

Abh. Ber. Naturkundemus. Görlitz	Band 75 Heft 1	S. 61 – 81	2003
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***Hypoponera punctatissima* (Roger) and *H. schauinslandi* (Emery) – Two morphologically and biologically distinct species (Hymenoptera: Formicidae)**

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Abstract

The ant known so far under the name »*Hypoponera punctatissima*« consists of two sibling species: *H. punctatissima* (Roger, 1859) and *H. schauinslandi* (Emery, 1899), which can be reliably distinguished by high-precision morphometry and discriminant functions. Phenotypic separation is clearly supported by a number of biological differences. *H. punctatissima* is capable of long-range flight-dispersal and of nesting in several types of outdoor habitats. For Europe north of 48° N, nesting in natural or semi-natural habitats without endogenous heat production was unknown or extremely rare before 1950 (0 – 6 % of 16 overall observations) but documented in 25 % of 24 overall observations after 1950, which is interpreted as a consequence of global climate change. *H. punctatissima* does not depend on passive anthropogenic transport to invade temperate Europe north of 48° N. Most certainly it has been present in England 1600 years b.p. or much earlier. *H. schauinslandi*, in contrast, is not capable of outdoor nesting and long-range flight-dispersal in Europe north of 48° N and occurs there exclusively in greenhouses, where soil arthropods are available as a main food source. This tropical-cosmopolitan species depends on passive human transport when introduced to the temperate zone. Both species show gynomorphic and ergatoid females, major and minor ergatoid males, destructive fighting between major males but not between minor males, and a similar size of nest populations. Investigation of type material by high-resolution discriminant analysis established the following synonymies – in any case with error probabilities of $p < 0.006$: *H. androgyna* (Roger, 1859), *H. tarda* (Charsley, 1877), *H. punctatissima* r. *jugata* (Forel, 1892) and *H. punctatissima* var. *exacta* (Santschi, 1923) are junior synonyms of *H. punctatissima*, while *H. dulcis* var. *aemula* (Santschi, 1911) and *H. ergatandria* subsp. *bondroiti* (Forel, 1911) are junior synonyms of *H. schauinslandi*. Four names – *H. abeillei* (André, 1881), *H. indifferens* (Forel, 1895), *H. gibbinota* (Forel, 1912) and *H. lesnei* (Bondroit, 1916) – refer to species clearly different from both *H. punctatissima* and *H. schauinslandi*.

Zusammenfassung

***Hypoponera punctatissima* (Roger) and *H. schauinslandi* (Emery) – zwei morphologisch und biologisch trennbare Arten (Hymenoptera: Formicidae)** – Die bisher unter dem Namen »*Hypoponera punctatissima*« bekannte Ameise besteht aus den Zwillingsarten *H. punctatissima* (Roger, 1859) und *H. schauinslandi* (Emery, 1899), die mittels hochauflösender Diskriminanzanalyse sicher unterscheidbar sind. Die phänotypische Unterscheidung wird durch eine Reihe biologischer Unterschiede bestätigt.

H. punctatissima ist zu einem weitreichenden Ausbreitungsflug und zur ganzjährigen Etablierung von Nestern in verschiedenen Typen von Freilandlebensräumen befähigt. Nestgründungen in Freilandhabitaten, die keine endogene Wärmeproduktion aufweisen, waren vor 1950 in Europa nördlich 48° N unbekannt oder extrem selten (höchstens einer von 16 Nachweisen), wurden hier aber für sechs von 24 Nachweisen nach 1950 dokumentiert. Diese Zunahme wird als Folge der globalen Erwärmung, insbesondere der mildernden Winter interpretiert. *H. punctatissima* war bei der Besiedlung der temperaten Zone nördlich 48° N nicht von passivem anthropogenen Transport abhängig und könnte schon im Atlantikum hier eingewandert sein. Zumindest England wurde sehr wahrscheinlich spätestens im 4. Jahrhundert besiedelt. *H. schauinslandi* ist dagegen nicht zu einem weitreichendem Ausbreitungsflug oder zur Etablierung von Freilandnestern in Europa nördlich 48° N befähigt und tritt hier ausschliesslich in Warmhäusern auf, wo kleine Bodenarthropoden als Hauptnahrungsquelle verfügbar sind. Sie ist ein tropischer Kosmopolit, dessen Einführung in die temperate Zone unter gegenwärtigen klimatischen Bedingungen von passivem anthropogenen Transport zwingend abhängig ist. Beide Arten zeigen gynomorphe und ergatoide Weibchen, einen Grössenbimorphismus der ergatoiden Männchen, Beschädigungskampf zwischen den Major-Männchen, Fehlen eines solchen zwischen Minor-Männchen und eine vergleichbare Demographie der Nester. Die Untersuchung von Typenmaterial mittels hochauflösender Diskriminanzanalyse konnte folgende Synonymien mit einer Irrtumswahrscheinlichkeit $p < 0.006$ zeigen: *H. androgyna* (Roger, 1859), *H. tarda* (Charsley, 1877), *H. punctatissima* r. *jugata* (Forel, 1892) und *H. punctatissima* var. *exacta* (Santschi, 1923) sind jüngere Synonyme von *H. punctatissima*, während *H. dulcis* var. *aemula* (Santschi, 1911) und *H. ergatandria* subsp. *bondroiti* (Forel, 1911) jüngere Synonyme von *H. schauinslandi* sind. Vier Namen – *H. abellei* (André, 1881), *H. indifferens* (Forel, 1895), *H. gibbinota* (Forel, 1912) und *H. lesnei* (Bondroit, 1916) – beziehen sich auf vier deutlich von *H. punctatissima* und *H. schauinslandi* verschiedene Arten.

