Cardiocondyla atalanta Forel, 1915, a cryptic sister species of *Cardiocondyla nuda* (Mayr, 1866) (Hymenoptera: Formicidae)

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Abstract

A numeric morphology-based alpha-taxonomy (NUMOBAT) analysis confirmed cryptic heterospecificity of *Cardiocondyla atalanta* Forel, 1915 from *Cardiocondyla nuda* (Mayr, 1866). A discriminant analysis (DA) considering 14 morphological characters confirmed all *a-priori*-determinations of 48 *C. atalanta* and 84 *C. nuda* worker specimens and allocated the holotypes of *C. atalanta* and *C. nuda* to the corresponding cluster with p = 0.999 and p = 1.000, respectively. The Leave-One-Out Cross-Validation (LOOCV) test indicated an error rate of 0 %. *Cardiocondyla atalanta* differs from *C. nuda* in the worker caste by having a shorter and less dense pubescence on first gaster tergite and a shorter scape. Simulations indicate that a single character, absolute pubescence length on first gaster tergite, should enable a safe species discrimination if nest samples containing three workers are available. The distribution of both species differs considerably. *Cardiocondyla nuda* is distributed in Polynesia east to 170° W, in New Guinea and along the coast of northern and eastern Australia. It avoids continental parts of Australia and is apparently best adapted to climate zones with annual rainfalls above 1000 mm. *Cardiocondyla atalanta* ranges all over the Australian continent, including its innermost parts, and is only exceptionally found on offshore islands of Australia. It is better adapted to a xerothermous climate with annual rainfall below 1000 mm. Both species are sympatric in the coastal areas of northern and eastern Australia. Syntopic occurrence was only once observed but is most certainly underrecorded because of low sample numbers.

Key words: Numeric morphology-based alpha-taxonomy, cryptic species, discriminant analysis, Australasian faunal region.

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Introduction

The *Cardiocondyla nuda* group in the definition of Seifert (2003) contains three major clades each of which has a very large geographic range: clade 1 with the cosmopolitan tramp species *Cardiocondyla mauritanica* Forel, 1890; clade 2 with the different forms (possibly cryptic species) of the *C. kagutsuchi* Terayama, 1999 complex, which largely replace *C. mauritanica* in the Oriental, Australasian and Japanese region; and clade 3 formed by *C. nuda* (Mayr, 1866) and *C. atalanta* Forel, 1915, which are both known from the Australasian faunal region. The clear morphological separation of these three clades is unquestionable (Seifert 2003, see also below) and has also been confirmed by genetic data (Heinze & al. 2005).

Seifert (2003) provisionally considered *C. atalanta* as a species separate from *C. nuda* but this statement was based on only two available worker specimens – the holotype and a second specimen from Australia. Since then, I had the opportunity to investigate much more material of *C. atalanta* and also further specimens of *C. nuda*. This enabled the separate species hypothesis to be checked by the objective test systems of NUMOBAT.

Methods

Fifteen numerically described continuous morphological characters were used. All measurements were made on mounted and dried specimens using a pin-holding stage, permitting full rotations around X, Y and Z axes. A Wild M10 high-performance stereomicroscope equipped with a 1.6× planapochromatic objective was used at magnifications of 160 - 320×. 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 visualisation of silhouette lines. A Schott KL 2500 LCD cold-light source in combination with a Leica coaxial polarised-light illuminator provided optimum resolution of tiny structures and microsculpture at highest magnifications. Simultaneous or alternative use of the cold-light sources depending upon the required illumination regime was quickly provided by regulating the voltage up and down. A Leica cross-scaled ocular micrometer with 120 graduation marks ranging over 65 % of the visual field was used. To avoid 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.

Definition of numeric characters

CL   Maximum cephalic length in median line; the head must be carefully tilted to the position yielding the

true maximum; excavations of hind vertex and/or clypeus reduce CL.

