster significantly darker—this is the most frequently observed coloration but populations with dark headed specimens or such with concolorous amber specimens do occur. For morphometric data of 52 workers see Tab. 2.
A TAXONOMIC REVISION OF THE CARDIOCONDYL A NUDA GROUP

Geographic range. Australia, only species of the whole genus Cardiocondyla occurring in inner Australia.

Diagnosis. see key. The very short gastral pubescence is the most obvious difference to the sister species C. atalanta.

Biology. C. paranuda is apparently well adapted to arid and very hot climate and the only species of the whole genus Cardiocondyla occurring in inner Australia. This is demonstrated by significant differences between C. atalanta and C. paranuda in the continentality of the sites. The mean distance from sea shore and mean annual rainfall are 23 ± 51 [0,252] km and 1430 ± 716 [500, 4500] mm in 27 sites of C. atalanta and 329 ± 332 [0, 904] km and 588 ± 385 [150, 1250] mm in 27 sites of C. paranuda. These differences are significantly different in both sea shore distance (ANOVA $F_{1,52} = 22.39$, $p<0.0005$) and annual rainfall (ANOVA $F_{1,52} = 28.90$, $p<0.0005$). As yet only foragers have been collected and colony structure, male morphology, and behavior are unknown.

Comments. There is a serious problem with the site documentation in the holotype of C. paranuda. The specimen was sent by C.A. Collingwood to the senior author in the 1980s with the labelling "TUNISIA: Medinine-32 km SE Chabania-6 km NW leg. H. Heatwole 1976". If run as a wild-card in a LDA considering all 16 morphometric characters and collecting all samples of the C. mauritanica species complex in class 1 and all of the C. nuda complex in class 2, the holotype C. paranuda is allocated to the C. nuda complex with $p=1.0000$. This is problematic because species of the C. nuda species complex are completely absent from the West Palaearctic and North Africa and it appears also most unlikely that ants from Australia should have been anthropogenically introduced to a site in the Sahara desert. Furthermore, NC-clustering places the holotype in a cluster of C. nuda group specimens that are treated as a single species that is restricted to the Australian continent and sister to C. atalanta (Fig. 8). A wild-card run in a LDA confirms this allocation with $p=0.9916$ (see section 4.4). The most
probable explanation for this conflicting situation is a confusion of labels. Harold Heatwole collected in North Africa, Tibet and Australia—for instance, the two *C. paranuda* samples from Queensland: Chilcott Island in 1967 were taken by him. He usually gave his specimens to Collingwood stored in tubes with ethanol. As repeatedly witnessed by the senior author in personal contacts during laboratory work in 1982 and 1990, Collingwood had the dangerous habit of placing similar ethanol-stored ants from different tubes side-by-side under the microscope for better comparison and sometimes he confused from which tube he had taken the specimens. We conclude that the type of *C. paranuda* has most probably been collected somewhere in Australia.

*Cardiocondyla atalanta* Forel 1915
Tab. 2, Fig. 13


**Material examined.** A total of 34 nest samples with 63 workers were subject to NUMOBAT investigation.

Queensland: Moggil, 1951.05.17, [-27.58, 152.87]; Queensland: Myall Lake, N side, 1977.12.28, [-32.42, 152.40];
Hill- 1 km N, 1981.05.xx, [-15.27, 145.21]; Queensland: Townsville-45km NW, 1976.04.14, [-19.18, 146.55];
Queensland: Woodstock-52 km S, 1976.04.11, [-20.07, 146.82]; Western Australia: Gayamin Pool, Chittering,
without date, [-31.47, 116.09]; Western Australia: Kimberley district, type Cardiocondyla atalanta, [-17.40,
126.60]; Western Australia: Koolan Island, 1987.xx.xx, [-16.13, 123.75]; Lord Howe Island, 1966.xx.xx, No "soil
nest", No "stray sample", [-31.56, 159.09]; Norfolk Island, 1984.03.xx, [-29.03, 167.95]; Norfolk Island,
9.538, 147.291].

Geographic range. C. atalanta is known from all of Australia except its inner desert territories, from Papua
New Guinea and the Lord Howe and Norfolk Islands.

Diagnosis. The species differs from C. nuda by a less elongated head and scape, a higher petiole and a higher
and wider postpetiole. The main difference to the sister species C. paranuda is the longer pubescence on the gastral
tergites (Tab. 2, Fig. 13).

Biology. Colony structure and behavior does not seem to differ from C. nuda. Multiple fertile queens were
present in four of six colonies excavated in 2014 in Kutini Payamu National Park near Lockhart. Males are
ergatoid, kill callow males and fight with adult males (observation in the laboratory of J. Heinze). Slightly larger,
ergatoid males with stubby wings, as previously described for related taxa (Yamauchi et al. 2005), may
occasionally occur.

Cardiocondyla compressa sp. nov. Seifert
Tab. 2, Figs. 17–19

Etymology. The species epithet refers to the extremely narrow petiole.

Type material. The holotype worker and one paratype worker without gaster are on the same pin labelled
"TORRES STRAIT Hammond I. 10.33Sx142.12E", "4–8 July 1974 H. Heatwole et E. Cameron" and "Holotype
(top specimen) & Paratype Cardiocondyla compressa Seifert". The types are deposited at SMNG.