1. Introduction

The ant genus *Hypoponera* (Santschi, 1938) is of mainly tropical distribution and differs from *Ponera* Latreille, 1804 in the female castes by the absence of a fenestra or thin translucent spot on anteroventral subpetiolar lobe. According to the conceptions followed so far (KUTTER 1977, COLLINGWOOD 1979, SEIFERT 1996), only two species of *Hypoponera* have invaded Central Europe: *H. eduardi* (Forel, 1894) and »*H. punctatissima*« (Roger, 1859)«. *H. eduardi* is widely distributed in the Mediterranean but only exceptionally found in S Central Europe. »*H. punctatissima*«, in contrast, is known from all countries in Central Europe and has extended its range to Fennoscandia. Within the myrmecofauna of these regions, it is outstanding for its peculiarity of nesting in heaps or mounds of various decomposing organic materials (DONISTHORPE 1915, STRADLING 1965, SEIFERT 1982, DESSART & CAMMAERTS 1995, DEKONINCK & VANKERKHOVEN 2001) or for being recorded deep in a coal mine in S England (YARROW 1967).

A recent morphological investigation had the surprising result that »*H. punctatissima*« in the conception of all contemporary authors consists of two clearly different species and that the natural history of these ants must be written anew. An improved morphometric methodology very near to that described by Seifert (2002) enabled a certain discrimination of both workers and gynes of the two sister species on the individual level. Despite this clear separation, a diagnostic character perceptible by simple visual inspection (such as characteristic setae, carinae, curvatures, dents etc.) was not discovered. Hence, the distinction of *H. punctatissima* from its sister species *H. schauinslandi* (Emery, 1899) is purely morphometric at the present stage. The results of these studies, of type investigations in 12 related taxa, and a differential biology of the two sister species are presented in this paper.

2. Materials and methods

2.1. Equipment, measuring, and data evaluation

Workers were evaluated for a minimum of 10 and gynes for a minimum of 9 numeric characters, at magnifications of 200–320 x using a Wild M10 high-performance stereo-microscope equipped with a 1.6 x planapochromatic objective. 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 ranging over 65 % of the visual field was used. A cross-scale is inevitable for exact measurements of characters such as PrOc or FoDG. A mean measuring error of $\pm 0.6 \mu\text{m}$ was calculated for small and well-defined structures such as petiole width, but one of $\pm 2 \mu\text{m}$ for larger structures with difficult positioning and some definition error such as mesosoma length. To avoid rounding errors, all measurements were recorded in μm even for characters for which a precision of $\pm 1 \mu\text{m}$ is impossible. In order to reduce irritating reflections of the cuticular surfaces, a plastic diffuser was positioned as close as possible to the specimen. This method considerably improved the resolution of micro-sculpture and the measuring accuracy for tiny structures such as pubescence hairs. Any measurement refers to real cuticular surface and not to the diffuse pubescence surface (important in CW, PEW, FR, MW).

The process to discriminate the most similar sister species included (a) the reduction of variance in primary data (SEIFERT 2002), (b) the removal of allometric variance by species-specific functions valid for species pairs (SEIFERT 2002), and (c) a canonical discriminant analysis with an SPSS program.

