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Hypoponera ergatandria (Forel, 1893) – a cosmopolitan tramp species different from *H. punctatissima* (Roger, 1859) (Hymenoptera: Formicidae)

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Abstract

Strong evidence is presented that the ponerine tramp ants frequently found in hothouses around the globe and named for many decades *Hypoponera punctatissima* consist of two clearly separable species: *Hypoponera punctatissima* (Roger, 1859) and *H. ergatandria* (Forel, 1893). Exploratory data analyses using eleven morphometric characters were performed in a total of 95 samples with 213 specimens from the worldwide range. They showed that both species are clearly separable in ergatoid males, gynomorphic females, workers and ergatoid females. Hierarchical NC-Ward clustering, non-hierarchical NC-K-Means clustering, NC-NMDS-K-Means ordination and principal component analysis provided identical classifications with a striking clustering structure. A linear discriminant analysis confirmed the results of these exploratory data analyses by 100% and allocated each of the 27 type specimen to either cluster with posterior probabilities of $p > 0.989$. As junior synonyms of *Hypoponera punctatissima* (Roger, 1859) were established by type investigation: *Hypoponera androgyna* (Roger, 1859), *Hypoponera tarda* (Charsley, 1877), *Hypoponera punctatissima* r. *jugata* (Forel, 1892) and *Hypoponera punctatissima* var. *exacta* (Santschi, 1923). As junior synonyms of *Hypoponera ergatandria* (Forel, 1893) were established by type investigation: *Hypoponera kalakauae* (Forel, 1899), *Hypoponera punctatissima* var. *schauinslandi* (Emery, 1899), *Hypoponera dulcis* var. *aemula* (Santschi, 1911) and *Hypoponera ergatandria* subsp. *bondroiti* (Forel, 1911). Both species are highly sympatric in Europe with one known example to occur in the same greenhouse. Not a single nest sample in the global material contained workers of both *H. punctatissima* and *H. ergatandria* and there was also no nest sample containing conflicting ergatoid males or gynomorphic females. The species obviously maintain separate reproductive cycles under conditions of a broadly sympatric occurrence and developed significant differences in phenology of sexual development, dispersal of alate gynes, habitat selection in the temperate zone and global distribution. These data clearly rebut the recent judgement of Bolton & Fisher (2011) '...that the discriminant functions applied by Seifert (2004) do not isolate discrete species, but rather indicate allopatric populations of the same species, or even different eco-morphs of a single species.' A simple method providing a complete separation of the two species and taking a trained investigator three minutes of working time is presented for males, workers, ergatomorphic females and gynomorphs.

Keywords sibling species | tramp species | morphometrics | allometric growth | exploratory data analysis | nest centroid clustering

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1. Introduction

The ant genus *Hypoponera* (Santschi, 1938) is of mainly tropical distribution and differs in the female castes from *Ponera* Latreille, 1804 by the absence of a fenestra or thin translucent spot on anteroventral subpetiolar lobe. Seifert (2004) has presented evidence that those cosmopolitan tramp ants frequently found in hothouses around the globe and named for many decades *Hypoponera punctatissima* (Roger, 1859) consist of two clearly separable species: *H. punctatissima* and *H. schauinslandi* (Emery, 1899). Seifert (2004) based his argumentation on significant differences in morphology of all three castes, phenology of sexual development, flight behavior, geographic distribution and habitat selection. Seifert's species delimitation has recently been rejected by Bolton & Fisher (2011) who assumed '...that the discriminant functions applied by Seifert do not isolate discrete species, but rather indicate allopatric populations of the same species, or even different eco-morphs of a single species.' The intended immediate response to this statement, however, has been delayed for more than 12 months because the crucially important types of *H. ergatandria* (Forel, 1893) could not then be obtained. The list of junior synonyms of *Hypoponera punctatissima* presented by Bolton & Fisher (2011) contained the incredible number of 22 available names. Seifert (2004) had examined type specimens of twelve taxa he considered to be relevant but he was not able to conclude from original descriptions that *H. ergatandria* (Forel, 1893) and *H. kalakauae* (Forel, 1899) could possibly represent senior synonyms of *H. schauinslandi* (Emery, 1899). As a consequence, Seifert did not investigate types of the former two taxa.

This paper has three goals: (a) to further strengthen the argumentation in favor of a two-species hypothesis by application of advanced forms of exploratory data analysis, (b) to demonstrate by type investigation that the oldest available names for the species in question are *Hypoponera punctatissima* (Roger, 1859) and *H. ergatandria* (Forel, 1893) and (c) to show that very simple means of species discrimination are successful in all three castes.

1.1. Origin of investigation material

Institutions or private collections from which material was studied have the following acronyms:

MCSN Genova – Museo Civico di Storia Naturale Genova, **MHN Genève** – Muséum d'Histoire Naturelle Genève, **NHM Basel** – Naturhistorisches Museum Basel, **NHM London** – Natural History Museum London, **NHM Wien** – Naturhistorisches Museum Wien, **NM Leipzig** – Naturkundemuseum Leipzig, **MNHN Paris** – Muséum National d'Histoire Naturelle Paris, **SDEI Müncheberg** – Senckenberg Deutsches Entomologisches Institut Müncheberg, **SM Frankfurt** – Senckenberg Museum Frankfurt, **SMN Görlitz** – Senckenberg Museum für Naturkunde Görlitz, **UM Oxford** – University Museum Oxford: Hope Entomological Collections, **ZMHU Berlin** – Zoologisches Museum der Humboldt-Universität Berlin

1.2. Material subject to numeric data recording

For both sibling species, numeric data recording was performed in a total of 95 samples containing 18 ergatoid males, 78 gynes and 117 workers.

Hypoponera punctatissima

Numeric data recording was performed in a total of 11 ergatoid males, 42 gynes and 49 workers from 47 different samples and 39 localities. These are in detail (collecting date given in the format yyyy.mm.dd):

Austria: Dornbach, 1862; Linz–27 km ESE; Gutau, 1974.07.30; Purgstall (15.07.53E, 48.03.05N), 1978.07.28. **Belgium**: Bruxelles, Quartier Leopold, railway station, 1994.08.16; Leuven, centre of the city, 1998.07.10; Limburg, Overbroek, Gelinden, 1998.08.16. **Canada**: Montreal, Insectarium, 2003.05.28; Montreal, St. Mary's Hospital 2009.05.14. **England**: Oxford, St.Giles Road West, greenhouse, 1877, type *H. tarda*; Kent: Westerham 1921.10.29; Kent: Westerham, 1921.06.05. **Finland**: Jyväskylä, pre 1925 (leg. Sahlberg). **France**: Reims, 1934.06.24; Reims, 1934.07.18. **Germany**: Berlin, pre 1860, type *H. punctatissima* (Roger); Leipzig-City, 1912.07.15; Miltitz near Leipzig, 1912.06.01; Fahrnau, Hühnerberg, pre 1925; Berlin, pre 1945; Marburg/Lahn, Niederweimar, 1949.07.04; Halle, Passendorfer Wiesen, 1953.07.22; Dresden, Dresdener Heide, 'Saugartenmoor', vii.1975; Untergrochlitz near Greiz, 1977.01.14; Untergrochlitz near Greiz, 1977.07.05; Leipzig-City, 1978.08.; Doberschütz near Eilenburg, 1981.09.27; Doberschütz near Eilenburg, 1981.10.04; Moschwig near Bad Schmiedeberg, 1982.08.15; Leipzig, Auwald, 1983.08.08.; Leipzig, Auwald, 1983.08.12; Leipzig, Zoo 2012.07.05; Ruhla, 1987.06.28; Rudingshain-E, Niddahänge, 1990.07.23; Mainz-Finthen-W, Höllenberg, chalky sand dune, 1990.09./10.; Mainz-Finthen-W, Höllenberg, young orchard, 1990.09./10.; Gotha, Seeberge, Heilige Lehne, 1993.08.14; Königshain near Görlitz, Hochstein–0.5 km SE, 1994.08.09; Rottewitz near Meissen, 2001; Hamburg-Eimsbüttel, 2002.06.26; Großhennersdorf near Herrnhut, 2009.03.05; Mücka near Niesky, 2012.10.20. **Luxemburg**: Luxemburg-City, City Bath 1918.08. **Madagascar**: Imerina, pre 1893, type *H. jugata*. **Morocco**: Tanger, 1904; Volubilis,pre 1921; Rabat, pre 1921. **The Netherlands**: Mijdrecht, 1926.10.08 (van der Wiel). **Norway**: Röa near Oslo, pre 1945 (Eidmann). **Poland**: Rauden, pre 1860, type *H. punctatissima*; **Tunisia**: Al Hammamat (36.24N, 10.37E), 1917.08., type *H. exacta.*