Description of worker caste. Worker (Tab. 2, Figs. 17–19): Small body size, CS 410 µm. Head elongated, CL/
CW 1.200. Postocular distance large, PoOc/CL 0.476. Eyes small, EYE 0.225. Frontal carinae immediately caudal
of the FRS level parallel or slightly converging. Sculpture on head, mesosoma and waist much weaker than usually
seen in the C. nuda group (Figs. 17–19); foveolae on vertex less deeply impressed, of 14–19 µm diameter, and with
an inner corona (a flat tubercle) of 7–9 µm diameter having the base of a decumbent pubescence hair in its center.
Longitudinal sculpture on vertex almost absent, 1–2 weak longitudinal carinulae run parallel to frontal carinae in
short distance to these. Weak semicircular rugae are found around the antennal fossae. Lateral mesosoma on whole
surface regularly microreticulate-foveolate; longitudinal sculpture except for 4–6 weak and short carinulae on
metapleuron completely absent; dorsal mesosoma rather shining (Fig. 19) and with shallow reticulate-foveolate-
shagrinate microsculpture. Sides of petiole with a weakly sculptured microreticulum, dorsal petiole and postpetiole
with shining, with only a delicate microreticulum. Cuticular surface of first gaster tergite rather smooth and shining
but on its whole surface with a well-developed microreticulum. Pubescence hairs on gaster tergites moderately
long, PLG/CS only 5.88%. Metanotal depression very shallow, MGr/CS 1.1%. Propodeal spines short but clearly
longer than in the C. mauritanica species complex. Dorsal propodeum sloping down to base of spines under an
angle of 20°. Petiole very narrow, PEW/CS 0.250; petiole node much longer than wide. Postpetiole in dorsal view
with convex (not angulate) sides and rather low, PPH/CS 0.327; postpetiolar sternite not bulging, thus approaching
the condition in the C. mauritanica complex. Head, mesosoma, waist and appendages yellowish, gaster
significantly darker. For morphometric data of 2 workers see Tab. 2.
FIGURE 17. Head of the holotype of *Cardiocondyla compressa* sp. nov. in dorsal aspect.

FIGURE 18. Holotype of *Cardiocondyla compressa* sp. nov. in lateral aspect.
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FIGURE 19. Holotype of Cardiocondyla compressa sp. nov. in dorsal aspect.

Geographic range. Australia. The only known site is Hammond Island (-10.55, 142.20) in the Torres Strait in North Queensland.

Diagnosis. The species is characterized by a very narrow petiole, small size and reduced sculpture.

Comments. The arguments for describing C. compressa as species different from C. atalanta are presented in section 4.4.

Cardiocondyla shuckardi sculptinodis Santschi 1913 Revived Combination


The type gyne has no head but the conserved mesosoma and waist characters clearly exclude that it from the C. nuda group. Comparisons were made with 114 gynes of C. nuda, C. mauritanica, C. atalanta, C. kagutsuchi, and C. itsukii and NUMOBAT files of these specimens hosted in SMN Görlitz. The C. sculptinodis type differs from this C. nuda group material by a wide petiole with a node appearing globular in dorsal view and a ratio PEW/PPW of 0.68. This ratio is 0.576 ± 0.027 [0.511, 0.654] in 114 measured gynes of the C. nuda group—in other words, the C. sculptinodis type has a probability of p<0.00005 of belonging to this cluster. Furthermore, the propodeum of the C. sculptinodis type shows in lateral view spines reduced to a blunt angle of 125°. The spines of the C. nuda group gynes are developed as more or less sharp dents the upper and lower margins of which form an angle of 75–95°. Thirdly, the color of the C. sculptinodis type is uniformly dark or blackish brown—this has never been observed in the two species of the C. nuda group possibly occurring in Madagascar (C. mauritanica and C. itsukii). On the
other hand, there is no single character of the *C. sculptinodis* type which contradicts an allocation to the *C. shuckardi* group. The character combination is close to *C. shuckardi* Forel 1891 itself, the type of which is also from Madagascar. The *C. shuckardi* group contains a minimum of four and a maximum of six species (unpub. data). It is not clear if there is more than one species of this group on Madagascar, so synonymization at this point would be premature.

**Acknowledgments**

We wish to thank Steven Shattuck for enabling a loan of *Cardiocondyla* material from the ANIC-CSIRO collection Canberra, Mostafa Rizk-Sharaf (Riyadh), Paul Krushelnicky (Honolulu), Andreas Schulz (Leverkusen) and Alan Andersen (Winnellie) for donating field samples. Robyn Meier (Canberra) helped in the clarification of sampling localities. We are indebted to Roland Schultz (Görlitz) for producing the z-stack pictures of the ants. Collection and exportation of *Cardiocondyla* was granted by the Department of Environment and Heritage Protection of Queensland, WITK 14626014 to J. Oettler, University of Regensburg, and export permit PWS2014-AU-001218 issued by the Wildlife Trade and Biosecurity Branch of the Australian Department of the Environment to L. Schrader, University of Regensburg.

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