CW Maximum cephalic width; the maximum in *Cardiocondyla* 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 either real foveolae or meshes of a reticulum and usually have the base of a decumbent pubescence hair in their centre. In species whose foveolae or mesh-like structures are reduced (e.g., in the *C. stambuloffii* group) the mean diameter of the small punctures or tubercles at hair bases is measured as dFOV. At least six measurements are averaged. Use magnifications ≥ 250× and light diffusers to suppress irritating reflections.

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

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.

PEL Diagonal maximum length of petiole in lateral view, measured from anterior corner of subpetiolar process to dorsocaudal corner of caudal cylinder.

PEW Maximum width of petiole.

PLG Mean length of pubescence hairs on dorsum of first gaster tergite as arithmetic mean of 6 measurements at least. Use magnifications > 250× and light diffusers to suppress irritating reflections.

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.

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. Left and right spine lengths are averaged. This mode of measuring is less ambiguous than other methods and yields higher spine length values in species with reduced spines.

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 normalise 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 320×. 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.

Canonical discriminant analysis

A canonical discriminant analysis (DA) was performed using the SPSS 10.0 statistical package for the whole *C. nuda* group based on sample means, and for the species pair *C. nuda* and *C. atalanta* based on individual workers. All characters passed the tolerance test in a DA to the level of 0.001 as implemented by SPSS both when calculated as primary (crude) or as indexed data. After running a "Leave-One-Out Cross-Validation" analysis (LOOCV, LACHENBRUCH & MICKEY 1968, LESAFFRE & al. 1989), the performance / reliability of a DA was assessed by the degree of coincidence of *a-priori-* and *a-posteriori*-hypotheses (error rate) and by a statistics of *a-posteriori*-probabilities.

Material

The detailed data on field samples are arranged as follows: locality, collecting date, geographical coordinates in decimal format [in square brackets]. In samples without exact collecting dates available, names of collectors are given to allow an approximate estimation of the collecting period. A detailed account of the samples is not given for *C. mauritanica* and the *C. kagutsuchi* complex because these species are only marginally treated in this paper.

Cardiocondyla atalanta

Twenty-eight samples with 48 workers in normal print are the basis of the morphological data sets. In further five samples marked with "**", it was not possible to investigate the full character set. These samples could be determined based on PLG and sqPDF and are included in the distribution map.

Australia: Alice Springs: Kunoth Polk (leg. Greenslade, No 22110174) [23.51° S, 133.59° E]; Alice Springs: Kunoth Polk (leg. Greenslade, No 24110174) [23.51° S, 133.59° E]; Alton Downs, Birdsville - 48 km SW, 19.IX.1972 [26.28° S, 139.10° E]; Ayers Rock, 29.X.1981 [25.35° S, 131.03° E]; Belanglo State Forest, 16.II.1991 [34.53° S, 150.25° E]; Black Mountain, II.1997 [35.28° S, 149.09° E]; Broken Hill, Parkland, 18.V.1971 [31.96° S, 141.46° E]; Chilcott Islands, 8.IX.1967 [16.25° S, 150.00° E]; Chilcott Islands, 8.IX.1967 [16.95° S, 149.91° E]; Coongie - 25 km S, VIII. 1975 [27.50° S, 140.00° E]; Cunnamulla, 17.IX.1974 [28.07° S, 145.67° E]; Derby-City, X.1982 [17.31° S, 123.62° E]; Flinders Ranges, 6.I.1999 [31.37° S, 138.63° E]; Flinders Ranges: Elatina Hut - 1 km NW (leg. Greenslade) [31.35° S, 138.63° E]; Flinders Ranges: Westwloona - 14 km WSW (leg. Greenslade) [31.50° S, 138.50° E]; Fowlers Gap, 19.II.1979 [31.02° S, 146.60° E]; Kimberley district (leg. Mjöberg), holotype *C. atalanta* [17.4° S, 126.6° E]; Lake