Hypoponera ergatandria

Numeric data recording was performed in a total of 7 ergatoid males, 36 gynes and 68 workers from 46 different samples and 38 localities. These are in detail:

Belgium: Bruxelles, Botanical Garden, greenhouse, 1909.11., type *H. bondroiti*; Maarkedal (50.47°N, 3.37°E), home for the aged, 1997.01. **England**: London, butcher's shop, from electrocutor trap, 2000; Berks, Wilden, butterfly house, 2000.02.25; Yorks: Armthorpe, 1976.02.12; Yorks: Carrside Hatfield, 1973.07.22. **Germany**: Potsdam: Babelsberg, greenhouse Orchidflora, 1939.07.21; Potsdam–1.5 km WNW, Sanssouci, greenhouses, 1939.07.19; Potsdam–1.5 km WNW, Sanssouci, orchid houses, 1940.10.08; Potsdam–1.5 km WNW, Sanssouci, orchid houses, 1940.06.19; Berlin, Zoo (aquarium), pre 1945; Berlin, Zoo, pre 1945 (Heinroth); Berlin-Neukölln, Britzer Garten, butterfly house, 1995.01.12; Berlin-Friedrichsfelde, Tierpark, greenhouse, 2002.10.02; Berlin-Friedrichsfelde, Tierpark, 2004.02; Dienslaken-Hiesfeld, 2007.10.07; Leipzig, Botanical Garden, greenhouse, 1955.03.11; Leipzig, Botanical Garden, greenhouse, 1978.08; Leipzig, Zoo, 2012.05.17; Leipzig, Zoo, 2012.05.24; Leipzig, Zoo, 2012.08.02; Wuppertal, Zoological Garden, 1960.04; Frankfurt/M., Senckenberg-Anlage, at window, 1973.07.13; Frankfurt/M., Senckenberg-Anlage, at window, 1974.07.10; Frankfurt/M., Bockenheim, 2000.07.03; Erfurt, butterfly house, 1999.02.27; Düsseldorf-City, Aquazoo, greenhouse, 2002; Görlitz, Naturkundemuseum, greenhouse, 2002.03.21; Görlitz, Naturkundemuseum, greenhouse, 2005.04.10; Konstanz,botanical garden of university, greenhouse, 2003.04.24; Hannover, Vinnhorsten, 2005.04.27; Heidelberg, Zooschule, 2007.04.27. **Hawaii**: Laysan Island (25.46°N, 171.44°W): Schauinsland, pre 1900, type *H. schauinslandi*; Oahu: Honolulu 1896.11, type *H. kalakauae*; Kauai: Lahue 1896.07, type *H. kalakauae*; **Indonesia**: Java: Cibodas, 2000.01.05. **Japan**: Okinawa: Yona, 1999.10.03; Okinawa: Miyake Isl., 2001.07.26; Okinawa: Miyake Isl., 2003.11.29. **Poland**: Breslau, Botanical Garden, greenhouse pre 1945. **Spain**: Almeria, greenhouse, 2005.03. **St. Vincent**: Bowwood Valley near Kingstown, pre 1893, type *H. ergatandria*; Islet fronting Chateaubelais Bay, pre 1893, type *H. ergatandria*; southern part of St. Vincent: Villa Estate, pre 1893, type *H. ergatandria*. **Switzerland**: Zürich, Zoological Garden, greenhouse, 2001.01.28. **Tanzania**: Kilimandjaro: Kiboscho, 1400 m, 1904, type *H. aemula*. Victoria: Nyanza, Acip. di Sesse, Bugala, 1908.

1.3. The type material and its labeling

Ponera punctatissima (Roger, 1859)

1 lectotype worker [by present designation] apparently labeled by Roger himself 'Roger', '*Ponera punctatissima* n. sp. ♀ Rauden Berlin', 'Museum Paris Coll. O. Sichel 1867', and a copy of a handwritten comment of Roger in German, MNHN Paris; 1 paralectotype worker labeled not in Roger's handwriting 'Schlesien Rauden Roger, S.', '*Ponera punctatissima* Rog.' and 'Type', 2 paralectotype 'Rauden', SDEI Müncheberg; 1 paralectotype worker labeled not in Roger's handwriting 'Schlesien Rauden Roger, S.,'*Ponera punctatissima* Rog.' and 'Type', 2 paralectotype gynomorphs with similar labeling, all ZMHU Berlin.

Ponera androgyna Roger, 1859

Two ergatoid syntype males labeled not in Roger's handwriting 'Schlesien Rauden Roger, S.', '*Ponera punctat.* Rog. *v. androgyna* Rog' and 'Type', ZMHU Berlin.

Ponera tarda Charsley, 1877

2 syntype workers labeled 'Ex Coll. J.O. Westwood. Pres. 1857 by Rev. F. W. Hope. Named 1896 by Edw. Saunders as *Ponera punctatissima* [printed and handwritten], 'burrowing in loose earth in greenhouse R. S. Charsley Oxford' [in Charsley's handwriting], '*Ponera tarda* Charsley. In greenhouse near the Woodstock R Oxford-An *P. punctatissima*? sec. W. J. White + F. Smith in litt. Sept. 1879' [in Westwood's handwriting] and 'Type Hyme 2500 172; 2/2 *Ponera tarda* Charsley, 1877 Syntypes ♀♀ Hope Ent Coll., OUMNH' [printed label]; UM Oxford.

Ponera punctatissima r. *jugata* Forel 1892

1 type gyne labeled 'Typus', '*P. punctatissima* Roger *R. jugata* Forel Imerina (Sikora)' and 'r. *P. jugata* Forel', MHN Genève.

Ponera ergatandria Forel, 1893

1 alate syntype gyne labeled 'Typus', '41d moi ' and '*P. ergatandria* Forel ♀ type St. Vincent'; 3 syntype workers labeled 'Typus', '41a moi ' and '*P. ergatandria* Forel ☿ type St. Vincent'; 2 workers (one without head, one without gaster) labeled 'Typus', '41b moi ', '*P. ergatandria* Forel ☿ type St. Vincent'; all MHN Genève.

Ponera kalakauae Forel, 1899

1 syntype worker labeled '*P. Kalakauae* ☿ Type Hawaii', MHN Genève. 1 syntype worker labeled 'Lahue 2000ft Kauai VII.96', 'Hawaiian Islands. R.C.L. Perkins 98.60', 'Syntype', 'Type', '*Ponera Kalakauae* Forel ☿ type' [Forel's handwriting], NHM London. 1 alate syntype gyne labeled 'Type', 'Hawaiian Islands. R.C.L. Perkins 98.60', 'Syntype', '*Ponera Kalakauae* Forel ♀ type' [Forel's handwriting], NHM London.