2.2. The morphometric characters

- 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 (do not use 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.
- EyePos** – a distance between a posterior and anterior reference point measured when head adjusted as given for CL. *Posterior reference point*: intersection point of the median line of head with an orthogonal line directed to eye centre. Because of bilateral head asymmetries use an average of both eyes. *Anterior reference point*: anteriormost point of clypeus as given for CL.
- FoDG** – mean distance of foveolae on dorsum of 1st gaster tergite. Count the number of foveolae n in an area A . FoDG is then $\sqrt{A/n}$. To enable most effective counting, select a mirroring part and align the counting areas longitudinally. Explicitly, counting was performed within squares of 10 x 10 graduation marks (GRM) at a magnification of 320 x. In this case, 10 GRM corresponded to 42.5 μm . For example, if 40 foveolae in seven 10 x 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. In *Hypoponera*, pubescence may be patchily removed to reduce the counting error.
- FL** – maximum divergence of frontal lobes.
- 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, measure to the suture and multiply with 1.03).
- MW** – maximum overall mesosoma width (workers) or maximum width before the tegulae (gyenes).
- 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).
- PEL** – petiole length; horizontal distance from the tip of the frontolateral node corner to the caudalmost point of petiole (Fig. 1).
- PEW** – maximum width of petiole.
- PrOc** – a preocular distance between a posterior and anterior reference point measured when head adjusted as given for CL. *Posterior reference point*: intersection point of the median line of head with an orthogonal line directed to anterior eye margin. Because of bilateral head asymmetries use an average of both eyes. *Anterior reference point*: anteriormost point of clypeus as given for CL.

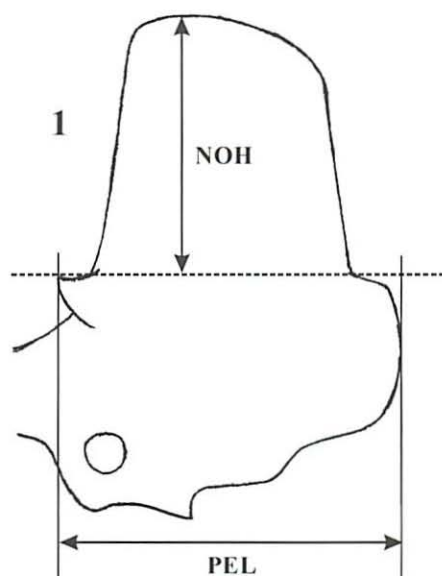


Fig. 1 Measuring of petiole length (PEL) and of petiolar node height (NOH) in *Ponera* and *Hypoponera*

2.3. Sources of material

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

coll.Burger	collection of F. Burger/Weimar
coll.Dauber	collection of J. Dauber/Giessen
coll.Yamauchi	collection of K. Yamauchi/Gifu
DEI	Deutsches Entomologisches Institut Eberswalde
MCSN Genova	Museo Civico di Storia Naturale Genova
MHN Genève	Muséum d'Histoire Naturelle Genève
MNHN Paris	Muséum National d'Histoire Naturelle Paris
NM Leipzig	Naturkundemuseum Leipzig
NHM Basel	Naturhistorisches Museum Basel
NHM Wien	Naturhistorisches Museum Wien
SM Frankfurt	Senckenberg-Museum Frankfurt
SMN Görlitz	Staatliches Museum für Naturkunde Görlitz
UM Oxford	University Museum Oxford: Hope Entomological Collections
ZMHU Berlin	Zoologisches Museum der Humboldt-Universität Berlin

2.4. Investigated material of *H. punctatissima* and *H. schauinslandi*

45 samples of *H. punctatissima* with 11 ergatoid males, 38 gynomorphic and 48 workers ergatoid female specimens were morphometrically investigated:

AUSTRIA: Dornbach, 1862; Linz–27 km ESE; Gutau, 1974.07.30; Purgstall (15.07.53 E, 48.03.05 N), 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. ENGLAND: Oxford, St.Giles Road West, greenhouse, 1877, type *H. tarda*; Westerham 1921.10.29; 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; 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. 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: Røa near Oslo, pre 1945 (Eidmann). POLAND: Rauden, pre 1860, type *H. punctatissima*; TUNISIA: Al Hammamat (36.24 N, 10.37 E), 1917.08., type *H. exacta*.