Menindee, 19.V.1971 [32.32° S, 142.40° E]; Ti-Tree Well - 11 km S, 28.X.1962 [22.26° S, 133.38° E]; Perth, Kings Park, 14.XII.1969 [31.97° S, 115.84° E]; Ayr - 24 km NW, 14.XI.1962 [19.45° S, 147.23° E]; SW Katherine: Manaulloo [14.50° S, 132.20° E]; Simpson Gap, 6.X.1972 [23.71° S, 133.71° E]; Sydney-Concord, 1.V.1960 [33.86° S, 151.10° E]; Perth (leg. J. Clark) [31.96° S, 115.87° E]; Gayamin Pool, Chittering [31.47° S, 116.09° E]; Woodstock-52 km S, 11.IV.1976 [20.07° S, 146.82° E]; above Baroalba springs, 17.XI.1972 [12.47° S, 132.51° E]. **Kalamurina - 2 km NE, 17.IX.1972 [27.70° S, 138.27° E]; **Jabiru, VI.1984 [12.67° S, 132.87° E]; ** Cameron Corner - 40 km E, XI.1976 [29.01° S, 141.41° E]; **Coonabarabran - 50 km E, 29.III.1980 [31.27° S, 149.80° E], **Mining Camp Mitchel Plateau, V.1983 [14.81° S, 125.83° E].

Cardiocondyla nuda

Fifty-eight samples with 84 workers in normal print are the basis of the morphological data sets. In further two samples marked with "**", it was not possible to investigate the full character set. These samples could be determined based on PLG and sqPDF and are included in the distribution map.

Australia: Cairns district [16.90° S, 145.80° E]; Cedar Creek NP, 13.X.1991 [27.75° S, 153.20° E]; Giru, 1981 [19.51° S, 147.13° E]; Hartleys Creek, 13.VIII.1983 [16.41° S, 145.36° E]; Horne Creek, 23.VIII.2004 [13.73° S, 143.20° E]; Koolan Island, I.1987 [16.13° S, 123.75° E]; Lansdown near Woodstock, 13.IV.1976 [19.67° S, 146.83° E]; Lord Howe Island, 3.XII.1966 [31.56° S, 159.09° E]; Lord Howe Island, 2.XII.1966 [31.56° S, 159.09° E]; Myall Lake, N-side, 28.XII.1977 [32.60° S, 152.40° E]; Cardwell, Kirrama, XII.1957 [18.00° S, 146.80° E]; Kuranda, 1.XI.1950 [16.82° S, 145.63° E]; Barham, 23.III.1960 [35.62° S, 144.15° E]; Bulli, V.1915 [34.31° S, 150.93° E]; Gove, VII.1982 [11.30° S, 132.30° E]; Norfolk, IV.1984 [29.00° S, 167.93° E]; Norfolk, Philip Island, III.1984 [29.03° S, 167.95° E]; Norfolk, Philip Island, XI.1984 [29.03° S, 167.95° E]; Norfolk, Philip Island, IX.1984 [29.11° S, 167.95° E]; Rimbija Island, II.1977 [11.10° S, 136.75° E]; Rounded Hill - 1 km N, V.1981 [15.17° S, 145.13° E]; Rounded Hill, 1980 [15.28° S, 145.21° E]; Rounded Hill, 1981 [15.28° S, 145.21° E]; Moggil, 17.V.1951 [27.58° S, 152.87° E]; S.W. Rocks, 19.V.1983 [30.88° S, 153.03° E]; Thurling Farm, Paddock, X./XI.1977 [17.22° S, 145.36° E]; Townsville - 45 km NW, 14.IV.1976 [19.18° S, 146.55° E]; Woodstock - 52 km S, 11.IV.1976 [20.07° S, 146.82° E]; **Torres Strait, Murray Isl., VII.1974 [9.92° S, 144.05° E]. **Fiji:** Ovalau (leg., Godeffroy, No. 2768), holotype *C. nuda* [17.68° S, 178.79° E]; Saiaro (leg. W.M. Mann) [17.90° S, 178.00° E]; Viti Levu, 17.IV.1976 [17.83° S, 177.94° E]; **Micronesia:** Pohnpei, 30.VII.1994 [6.97° S, 158.22° E]; Pohnpei, 19.III.2000 [6.97° S, 158.22° E]; Pohnpei, Ace, 26.XI.1995 [6.97° S, 158.22° E]; Pohnpei, clear area, 26.XI.1995 [6.97° S, 158.22° E]. **New Guinea:** Seleo, 1896 (leg. Biró) [3.15° S, 142.48° E]; Huon Peninsula, lower Busu River [6.73° S, 147.05° E]; Okapa - 15 km NW, Moife, X.1959 [6.44° S, 145.51° E]; Lae - 16 km NW, 12.VI.1972 [6.64° S, 146.89° E]; Loloata Island, 24.X.2004 [9.54° S, 147.29° E]; Manus: Ndrova Island, 7.V.1972 [2.22° S, 147.24° E]; Morobe: Bulolo, 18.XII. 1967 [7.76° S, 147.59° E]. **Samoa:** Upolu (leg. Godef-
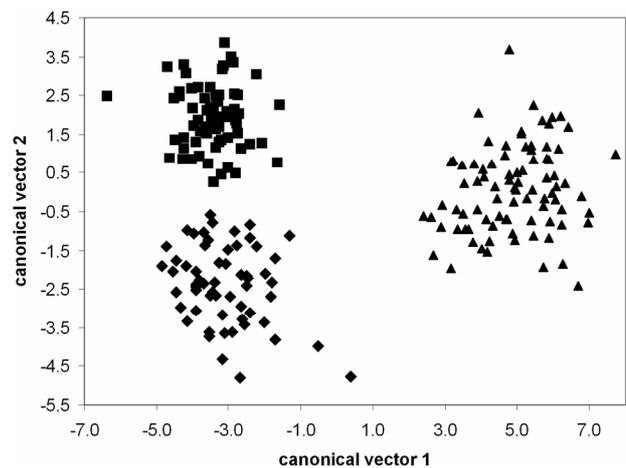