Ponera punctatissima var. schauinslandi Emery, 1899

Two syntype gynes on two different pins, each labeled 'Ins. Laysan Schauinsland' and '*Ponera punctatissima* var *Schauinslandi* Emery' [in Emery's handwriting], 'Syntypus *Ponera punctatissima* var. *schauinslandi* Emery, 1899', MCSN Genova.

Ponera dulcis var. *aemula* Santschi, 1911

1 worker lectotype [designated by Seifert 2003] and 1 worker paralectotype on separate pins, both labeled 'Type' [handwritten], 'Museum Paris Afrique Orient. All. Kilimandjaro (Zone Des Cultures, Kiboscho (1400 m.) Ch. Alluaud 1904' [printed] and '*Ponera dulcis* var. *aemula* Sant' [handwritten]; lectotype with CW 532, paralectotype CW 545; NHM Basel.

Ponera ergatandria subsp. *bondroiti* Forel 1911

1 syntype worker labeled 'Typus','Jardin Botan. Bruxelles 15-11-09', 'ergatoide minor' [Bondroit´s handwriting], '*P. ergatandria* Forel r. Bondroiti For type Bruxelles Serre chaud' [Forel's scribbling] and 'A Synonym of *P. gleadowi* For. DET. R. W. Taylor 24/III/63' [Taylors handwriting].
3 syntype workers labeled 'Bruxelles 11-09' [Bondroit´s handwriting], '*P. ergatandria* Forel r. Bondroiti For ♀ type Serre chaud Bruxell' [Forel's scribbling] and 'A Synonym of *P. gleadowi* For. DET. R. W. Taylor 24/III/63' [Taylor's handwriting]. 1 alate syntype gyne labeled 'Bruxelles Jardin Botan. 5-11-09' [Bondroit´s handwriting], '*P. ergatandria* Forel r. Bondroiti For type Bruxelles Serre chaud \ r. *P. Bondroiti* Forel' [Forel's scribbling] and 'A Synonym of *P. gleadowi* For DET. R. W. Taylor 24/III/63' [Taylor's handwriting]. 1 ergatoid syntype male labeled 'Jardin Botan. Bruxelles 15-11-09 \ ergatoide' [Bondroit´s handwriting]. All this material in MHN Genève.

Ponera punctatissima var. *exacta* Santschi, 1923

1 lectotype [designated by Seifert (2003)] and 2 paralectotype workers on the same pin, labeled '*Tunisie Hammamat* (Santschi VIII)' and '*P. punctatissima* v. *exacta* Sat'; lectotype (top specimen) with CS 617, SL/CS 0.777 and MW/CS 0.647; NHM Basel.

2. Investigation Methods

Workers and males were evaluated for a minimum of 10 and gynes for a minimum of 9 numeric characters. A Wild M10 high-performance stereomicroscope equipped with a 1.6x planapochromatic objective (resolution 750 lines/mm) was used at magnifications of 200–320x. Beginning with the year 2009, a Leica M165C high-performance stereomicroscope equipped with a 2.0 planapochromatic objective (resolution 1050 lines/mm) was used at magnifications of 200–384x. 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 optimum

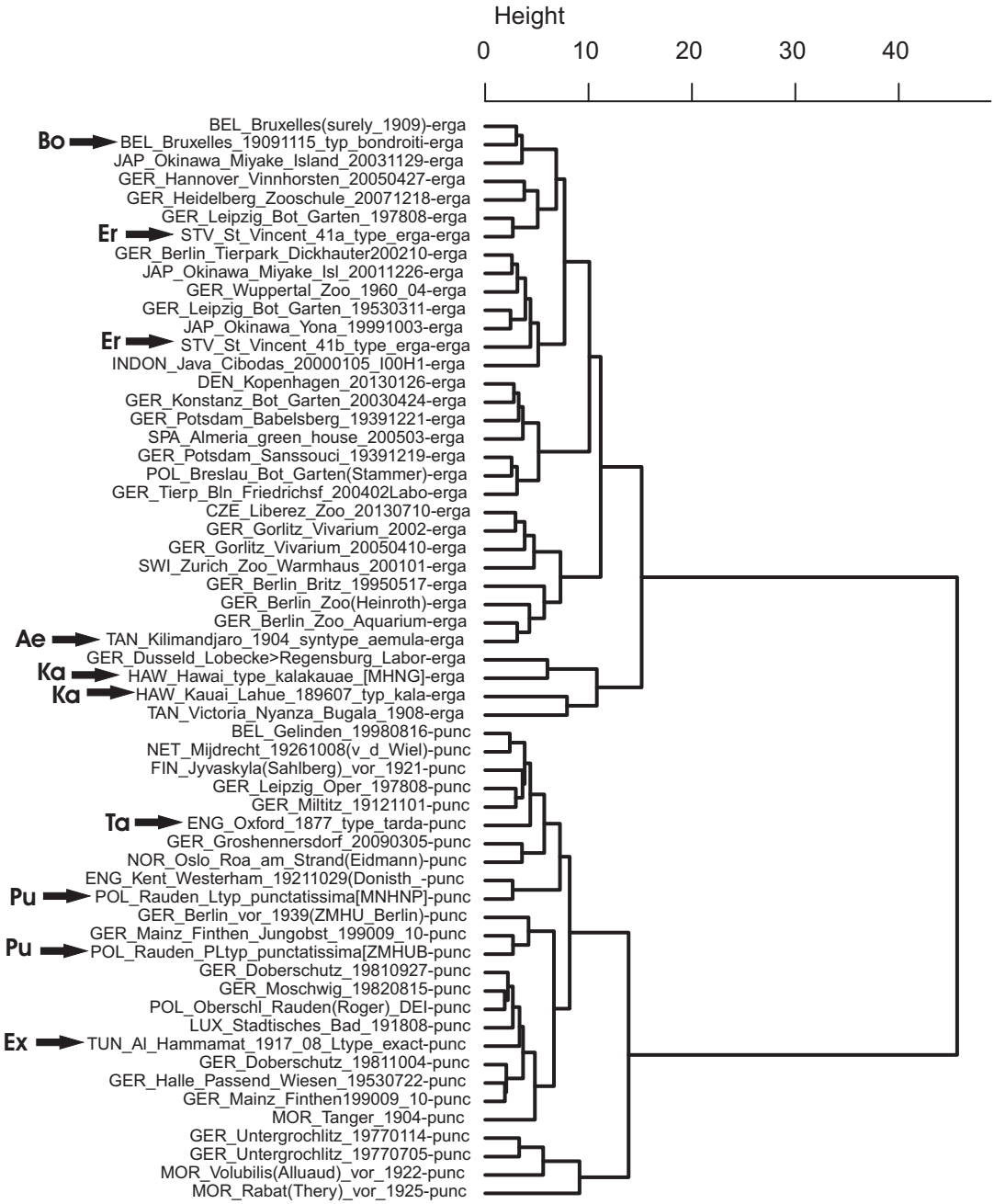

Figure 1. NC-Ward clustering of worker samples of *Hypoponera punctatissima* and *H. ergatandria*. Arrows indicate type samples with the acronyms meaning: **Ae** – *aemula* (Santschi), **Bo** – *bondroiti* (Forel), **Er** – *ergatandria* (Forel), **Ex** – *exacta* (Santschi), **Ka** – *kalakauae* (Forel), **Pu** – *punctatissima* (Roger) and **Ta** – *tarda* (Charsley).