29 samples of *H. schauinslandi* with 2 ergatoid males, 24 gynomorphic and 45 ergatoid female specimens were morphometrically investigated:

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. GERMANY: Potsdam–1.5 km WNW, Sanssouci, greenhouses, 1939.07.19; Potsdam: Babelsberg, greenhouse Orchidflora, 1939.07.21; Potsdam–1.5 km WNW, Sanssouci, orchid houses, 1940.10.08; Potsdam–1.5 km WNW, Sanssouci, orchid houses, 1940.06.19; Berlin, Zoological Garden (aquarium), pre 1945; Berlin, Zoological Garden, pre 1945 (Heinroth); Leipzig, Botanical Garden, greenhouse, 1955.03.11; Wuppertal, Zoological garden, 1960.04; Frankfurt/M., Senckenberg-Anlage, at window, 1973.07.13; Frankfurt/M., Senckenberg-Anlage, at window, 1974.07.10; Leipzig, Botanical Garden, greenhouse, 1978.08; Berlin-Neukölln, Britzer Garten, butterfly house, 1995.01.12; Erfurt, butterfly house, 1999.02.27; Düsseldorf-City, Aquazoo, greenhouse, 2002; Görlitz-City, Naturkundemuseum, greenhouse, 2002.03.21; Berlin-Friedrichsfelde, Tierpark, greenhouse, 2002.10.02; Konstanz, botanical garden of university, greenhouse, 2003.04.24. HAWAII: Laysan Island (25.46 N, 171.44 W): Schauinsland, pre 1900, type *H. schauinslandi*. INDONESIA: Java: Cibodas, 2000.01.05. JAPAN: Okinawa: Yona, 1999.10.03; Okinawa: Miyake Isl., 2001.07.26. POLAND: Breslau, Botanical Garden, greenhouse pre 1945. SWITZERLAND: Zürich, Zoological

Garden, greenhouse, 2001.01.28. TANZANIA: Kilimandjaro: Kiboscho, 1400 m, 1904, type *H. aemula*. Victoria: Nyanza, Acip. di Sesse, Bugala, 1908.

2.5. Investigated type material of *Hypoponera*

For any of the 12 names treated here type material was available and any of the names could be referred to *Hypoponera*. The text on the type labels is cited with each writing error, abbreviation or sign and illegible syllables are mentioned. A backslash between the citations means a change to the next label on the same pin. Differences between text of labels and statements in original descriptions were in no case as strong that genuine type identity might be doubted. Material is listed here under the original names in chronological order.

***Ponera punctatissima* Roger, 1859:** 1 paralectotype worker (des. by Seifert 2003) in MNHN Paris, apparently labelled 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. 1 paralectotype worker in DEI, labelled not in Rogers handwriting »Rauden«. 1 paralectotype worker in ZMHU Berlin, labelled not in Rogers handwriting »Schlesien Rauden Roger, S. \ *Ponera punctatissima* Rog. \ Type«.

***Ponera androgyna* Roger, 1859:** 2 ergatoid syntype males in ZMHU Berlin, labelled not in Rogers handwriting »Schlesien Rauden Roger, S. \ *Ponera punctat.* Rog. v. *androgyna* Rog \ Type«.

***Ponera tarda* Charsley, 1877:** 2 syntype workers in UM Oxford with the following labels: »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 Westwoods handwriting), and »TYPE HYME 2500 172;2/2 *Ponera tarda* Charsley, 1877 SYNTYPES ♀♀ HOPE ENT COLL., OUMNH« (printed label).

***Ponera abeillei* André, 1881:** 2 syntypes in MNHN Paris: 1 worker type labelled »Ajaccio Abeille \ MUSEUM PARIS COLLECTION ERNEST ANDRÉ 1914 \ TYPE \ *H. abeillei* (André)«; 1 type worker with same labelling but bottom label »abeillei (André)«.

***Ponera punctatissima* r. *jugata* Forel, 1892:** 1 type gyne without scapes, labelled »Typus \ *P. punctatissima* Roger R. *jugata* Forel Imerina (Sikora) \ r. *P. jugata* Forel«, MHN Genève.

***Ponera punctatissima* r. *indifferens* Forel, 1895:** 4 syntypes in MHN Genève: 1 gyne labelled »Typus \ *P. punctatissima* Rog ♀ r. *indifferens* Forel Moramanga (Sikora Juli 93) Z5 type«; 2 workers »Typus \ Pon. *punctatissima* ♀ r. *indifferens* type Moramanga (Sikora Juli 93) 75 \ 7. *P. indifferens* Forel«; 1 gyne, labelled »50 Mg \ *Ponera punctatissima* Roger ♀ r. *indifferens* Forel Mockay« (possible reading also »Mokay« or »Mackay«).