Fig. 1: Canonical discriminant analysis of the three major clades of the *Cardiocondyla nuda* group based on sample means: *C. mauritanica* (squares, n = 69), the forms of *C. kagutsuchi* complex (rhombs, n = 59) and *C. nuda et atalanta* (triangles, n = 86).

froy) [13.92° S, 171.74° W]; Tutuila: Pago Pago, 10.I. 1923 [14.28° S, 170.70° W]; Upolu, Le Mafa, 30.III. 1962 [13.88° S, 171.90° W]; Upolu: Alagaogao, 19.III. 1962 [13.90° S, 171.70° W]. **Solomon Islands:** Honiara, 16.VI.1954 [9.43° S, 159.94° E]; Guadalcanal, 23.XII.1964 [9.64° S, 160.19° E]; Isabel: Buala, 14.XII.1964 [8.16° S, 159.62° E]; Malaita, 16.II.1965 [9.05° S, 161.00° E]; Santa Catalina, 5.VII.1933 [9.70° S, 160.00° E]; **Guadalcanal, Tenavatu, 13.XII.1954 [9.43° S, 160.10° E]. **Tonga:** Tonga Tabu (leg. Godeffroy) [21.18° S, 175.22° W]. **Vanuatu:** Aneityum, IX.1930 [16.50° S, 167.60° E]. **Wallis and Futuna:** Futuna: Mt. Puke, 1965 [14.30° S, 178.15° W]; Futuna: Nuku, III.1965 [14.30° S, 178.15° W]; Nuku Hifala, 30.III.1965 [14.30° S, 178.00° W]; Nuku Tapu, III./IV.1965 [14.30° S, 178.00° W]; Uvea, Matu-Utu, II. 1965 [13.26° S, 176.16° W].

Cardiocondyla mauritanica

69 samples with 138 workers from Afghanistan, Egypt, Greece, India, Indonesia, Iran, Iraq, Israel, Jordan, Kiribati, Libya, Malta, Morocco, Oman, Puerto Rico, Pakistan, Portugal, Spain, Tunisia, Turkey, United Arab Emirates, Ukraine, and USA (Arizona, California, Florida).