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. The mean relative measuring error over all magnifications was 0.3 %. All measurements were made on mounted and dried specimens using a pin-holding stage, permitting endless rotations around X, Y, and Z axes. A Leica cross-scaled ocular micrometer with 120 graduation marks was used. To avoid rounding errors, all measurements were recorded in µm even for characters for which a precision of ± 1 µm was impossible.

The process of species discrimination included five major routines:

(a) Reduction of errors in primary data recording as described in Seifert (2002).
(b) Removal of allometric variance (RAV) performed with the procedure described by Seifert (2008).
(c) Application of the exploratory data analyses Nest Centroid Clustering (NC-Clustering). This included a hierarchical method (NC-Ward), a non-hierarchical method (NC-K-Means) and a highly flexible ordination method (NC-NMDS-K-Means). 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: http://sourceforge.net/projects/agnesclustering/.
(d) Principal Component Analysis (PCA) provided by the SPSS 16.0 software package.
(e) Checking of the demonstrated species clusters by linear discriminant analysis (LDA) also provided by SPSS 16.0.

2.1. The morphometric characters

Any measurement refers to real cuticular surface and not to the indeterminate pubescence surface (important in CS, CW, PEW, NOH, MW, SL).

CL – maximum cephalic length in median line; the head must be carefully tilted to the position with the true maximum. Excavations of occiput reduce CL. Anterior reference point in *Ponera* and *Hypoponera* is the upper clypeal protrusion (attention: not the clypeal protrusion below mandibular level!).

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

CW – maximum cephalic width.

FoDG – mean distance of foveolae on dorsum of 1st gaster tergite. Count the number of foveolae *n* in an area *A*. FoDG is then sqrt *A*/sqrt *n* . To enable most effective counting, select a mirroring part and align the counting areas longitudinally. Counting was performed within squares of 10 × 10 graduation marks (GRM) at the maximum magnification provided by the microscopes. In the Wild M10, for example, 10 GRM corresponded to 42.5 µm. If, e.g., 40 foveolae in seven 10 × 10 GRM squares were counted, then FoDG is calculated as 42.5 * sqrt (7/40) = sqrt(7 * 42.5 * 42.5)/sqrt(40). In the LEICA cross-scaled ocular micrometer the space between the GRM and the cross line is exactly 10 GRM wide. Hence, various numbers of 10 * 10 GRM squares, connected or not, can be easily defined. A dense pubescence obscuring foveolae may be patchily removed to reduce the counting error.

FR – minimum distance between frontal carinae.

ML – mesosoma length measured in lateral view. **Anterior reference point in the worker**: the point where anterior pronotal slope curves in anterior pronotal extension(shield). **Anterior reference point in the gyne**: the anteriormost point of the face of pronotal slope. **Posterior reference point in both castes**: caudalmost point of median propodeum. (Note: after the first suture at propodeal end there is still a sclerite sometimes partially hidden by petiole. If this sclerite is not fully visible, the measure to the suture was taken and multiplied with 1.03).

MW – maximum overall mesosoma width (workers) or maximum width before the tegulae (gynes).

NOH – petiole node height; measured in a right angle from a reference line beginning at the transition point between caudal node profile and caudal petiolar neck and ending at the most frontodorsal point of node corner (Fig. 1 in Seifert 2004).

PEL – petiole length; horizontal distance from the tip of the frontolateral node corner to the caudalmost point of petiole (Fig. 1 in Seifert 2004).

PEW – maximum width of petiole.

SL – maximum straight line scape length excluding the articulatory condyle and its neck. Care is required to measure real cuticular surface at distal scape end and to find the most distant proximal measuring point.

2.2. Removal of allometric variance (RAV)

In ant groups without extreme allometries removal of allometric variance (RAV) does not change the results of linear discriminant functions (Seifert 2008) but it may improve the success of exploratory data analyses. Exposing which deviations in shape characters or counts are no consequence of interspecific body size differences, RAV improves the explanatory power of comparative tables (Tabs 1, 2). RAV was performed in the two considered *Hypoponera* species with the following functions with CS given in mm.

In workers and ergatoid gynes, RAV was calculated for the assumption of all individuals having the same head size of CS = 0.6 mm:

$CL/CW_{0.6}$ = CL/CW /(– 0.3279*CS + 1.3671) * 1.698
$SL/CS_{0.6}$ = SL/CS /(– 0.1267*CS + 0.8276) * 0.7516
$FR/CS_{0.6}$ = FR/CS /(+ 0.0411*CS + 0.0974) *0.1221
$MW/CS_{0.6}$ = MW/CS /(+ 0.3172*CS + 0.4735) * 0.6638
$PEW/CS_{0.6}$ = PEW/CS /(+ 0.5555*CS + 0.1364) * 0.4697
$PEL/CS_{0.6}$ = PEL/CS /(+ 0.0937*CS + 0.3143) * 0.3706
$NOH/CS_{0.6}$ = NOH/CS /(+ 0.3374*CS + 0.1589) * 0.3613
$FoDG_{0.6}$ = FoDG /(– 3.86*CS + 14.75) * 12.44
$ML/CS_{0.6}$ = ML/CS /(+ 0.3431*CS + 1.2810) * 1.4868
$PEL/NOH_{0.6}$ = PEL/NOH /(– 0.6903*CS +1.4403) * 1.0260

In gynomorphic females, RAV was calculated for the assumption of all individuals having the same head size of CS=0.66 mm:

$CL/CW_{0.66}$ = CL/CW /(– 0.4043*CS + 1.3909) * 1.1240
$SL/CS_{0.66}$ = SL/CS /(– 0.1807*CS + 0.8656) * 0.7474
$MW/CS_{0.66}$ = MW/CS /(– 0.0658*CS + 0.8220) * 0.7786
$PEW/CS_{0.66}$ = PEW/CS /(+ 0.1179*CS + 0.4211) * 0.4989
$PEL/CS_{0.66}$ = PEL/CS /(– 0.0389*CS + 0.4136) * 0.3879
$NOH/CS_{0.66}$ = NOH/CS /(– 0.0111*CS + 0.3886) * 0.3813
$FoDG_{0.66}$ = FoDG /(– 0.86*CS + 13.32) * 12.76
$ML/CS_{0.66}$ = ML/CS /(– 0.0040*CS + 1.6624) * 1.6597
$PEL/NOH_{0.66}$ = PEL/NOH /(– 0.0727*CS +1.0667) * 1.0188

In ergatoid males, RAV was calculated for the assumption of all individuals having the same head size of CS=0.67 mm:

$CL/CW_{0.67}$ = CL/CW /(– 0.5346*CS+1.6200) * 1.2618
$SL/CS_{0.67}$ = SL/CS /(– 0.3986*CS + 0.8656) * 0.5985
$FR/CS_{0.67}$ = FR/CS /(– 0.0211*CS + 0.1373) * 0.1232
$MW/CS_{0.67}$ = MW/CS /(– 0.1175*CS + 0.6412) * 0.5625
$PEW/CS_{0.67}$ = PEW/CS /(– 0.0271*CS + 0.4193) * 0.4011
$PEL/CS_{0.67}$ = PEL/CS /(– 0.1193*CS + 0.3916) * 0.3117
$NOH/CS_{0.67}$ = NOH/CS /(– 0.0316*CS + 0.3266) * 0.3054
$FoDG_{0.67}$ = FoDG /(+ 3.12*CS + 10.55) * 12.64
$ML/CS_{0.67}$ = ML/CS /(– 0.4434*CS + 1.6082) * 1.3110
$PEL/NOH_{0.67}$ = PEL/NOH /(– 0.2817*CS +1.2092) * 1.0205

3. Results and discussion

3.1. The morphological separation

Table 1 and 2 show significant differences of the two species in absolute size and number of size-corrected shape variables. These data permitted a clear demonstration of the two species *H. punctatissima* and *H. ergatandria* in each caste by exploratory data analyses.

NC-Ward clustering considering absolute head size and 10 RAV-corrected shape characters provided a complete and profound separation of all 59 worker samples (Fig. 1). This separation was fully confirmed by NC-K-means and NC-NMDS-K-Means clustering (data not given). A linear discriminant analysis (LDA) confirmed the proposed classification by 100%. All 117 worker individuals were allocated with posterior probabilities of $p > 0.985$ – an exceptionally clear result for sibling species in ants. The number of cases in the smallest class, $n = 49$ in *H. punctatissima*, was 4.5-fold larger than the number of variables considered. This ratio is clearly beyond the recommended 3.0 threshold above which an LDA has little chances to act as a 'compliant servant' of an unsound hypothesis. All 17 type workers of seven taxa were allocated to either cluster with $p > 0.989$ and they remained at $p > 0.960$ after running a leave-one-out cross-validation LDA. The synonymies derived from this analysis are given below.

In gynomorphic females, as much as 61% of the 54 samples consisted of a single specimen due to the high percentage of isolated specimens caught outside the nests during dispersal after mating. This is far from an ideal condition to run nest centroid clustering. Nevertheless, both NC-Ward (Fig. 2), NC-K-means and NC-NMDS-K-Means provided a complete and 100% coincident separation when the number of considered characters was reduced to CS, $SL/CS_{0.66}$, $PEW/CS_{0.66}$ and $NOH/CS_{0.66}$. In order to depict the data of all 78 individuals, the result of a principal component analysis (PCA) using the same characters is also given (Fig. 3). Using those four characters, a LDA confirmed this classification in all specimens with posterior probabilities of $p > 0.9999$. All 8 type specimens of six taxa were allocated to either cluster with $p > 0.9999$ and they remained above this level in a leave-one-out cross-validation LDA. The synonymies derived from these analyses are given below.

The material of ergatoid males was only 5 samples and 7 specimens in *H. ergatandria* and 5 samples and 11 specimens in *H. punctatissima*. Nevertheless, a PCA considering absolute head size and 10 RAV-corrected shape characters provided a strong separation of both species: the 1st factor of the PCA scored -1.14 ± 0.20 [-1.53, -0.92] in *H. ergatandria* and 0.73 ± 0.42 [0.04, 1.28] in *H. punctatissima*. Due to the low sample size, the confirmation of this clustering had to be performed by a stepwise LDA that reduced the number of considered characters to three: $SL/CS_{0.67}$, $PEL/CS_{0.67}$ and $FoDG_{0.67}$. This LDA separated both species including the types of *H. androgyna* (Roger) and *H. bondroiti* (Forel) with $p > 0.9999$ and they remained at this level in a leave-one-out cross-validation LDA. The synonymies derived from this analysis are given below.

3.2. A simple way of species delimitation

Considering multiple characters is essential when more species have to be separated and most complex procedures of species delimitation are adequate for fundamental taxonomic research to convincingly demonstrate the existence of cryptic species. However, methods such as presented above appear unacceptable for practiticioners engaged in routine biodiversity investigations. To achieve as much simplification as possible while keeping the error at a minimum is required. In the following, a determination method is presented, that can be executed by a trained investigator within three minutes. *H. punctatissima* and *H. ergatandria* can be fully separated

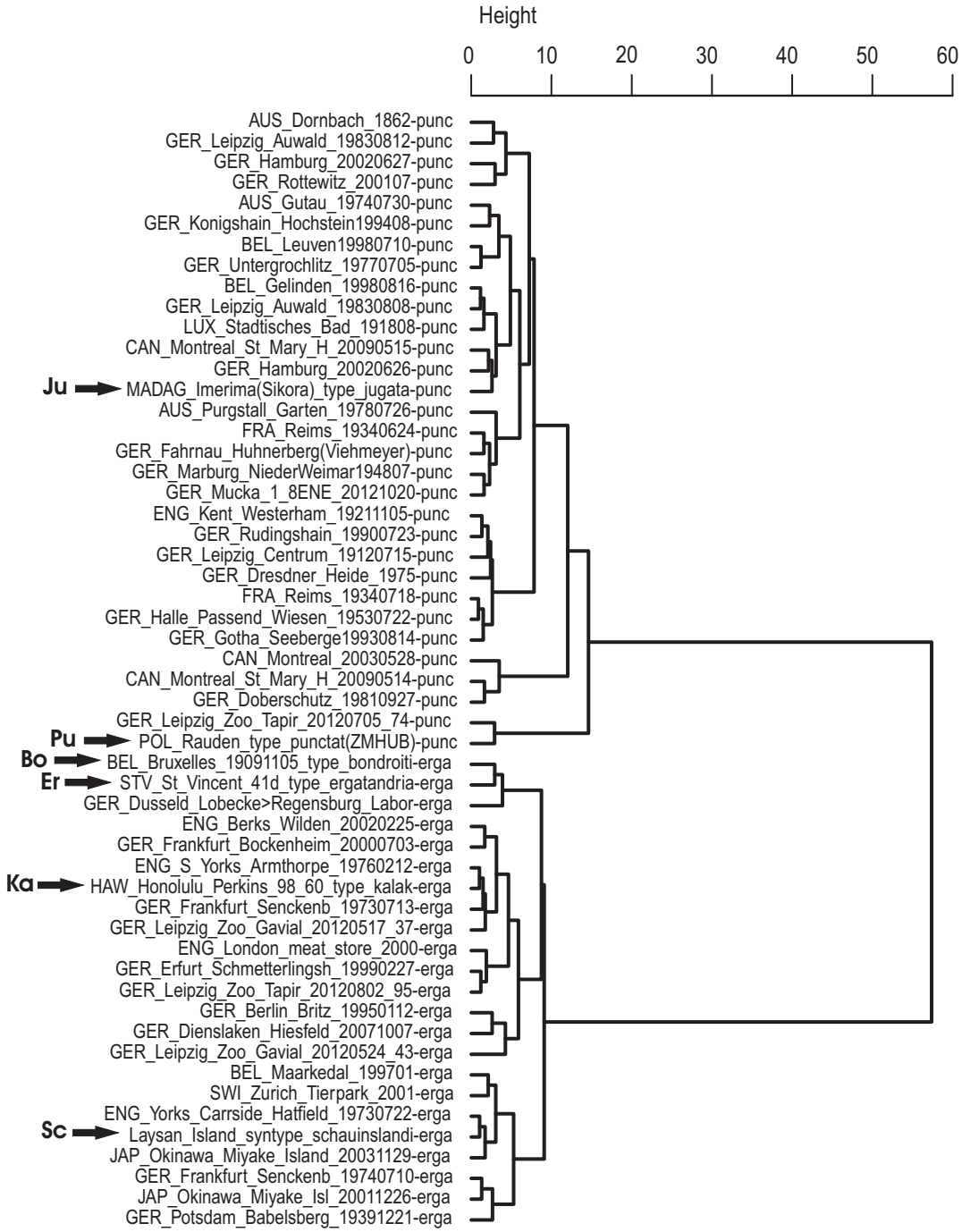

Figure 2. NC-Ward clustering of gynomorphic female samples of *Hypoponera punctatissima* and *H. ergatandria*. Arrows indicate type samples with the acronyms meaning: **Bo** – *bondroiti* (Forel), **Er** – *ergatandria* (Forel), **Ju** – *jugata* (Forel), **Ka** – *kalakauae* (Forel), **Pu** – *punctatissima* (Roger) and **Sc** – *schauinslandi* (Emery).