Cardiocondyla kagutsuchi complex

59 samples with 148 workers from Bhutan, south China, Guam, Hawaii, India, Indonesia, Japan, Malaysia, Nepal, New Guinea, the Philippines, Singapore, Sri Lanka, and Thailand.

Results and discussion

The major subdivision of the *C. nuda* group

The three major clades of the *C. nuda* group − *C. mauritanica* (clade 1), the different forms of *C. kagutsuchi* (clade 2) and *C. nuda et atalanta* (clade 3) − are safely separable based on sample means by a DA computing 14 characters (Fig. 1).
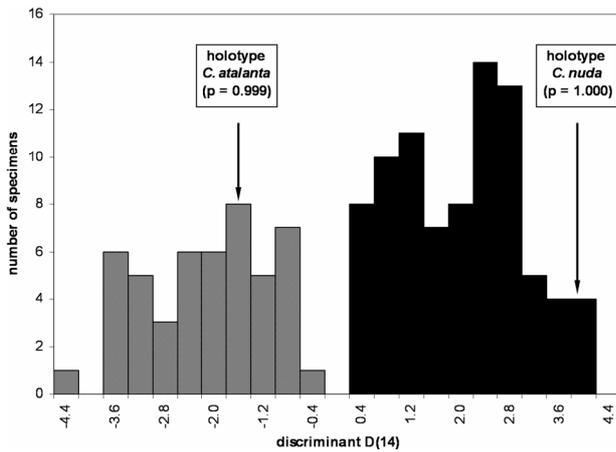
Fig. 2: Canonical discriminant analysis of worker individuals of the sibling species *C. atalanta* (grey bars, n = 48) and *C. nuda* (black bars, n = 84). The position of the holotypes of both taxa is marked by arrows.
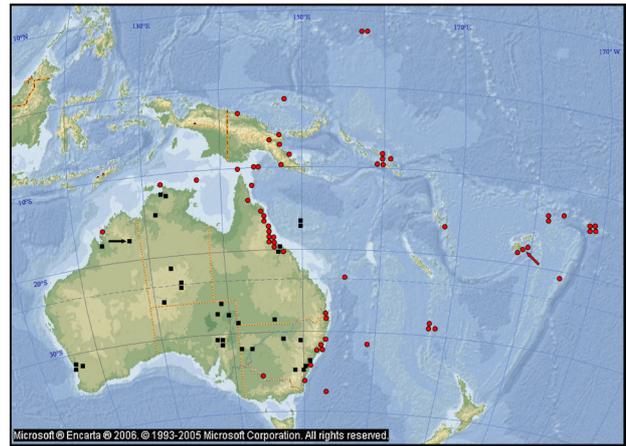

Fig. 3: Distribution map of *Cardiocondyla nuda* (red circles) and *C. atalanta* (black squares) in the Australasian region. Red and black arrows point to the type localities. Original map with permission of Microsoft Corporation.

With PLG/CS and MpGR/CS given in %, a canonical vector 1 of this DA is described by

18.481*CL/CW - 0.147*SL + 36.377*PEW/CS - 47.829*PPW/CS + 20.917*SP/CS + 0.416*sqPDG - 0.00466*PLG/CS - 15.449*PEH/CS + 88.464*PPH/CS - 0.137*dFov - 10.407*EYE/CS + 25.715*PoOc/CL - 3.68*MpGr/CS - 13.38*CS -31.385

and canonical vector 2 by

18.481*CL/CW - 5.062*SL - 59.433*PEW/CS + 49.329*PPW/CS + 50.300*SP/CS + 0.911*sqPDG - 0.00704*PLG/CS + 52.246*PEH/CS - 69.680*PPH/CS + 0.358*dFov + 4.483*EYE/CS - 25.763*PoOc/CL - 6.23*MpGr/CS - 11.648*CS - 16.301.