Table 1. Morphometric data of ergatoid males, workers and ergatoid females of *Hypoponera punctatissima* and *H. ergatandria*. Removal of allometric variance of shape variables was performed for the assumption of each individual having a head size of CS = 0.67 mm (in ergatoid males) and CS = 0.6 mm (in workers and ergatoid females).

	ergatoid males				workers and ergatoid females			
	H. punctatissima (n = 11)	ANOVA F p	***H. ergatandria*** (n = 7)		***H. punctatissima*** (n = 49)	ANOVA F p	***H. ergatandria*** (n = 68)
CS [µm]	754 ± 95 [615,879]	4.73 0.045	662 ± 73 [526,738]	CS [µm]	616 ± 110 [598,637]	235.37 0.000	557 ± 21 [518,604]
CL/CW 0.67	1.280 ± 0.031 [1.229,1.324]	9.52 0.007	1.239 ± 0.017 [1.218,1.262]	CL/CW 0.6	1.177 ± 0.013 [1.152,1.199]	13.37 0.000	1.167 ± 0.012 [1.140,1.193]
SL/CS 0.67	0.640 ± 0.013 [0.616,0.660]	136.30 0.000	0.564 ± 0.014 [0.545,0.580]	SL/CS 0.6	0.775 ± 0.008 [0.748,0.787]	687.82 0.000	0.730 ± 0.009 [0.716,0.748]
FR/CS 0.67	0.120 ± 0.007 [0.110,0.128]	3.40 n.s.	0.126 ± 0.005 [0.121,0.136]	FR/CS 0.6	0.121 ± 0.007 [0.104,0.137]	0.98 n.s.	0.119 ± 0.005 [0.108,0.128]
FoDG 0.67	12.49 ± 0.51 [11.8,13.3]	2.40 n.s.	12.96 ± 0.77 [11.7,14.0]	FoDG 0.6	12.70 ± 0.667 [11.6,14.5]	2.40 n.s.	12.49 ± 0.50 [11.3,13.9]
ML/CS 0.67	1.348 ± 0.013 [1.328,1.374]	67.63 0.000	1.277 ± 0.024 [1.252,1.320]	ML/CS 0.6	1.481 ± 0.019 [1.451,1.530]	0.85 n.s.	1.490 ± 0.025 [1.457,1.568]
MW/CS 0.67	0.570 ± 0.011 [0.550,0.585]	3.45 n.s.	0.560 ± 0.012 [0.540,0.573]	MW/CS 0.6	0.659 ± 0.015 [0.633,0.698]	36.11 0.000	0.677 ± 0.014 [0.649,0.713]
PEW/CS 0.67	0.423 ± 0.020 [0.397,0.459]	8.86 0.009	0.394 ± 0.020 [0.369,0.418]	PEW/CS 0.6	0.460 ± 0.017 [0.434,0.511]	20.98 0.000	0.479 ± 0.021 [0.446,0.540]
PEL/CS 0.67	0.327 ± 0.008 [0.319,0.344]	63.62 0.000	0.298 ± 0.007 [0.290,0.309]	PEL/CS 0.6	0.373 ± 0.005 [0.364,0.385]	22.16 0.000	0.365 ± 0.008 [0.347,0.385]
NOH/CS 0.67	0.318 ± 0.009 [0.303,0.333]	28.86 0.000	0.297 ± 0.007 [0.282,0.303]	NOH/CS 0.6	0.357 ± 0.012 [0.331,0.384]	7.32 0.008	0.365 ± 0.010 [0.349,0.384]
PEL/NOH 0.67	1.028 ± 0.028 [0.980,1.078]	2.13 n.s..	1.007 ± 0.035 [0.960,1.059]	PEL/NOH 0.6	1.046 ± 0.034 [0.978,1.126]	23.30 0.000	1.004 ± 0.037 [0.911,1.073]

Table 2. Morphometric data of gynomorphic females of *Hypoponera punctatissima* and *H. ergatandria*. Removal of allometric variance of shape variables was performed for the assumption of each individual having a head size of CS = 0.66.

	H. punctatissima (n = 42)	ANOVA F p	***H. ergatandria*** (n = 36)
CS [µm]	705 ± 22 [637,753]	314.04 0.000	618 ± 21 [572,651]
CL/CW 0.66	1.126 ± 0.013 [1.101,1.158]	10.82 0.002	1.113 ± 0.020 [1.055,1.156]
SL/CS 0.66	0.767 ± 0.014 [0.727,0.810]	307.07 0.000	0.720 ± 0.010 [0.698,0.743]
ML/CS 0.66	1.659 ± 0.030 [1.611,1.731]	4.26 0.042	1.642 ± 0.042 [1.545,1.750]
MW/CS 0.66	0.771 ± 0.023 [0.737,0.835]	10.40 0.002	0.755 ± 0.021 [0.715,0.791]
PEW/CS 0.66	0.508 ± 0.017 [0.481,0.565]	46.24 0.000	0.484 ± 0.014 [0.461,0.517]
PEL/CS 0.66	0.386 ± 0.008 [0.373,0.406]	26.79 0.000	0.377 ± 0.009 [0.354,0.395]
NOH/CS 0.66	0.391 ± 0.012 [0.366,0.420]	95.15 0.000	0.366 ± 0.010 [0.346,0.386]
PEL/NOH 0.66	0.988 ± 0.035 [0.917,1.054]	25.72 0.000	1.029 ± 0.037 [0.923,1.091]
FoDG 0.66	12.58 ± 0.56 [11.4,13.7]	5.59 0.021	12.26 ± 0.61 [11.0,13.7]

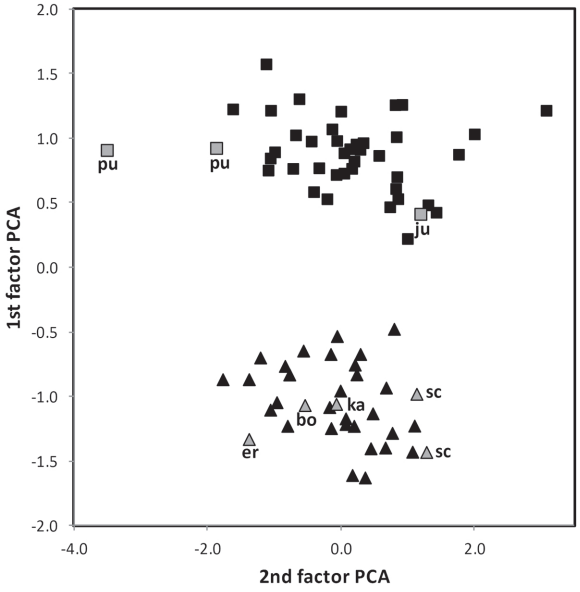

Figure 3. First and second factor of a principal component analysis of gynomorphic females of *Hypoponera punctatissima* (squares) and *H. ergatandria* (triangles). Type specimens are given with a grey filling with the acronyms meaning: **bo** – *bondroiti* (Forel), **er** – *ergatandria* (Forel), **ju** – *jugata* (Forel), **ka** – *kalakauae* (Forel), **pu** – *punctatissima* (Roger) and **sc** – *schauinslandi* (Emery).

in all three castes by using a discriminant function of two simple measurements: absolute head width CW and absolute scape length SL in dry mounted specimens. Care is needed to determine the real cuticular surface of head capsule and distal scape end. This is not always easily done due to a profuse pubescence partially concealing structures. Readers should also consider the more general comments below. The input of data has to be in millimeters and accurate for three decimal points.