98.6 % of the 214 samples were determined with *a-posteriori*-probabilities of p > 0.95, and the LOOCV test indicated an error rate of 0 %. Figure 1 also suggests the *C. mauritanica* and *C. kagutsuchi* clade to be more closely related, while the *C. nuda et atalanta* clade is more distant from these two clades. Molecular analysis of mtDNA and 16S RNA (HEINZE & al. 2005) seem to support the relationship among the three clades, although only one sample of the *C. nuda et atalanta* clade was used in the previous study.

Evidence for heterospecificity of *C. atalanta*

With PLG/CS and MpGR/CS given in %, a discriminant D(14) is calculated with the following 14 morphological characters as

D(14) = -0.818*CL/CW + 17.558*SL - 11.006*PEW/CS - 0.864*PPW/CS + 17.78*SP/CS - 2.201*sqPDG + 1.902*PLG/CS - 5.085*PEH/CS + 26.639*PPH/CS + 0.081*dFov + 3.558*EYE/CS + 45.912*PoOc/CL - 0.307*MpGr/CS - 10.105*CS - 49.533.

All *a-priori*-determinations of 48 *C. atalanta* and 84 *C. nuda* worker specimens were confirmed, and 90.9 % of the determinations had *a-posteriori*-probabilities of p > 0.95. The holotypes of *C. atalanta* and *C. nuda* were exactly allocated to the corresponding cluster, with p = 0.999 and p = 1.000, respectively (Fig. 2). The Leave-One-Out Cross-Validation (LOOCV) test indicated an error rate of 0 % and allocated the holotypes of *C. atalanta* and *C. nuda* to the right cluster with *a-posteriori*-probabilities of

p = 0.987 and p = 1.000 respectively. An analysis based on sample means was not performed because 57 % of the 86 samples (including the type samples of *C. nuda* and *C. atalanta*) consisted of only one specimen and because the remaining samples were mainly based upon random surface collecting and should usually not represent nest samples. This situation could distort the covariance, and mixed samples could generate confusion. In fact, one sample from eastern Australia had both *C. nuda* and *C. atalanta* mounted on the same pin.

The zoogeography of *C. nuda* and *C. atalanta* provides additional evidence for regarding them as different biological species. Figure 3 shows the distribution of both sister species in Australia, New Guinea and Polynesia. There is an area of sympatric occurrence in east Australia in which no signs of morphological convergence were evident. Only 1.7 % of the 60 *C. nuda* samples were found more than 120 km from the sea coast. The only exception (Barham, New South Wales) is 256 km from the sea. *Cardiocondyla atalanta* ranges all over the Australian continent, including its innermost parts, and is only exceptionally found on offshore islands of Australia. 61 % of the 33 known samples of *C. atalanta* were more than 120 km from the sea. From these data, the probability that *C. nuda* occurs at the type locality of *C. atalanta* in Kimberley district (about 250 km from the coast line) is very low.

The two species also show clear differences in relation to climatic factors. *Cardiocondyla nuda* avoids continental parts of Australia and is apparently adapted to climatic zones with higher annual rainfall, whereas *C. atalanta* is apparently better adapted to extremely dry climate (Tab. 1).

Tab. 1: Annual rainfall of sites with reliably determined worker material of *Cardiocondyla nuda* and *C. atalanta* given as arithmetic mean ± standard deviation [minimum, maximum]. Data are taken from BARTHOLOMEW AND TIMES BOOKS (1991).

	C. nuda (n = 58)	*C. atalanta* (n = 28)
annual rainfall (mm)	2381 ± 1277 [500, 4500]	629 ± 396 [150, 1250]

Including the square root of mean annual rainfall as the 15th discriminant variable improves the performance of the discriminant function compared to the exclusively morphological approach: 92.4 % of the determinations had *a-posteriori*-probabilities of p > 0.95, and the LOOCV test probabilities of the holotypes of *C. atalanta* and *C. nuda* were 0.998 and 1.000, respectively.

Habitat selection

Clear differences between *C. atalanta* and *C. nuda* regarding the macroclimatic zonation were determined above, but the sparse information provided by the labels and the documentation of collections do not allow a differentiation of habitat selection. Both species seem to occur along a wide gradient from natural to urban habitats, in fully open as well as in woodland sites. *Cardiocondyla nuda* was reported from a coastal dune, coastal grasslands, a pasture, human settlements, moist soils along river and lake sites, *Eucalyptus* savannah and true rain forest. *Cardiocondyla atalanta* was found in *Eucalyptus* and *Acacia-Eucalyptus* savannah, in open grassland, parkland and road sides in cities. It remains unclear whether this species really avoids inner parts of intact rain forest. Its occurrence on two coral sea island sites (Chilcott Island group, leg. H. Heatwole), about 370 km away from the Australian continent, seems exceptional and raises questions. Zoogeographic considerations would decidedly point to *C. nuda*, but all six investigated workers are clearly determined as *C. atalanta* with *a-posteriori*-probabilities of 0.995, 0.998, 0.999, 0.999, 0.999, and 1.000. Passive aerial transport of mated flying gynes from the continent in eastern directions and over such a long distance seems rather unlikely because the main wind directions in east Australia are southeast to northeast. If this case does not represent an error by confusion of locality labels (probably not), I assume a human introduction with soil material from Australia.

Diagnostic characters of *C. atalanta* and simpler approaches to determination

Complex NUMOBAT systems such as those presented above are powerful solutions to difficult identification problems and are indispensable for fundamental taxonomic research that aims to recognise true biodiversity. Practitioners such as ecologists, however, who are confronted with very large sample numbers and a wealth of species belonging to very different genera, can hardly use such methods.

Is a simpler method for recognising *C. atalanta* available? A search for subjectively perceptible characters failed in practice. A researcher could have the superficial impression that *C. atalanta* has a weaker sculpture, a lighter colour, a smaller propodeal lobe and the postpetiole in dorsal view with a less concave anterior margin and more rounded sides, but the intraspecific variability is so large that these characters are almost invalid discriminators. Moreover, the differential characters CL/CW, PEW/CS and SP/CS, proposed by SEIFERT (2003) based on only two available *C. atalanta* workers, only weakly contribute to species discrimination, as the current investigation of much larger material showed.

Table 2 compares morphometric data of both species. Both the correlation with the canonical vector and the significance level in a t-test on independent samples indi-

Tab. 2: Morphometric data of worker individuals of *Cardiocondyla nuda* and *C. atalanta* given as arithmetic mean ± standard deviation [minimum, maximum], their correlation with the canonical discriminant vector and their t-value and significance level in a t-test of independent samples. Data are arranged with falling discriminatory power.

	C. nuda (n = 84)	*C. atalanta* (n = 48)	canonical correlation	t-value p
PLG/CS [%]	6.24 ± 0.41 [5.48, 7.31]	5.07 ± 0.39 [4.34, 5.71]	0.707	16.106 0.000
sqPDG	3.75 ± 0.21 [3.30, 4.33]	4.26 ± 0.27 [3.73, 4.81]	-0.541	12.336 0.000
SL/CS	0.796 ± 0.021 [0.757 ,0.839]	0.776 ± 0.019 [0.745 ,0.829]	0.239	5.404 0.000
PoOc/CL	0.470 ± 0.009 [0.453, 0.498]	0.463 ± 0.006 [0.452, 0.477]	0.219	4.996 0.000
dFOV	15.9 ± 1.0 [13.1, 18.0]	15.2 ± 1.2 [13.2, 17.7]	0.163	3.718 0.000
PEW/CS	0.288 ± 0.013 [0.254, 0.321]	0.295 ± 0.016 [0.259, 0.338]	-0.123	2.797 0.006
PPW/CS	0.512 ± 0.023 [0.474, 0.564]	0.521 ± 0.017 [0.471, 0.560]	-0.106	2.415 0.017
CS	461 ± 22 [422, 526]	471 ± 28 [413, 549]	-0.099	2.268 0.025
CL/CW	1.220 ± 0.022 [1.170, 1.307]	1.212 ± 0.021 [1.157, 1.256]	0.082	1.872 0.063
SP/CS	0.123 ± 0.014 [0.095, 0.157]	0.119 ± 0.010 [0.096, 0.142]	0.068	1.709 0.090
EYE	0.232 ± 0.006 [0.221, 0.247]	0.233 ± 0.006 [0.223, 0.246]	-0.056	1.285 0.201
PPH/CS	0.352 ± 0.019 [0.315, 0.395]	0.353 ± 0.014 [0.329 ,0.380]	-0.009	0.210 0.834
MGr/CS [%]	1.32 ± 0.46 [0.2, 2.6]	1.34 ± 0.58 [0.2, 2.9]	-0.006	0.141 0.888
PEH/CS	0.351 ± 0.016 [0.321, 0.390]	0.350 ± 0.016 [0.322, 0.388]	0.005	0.123 0.903