Workers and ergatomorphic females can be separated by the function

D = 142.82 SL – 68.67 CW –26.12

Specimens with D < 0 belong to *H. ergatandria* and those with D > 0 to *H. punctatissima*. The classification error was 0 % in 117 individuals.

Gynomorphic females can be separated by the function

D = 85.90 SL – 18.54 CW – 30.312

Specimens with D < 0 belong to *H. ergatandria* and those with D > 0 to *H. punctatissima*. The classification error was 0 % in 78 individuals.

Ergatoid males, independent if representing major or minor morphs, can be separated by the function

D = 130.69 SL – 40.553 CW – 28.125

Specimens with D < 0 belong to *H. ergatandria* and those with D > 0 to *H. punctatissima*. The classification error was 0 % in 18 individuals.

Comments: Measuring small ants requires a sufficiently accurate recording. From personal contacts with ant taxonomists and statements in the methods section of published taxonomic papers, it is obvious that a majority of contemporary myrmecologists still use microscopic systems, measuring devices and working routines inadequate for most of the extant ant species. Measuring small ants with methods adequate for grasshoppers and a missing sense for the developments of modern light optics during the last 40 years is a common attitude among myrmecologists. Custom and paradigm of famous contemporary myrmecologists and naivety of their imitators are here the key words. Sufficient accuracy does not require the most expensive equipment – a 6,000 Dollar stereomicroscope may be sufficient because accuracy is largely a question of the applied working routine. Seifert (2002) described in detail the sources of error affecting stereomicroscopic measurement and how they can be minimized. Once an investigator was trained in executing this routine it does not require him much more time than for a less careful working procedure. Key words of Seifert (2002) are in this context: parallax error, calibration error, micrometer reading error, click-stop error, object positioning error, character definition error, desiccation error, illumination error, rounding error and diopter adjustment error.

3.3 Rebuttal of Bolton & Fisher (2011)

Regarding the very clear species separation shown by Seifert (2004), Bolton & Fisher (2011) argued '...that the discriminant functions applied by Seifert do not isolate discrete species, but rather indicate allopatric populations of the same species [argument 1, B.S.] or even different eco-morphs of a single species [argument 2, B.S].'

Argument 1 is easily rejected. *H. punctatissima* and *H. ergatandria* are strongly sympatric: they are sympatric in Belgium, England, Germany and Poland (67 % of the investigated 97 samples of both species are from this area!) and they will be found sympatric in many other countries once an adequate sampling will be done. They do even occur syntopic and synchronic in the Tapir house of the Leipzig Zoo.

Argument 2 is also untenable. Morphs, by definition, are provided by the same gene pool. Accordingly, intraspecific dimorphism in ants is indicated in the field by a sufficiently frequent occurrence of intranidal mixtures of distinct phenotypes. Apart from the well known and very obvious minor vs. major situations in worker ants of several genera (e.g. *Pheidole*), clear examples of a more hidden worker dimorphism were reported for *Formica pratensis* Retzius, 1783 (Seifert 1992), *Formica lugubris* Zetterstedt, 1838 (Seifert 2003a) and *Cardiocondyla mauritanica* Forel, 1890 (Seifert 2003b). Unpublished investigations of the present author provide further good examples in *Lasius umbratus* (Nylander, 1846) and *Camponotus lateralis* (Olivier, 1792). *C. lateralis* is outstanding by the presence of two independent systems of dimorphism superimposed in a single species: the classical minor vs. major dimorphism and a size-independent syndrome of shape-and-pilosity dimorphism. Returning to *H. punctatissima* and *H. ergatandria,* we must consider the strong degree of sympatric occurrence stated above and the polygynous and polyandrous nature of the colonies in both species (Yamauchi et al. 1996, Seifert 2004). Polygyny will allow an easier adoption of mated gynes from other colonies. Given this, a significant proportion of colonies in the area would produce both the phenotype of *H. punctatissima* and *H. ergatandria* if the morph hypothesis was true. The facts found during this study strongly disprove argument 2 of Bolton & Fisher. There was not a single nest sample in the material containing workers of both *H. punctatissima* and *H. ergatandria* and there was also no nest sample containing conflicting ergatoid males or gynomorphic females. All samples were clean. Obviously, the species maintain separate reproductive cycles under conditions of a broadly sympatric occurrence. They have significant differences in phenology of sexual development, dispersal of alate gynes, habitat selection in the temperate zone and global distribution. These matters and other aspects of

special biology of both species are treated in an appendix placed after References.

4. Synonymic lists

The following synonymic lists contain only taxa of which type specimens were available. Naming the smaller and short-scaped sibling species as *H. ergatandria* (Forel, 1893) can be considered as 'final' because the types of all taxa described before 1893 were studied and confirmed as synonyms of *H. punctatissima* (Roger, 1859). The probabilities given after the type specimens are posterior probabilities by which the linear discriminant analyses confirmed the clustering of explorative data analyses.

Hypoponera punctatissima (Roger, 1859)

Ponera punctatissima Roger, 1859
Lectotype worker (p = 1.000), two paralectotype workers (both p=1.000) and two paralectotype gynomorphs (both p=1.000), all from Poland: Rauden.

Ponera androgyna Roger, 1859
2 ergatoid syntype males from Germany: Berlin and Poland: Rauden (both p = 1.000)

Ponera tarda Charsley, 1877
2 syntype workers from England: Oxford (p = 0.989 and p = 1.000)

Ponera punctatissima r. *jugata* Forel, 1892
1 type gynomorph from Madagascar: Imerima (p = 1.000)

Ponera punctatissima var. *exacta* Santschi, 1923
1 lectotype and 2 paralectotype workers from Tunisia: Hammamat (all p = 1.000)

Hypoponera ergatandria (Forel, 1893); **stat. nov.**

Ponera ergatandria Forel, 1893
1 alate syntype gynomorph from St. Vincent: Villa Estate (p=1.000); 2 syntype workers from St. Vincent: Bowwood Valley (both p = 1.000), 1 syntype worker from St. Vincent: Chateaubelais Bay (p = 1.000).

Ponera kalakauae Forel, 1899; syn. nov.
1 syntype worker from Hawaii (p = 1.000), 1 syntype worker from Kauai: Lahue (p = 1.000), 1 alate syntype gynomorph from Oahu: Honolulu (p = 1.000).

Ponera punctatissima var. *schauinslandi* Emery, 1899; syn. nov.
Two syntype gynomorphs from Laysan: Schauinsland (both p = 1.000).

Ponera dulcis var. *aemula* Santschi, 1911; syn. nov.
1 worker lectotype and 1 worker paralectotype from Tanzania: Kilimanjaro (p = 0.998 and p = 1.000)

Ponera ergatandria subsp. *bondroiti* Forel, 1911; syn. nov.
3 syntype worker (all p = 1.000), 1 alate syntype gynomorph (p = 1.000), 1 ergatoid syntype male from Belgium: Bruxelles (p = 1.000)

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Appendix. This appendix provides a condensed information on what is currently known about the biology of *H. punctatissima* and *H. ergatandria*. It is an advance publication of the species chapters from my intended book 'The Ants of Central and North Europe' scheduled to appear by the year 2016. It provides an impression of the format according to which the specific biology of 178 outdoor species of that area will be presented. The treatment of several aspects of biology (habitat, abundance, nest construction, phenology of sexual development) concentrates on the situation in the north meridional, temperate and boreal zone of Europe.