cate PLG/CS, sqPDG, SL/CS and PoOc/CL to be the best discriminators. Gastral pubescence length, scape length and postocular distance are significantly smaller in *C. atalanta* while gastral pubescence density is larger than in *C. nuda*. However, character overlap is considerable. For the most discriminative characters, the following percentage of specimens is found outside the overlap range: PLG/CS 87.9 %, sqPDG 43.9 %, SL/CS 6.8 %, PoOC/CL 14.4 %.

PLG offers the best approach to a rather simple species recognition. I recommend collecting nest samples and then carefully measuring mean PLG in three workers. Not considering geographic variability, a random combination of the 48 *C. atalanta* and 84 *C. nuda* workers to hypothetic homospecific nest samples of three workers yielded a full separation in 1804 samples:
C. atalanta: PLG 23.82 ± 0.83 [21.6, 25.7] μm (n = 656)
C. nuda: PLG 28.77 ± 1.17 [25.9, 32.1] μm   (n = 1148).
Random combination of two workers to hypothetic nest samples predicts 6.9 % of the samples to be within the interspecific overlap range, while this ratio increases to 18.2 % in individual workers.

Zusammenfassung

Eine numerische Morphologie-basierte alpha-taxonomische Analyse (NUMOBAT) zeigte die Artverschiedenheit von *Cardiocondyla atalanta* FOREL, 1915 und *Cardiocondyla nuda* (MAYR, 1866). Eine Diskriminanzanalyse (DA), die 14 morphologische Merkmale berücksichtigte, bestätigte alle *a-priori*-Determinationen von 48 *C. atalanta*- und 84 *C. nuda*-Arbeiterindividuen und ordnete die Holotypen von *C. atalanta* und *C. nuda* mit *a-posteriori*-Wahrscheinlichkeiten von p = 0.999 und p = 1.000 den entsprechenden Clustern zu. Der "Leave-One-Out Cross-Validation" (LO OCV) Test zeigte eine Fehlerrate von 0 % an. Arbeiter der *C. atalanta* unterscheiden sich von jenen der *C. nuda* durch eine kürzere und weniger dichte Pubeszenz auf dem ersten Gastertergit und durch einen kürzeren Scapus. Die Verbreitung beider Arten differiert beträchtlich. *Cardiocondyla nuda* ist in Polynesien ostwärts bis 170° W, in Neuguinea und entlang der Küsten Nord- und Ostaustraliens verbreitet. Sie meidet kontinentale Bereiche Australiens und ist offensichtlich an Klimabedingungen mit Jahresniederschlägen von über 1000 mm angepasst. *Cardiocondyla atalanta* ist über den ganzen australischen Kontinent einschließlich seiner innersten Regionen verbreitet und wird nur ausnahmsweise auf küstenfernen Inseln gefunden. Sie ist wahrscheinlich besser an extrem xerotherme Umweltbedingungen angepasst. Beide Arten treten in den Küstengebieten Nord- und Ostaustraliens sympatrisch auf. Syntopes Auftreten wurde nur einmal nachgewiesen, sollte aber real häufiger sein, als es durch die geringe Sammelhäufigkeit der Gattung *Cardiocondyla* angezeigt werden kann.

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