Genus *Hypoponera* Santschi 1938

Small, mainly hypogaean and litter ants. More than 130 species occurring worldwide, largely in the tropics. In Central Europe only three species with established or potential outdoor nesting. Males often wingless, ergatomorphic, with strongly enlarged heads and well-developed mandibles, living permanently in the nests and showing a lifelong spermatogenesis. Males of some exotic species for hours cling to the cocoons of female sexuals, insert their genitalia into it and secure their reproductive success by mating with the still encased female sexual[5, 6]. Major-males of other species perform injury or lethal fights to dominate mating of young gynes. True workers without ovaries[7], but gamergates may reproduce. Trophallaxis is documented while being unknown in most other genera of Ponerinae.

Hypoponera punctatissima (Roger 1859)

Geographical range. Widely spread tramp species of subtropical origin but unknown so far from the Australasian, Indo-Australian, Oriental and Neotropical faunal regions. In Europe going north to southern Fennoscandia – the northernmost site in E Sweden is at 64°N. Due to independent colony foundation and long-range dispersal flight of mated gynes, active postglacial invasion of the temperate zone highly probable during warmer climatic periods, passive anthropogenous introduction facilitates spreading. Invasion of Western Europe (England) documented in the late Roman time (1600 b.p.). In colder climatic periods of the Holocene obviously confined to heated buildings or aggregations of organic matter with endogenous heat production. **Habitat.** Here only situation in Europe north of 48°N given: Among 32 reported nest sites, 25 % in heated buildings, 59 % outdoors in mounds or heaps of decomposing, heat-producing organic material (saw dust, shredded wood or straw, horse or cow dung with much straw, garden compost, coffee waste, flood refuse at shore, mowed grass) and 16 % in natural or semi-natural habitats without substantial substrate-dependent heat production. The latter fraction is not documented before 1978 (0 % of 8 nest records) but significant after 1977 (21 % of 24 nest records) which is interpreted as a consequence of global warming. Nest habitats without heat production always open and sun-exposed: a park meadow in a city, a *Molinia* stand in a bog, an orchard, a xerothermous grassland on sand and a bare granite rock. Potentially occurring in any heated building providing intact soil substrates with a sufficient microfauna to serve as prey organisms; minimum condition: big flower pots, optimum condition: greenhouses of botanical or zoological gardens. **Abundance.** Widely distributed but at present stage still very rare in natural habitats. Decline of horse dung heaps with the advent of motorized transport in the beginning of the 20th century and the increased or accelerated utilization of organic waste products (such as sawdust and shavings of wood-processing) in the beginning of the 21st century could have reduced the outdoor population. **Nest construction.** In soil and organic material. Heaps of decomposing organic material showing an enormous heat production may force the ants in summer to construct brood chambers 1–2 cm below the surface (K. Lippold) but prevents deeper layers from freezing even in the coldest winters. Preferred

temperature range within an English horse dung heap 22–32°C. **Colony demography.** Polygynous. Single isolated nests may contain up to 190 workers, 3 major males, 17 minor males, 3 gynomorphic queens and may produce 30 alate gynomorphic females. Colonies may become polydomous and moderately polygynous. A coherent colony stretching over many square meters of a sawdust heap was supposed to be supercolonial (K. Lippold). Singularity of ergatoid males within a nests seems to be rare: reported numbers 2, 2, 2, 3, 3 and 17. Major and minor males may occur within the same nest. **Sexuals, mating, colony foundation and development.** Males always ergatomorphic and never found outside colony boundaries. Distinct size-dimorphism of males: CS 615–722 µm in minors, 762–879 µm in majors. Healed injuries in major males and absence of injuries in minor males indicate major males to fight among themselves but to tolerate minor males which themselves probably never fight. Ergatomorphic female castes dimorphic – the morph with relatively larger eyes, larger absolute size and relatively thicker body than in true workers is thought potentially becoming an ergatomorphic queen (issue not studied but probably analogous to situation in *H. ergatandria*). Development of gynomorphic females in heated buildings almost exclusively during spring and summer, hence probably initiated by increasing day length. Long-range flight dispersal of mated alate gynes well documented: 18 July ± 24 days [28 May–25 Aug] n = 31; occurring at days with mean / maximum air temperatures of 18.6 ± 2.3°C/ 24.1 ± 3.2°C (n = 8). One direct observation of take-off of alate gynes from a nest 9 Aug 1994, at 18.00–18.25 h solar time and air temperatures of 22°C. Three findings of alate gynes in the period 5 Nov–24 Mar refer to specimens not being in dispersal. **Nutrition.** Largely or exclusively feeding on small invertebrates which hampers penetration of most human dwellings. Favored prey objects seem to be Collembola. **References:** 1–3.

Hypoponera ergatandria (Forel 1893)

Geographical range. Cosmopolitan tramp species with tropical and subtropical origin. Trend for a worldwide spreading stronger than in *punctatissima*. Anthropogenous introduction into the north temperate zone started in the 1860's when tropical plants and animals were imported in higher numbers and could be kept in greenhouses with stable heating conditions throughout the year. **Habitat.** In Europe confined to different kinds of heated buildings offering some sort of moist soil substrate or decomposing organic matter. 95% of 20 recorded nest sites were in greenhouses of zoological and botanical gardens, in butterfly parks, plant stores, museums etc. The only exception, an old people's home, most probably had a room with a lot of potted plants. Air temperatures in occupied buildings not falling below 14°C (usually between 22 and 27°C). Outdoor nesting not confirmed so far but the finding of a dealate gyne on a recultivated heap of mine wastes with endogenous heat production near Dinslaken in 2007 suggests this. **Abundance.** Widely distributed in Europe; in greenhouses sometimes abundant. **Nest construction.** In soil or organic material. In European greenhouse habitats, repeatedly observed to nest under very moist conditions in log or under bark. This corresponds to reports on outdoor nests in tropical regions. **Colony demography.** Weakly polygynous and occasionally polydomous. Data of 26 nests from Okinawa: 29.2 ± 34.8 [1,184] workers, 3.7 ± 4.5 [0,20] ergatoid queens (these found in 22 nests), 0.73 ± 1.06 [0,4] gynomorphic queens (found in 10 nests), 0.38 ± 0.64 [0,2] major males (found in 8 nests), 0.58 ± 1.24 [0,6] minor males (found in 9 nests) and 5.30 ± 9.47 [0,39] alate gynomorphs (found in 12 nests). **Sexuals, mating, colony foundation and development.** Occurrence of alate gynomorphs in heated buildings of the temperate zone in two periods: largely 20 Jan ± 38 d [9 Nov–15 Mar] n = 12 and 30 Jun ± 29 d [17 May–2 Aug] n = 7. Hence, and in contrast to *punctatissima*, development of alates apparently mainly under short-day conditions. Mating of both ergatomorphic and gynomorphic females always intranidal, both by minor and major males. The colonization of new sites in the temperate zone largely depends upon passive anthropogenous transport but one midsummer observation of a flying gynomorph outside a human settlement indicates occasional active dispersal. **Nutrition.** Collembola and other microarthropods seem to be most preferred prey. Dependence from small epigaeic and hypogaeic invertebrates and difficulties using other food sources prevents a wider synanthropic distribution. **Behaviour.** Members of greenhouse personnel repeatedly reported painful stinging. **Miscellaneous.** Distinct size dimorphism in ergatoid males: CS in minors 508–615 µm and 695–808 µm in majors. Majors fight with majors for dominance of matings – no killings but damage of appendages was observed in 7 of 8 cases. Majors do not attack minors because minors seem to mimic females chemically. Minors do not fight among themselves. Distinct polymorphism of female reproductives: gynomorphs with large eyes, 3 ocellae, a large mesosoma and 3 + 3 ovarioles are able to fly. Ergatoid queens similar to workers but with slightly larger size, larger eyes, a spermatheca (that is always inseminated) and 3 + 3 ovarioles. Workers always without ovarioles and spermatheca. **References**: 1–4, 5–7.

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