Ponera punctatissima var. *schauinslandi* Emery, 1899: 2 gyne syntypes on two different pins in MCSN Genova: the first syntype labelled »*Ins. Laysan Schauinsland*« and »*Ponera punctatissima* var. *Schauinslandi* Emery« in Emery's handwriting and a red label »SYNTYPUS *Ponera punctatissima* var. *schauinslandi* Emery, 1899«; the second syntype labelled »*Ins. Laysan Schauinsland*« in Emery's handwriting and a with a red label »SYNTYPUS *Ponera punctatissima* var. *schauinslandi* Emery, 1899«.

Ponera dulcis var. *aemula* Santschi, 1911: 1 worker lectotype (by present designation) and 1 worker paralectotype on separate pins, both labelled »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), stored in NHM Basel. Lectotype with CW 532 µm, paralectotype CW 545 µm.

Ponera ergatandria subsp. *bondroiti* Forel, 1911: following syntypes labelled with a printed »Typus« label, stored in MHN Genève: 1 worker labelled »*Jardin Botan. Bruxelles 15-11-09 \ ♂ ergatoide minor*« in Bondroit's handwriting and »*P. ergatandria* Forel r. *Bondroiti* For ♂ type *Bruxelles Serre chaud*« in Forels scribbling. This specimen shows a well-developed stinger and no trace of male genitalia. 3 workers labelled »*Bruxelles 11-09*« in Bondroit's handwriting and »*P. ergatandria* Forel r. *Bondroiti* For ♀ type *Serre chaud Bruxelles*« in Forels scribbling. 1 alate gyne labelled »*Bruxelles Jardin Botan. 5-11-09*« in Bondroit's handwriting and »*P. ergatandria* Forel r. *Bondroiti* For ♀ type *Bruxelles Serre chaud \ r. P. Bondroiti* Forel« in Forels scribbling. 1 ergatoid male labelled »*Jardin Botan. Bruxelles 15-11-09 \ ♂ ergatoide*« in Bondroit's handwriting.

Ponera opaciceps var. *gibbinota* Forel, 1912: 1 type worker, labelled »*Typus \ Ponera opaciceps* Mayr ♀ var. *gibbinota* Jery & Kew \ v. *gibbinota* Forel«, (other possible readings of Forel's scribbling »*Jery*«: Kery, Hery, Guy), MHN Genève.

Ponera lesnei Bondroit, 1916: 1 worker type, labelled »*1122 \ Bois.de.Colombes 7 Juillet 87. Sous les pierres \ MUSEUM PARIS FRANCE P.LESNE 19 \ TYPE \ Ponera lesnei* Bondr. Type« and in Forel's handwriting »*Ponera ragusai* Em. ssp. *santschii* Em (= *lesnei* Bondr.«, MNHN Paris.

Ponera punctatissima var. *exacta* Santschi, 1923: 1 lectotype (by present designation) and 2 paralectotype workers on the same pin, labelled »*Tunisie Hammamat (Santschi VIII) \ P. punctatissima* v. *exacta* Sat«, NHM Basel. The Lectotype (top specimen) with CS 617, SL/CS 0.777 and MW/CS 0.647.

3. Results and discussion

3.1. Synonymic lists of *H. punctatissima* and *H. schauinslandi*

Based upon investigation of type material the following synonymic lists are presented (an argumentation why these synonymies are established is given in section 3.2.).

Hypoponera punctatissima (Roger, 1859)

Ponera punctatissima Roger, 1859; POLAND and GERMANY: Rauden and Berlin

Ponera androgyna Roger, 1859; POLAND and GERMANY: Rauden and Berlin

Ponera tarda Charsley, 1877; ENGLAND: Oxford

Ponera punctatissima r. *jugata* Forel, 1892; MADAGASCAR

Ponera punctatissima var. *exacta* Santschi, 1923; TUNISIA: Hammamet

***Hypoponera schauinslandi* (Emery, 1899), stat. nov.**

Ponera punctatissima var. *schauinslandi* Emery, 1899; HAWAII: Laysan Island

Ponera dulcis var. *aemula* Santschi, 1911; TANZANIA: Kilimandjaro; syn. nov.

Ponera ergatandria subs. *bondroiti* Forel, 1911; BELGIUM: Bruxelles; syn. nov.

Hypoponera bondroiti, sensu YAMAUCHI et. al 1996 [morphometric data and investigation of syntopic material]

3.2. Differential diagnosis of *H. punctatissima* and *schauinslandi*

The types of all available names possibly representing synonyms of *H. punctatissima* and *H. schauinslandi* were investigated in this study to ensure that no senior synonym of *H. schauinslandi* remained undetected. The identity of 12 taxa was checked in this way. Four names – *H. abeillei* (André, 1881), *H. indifferens* (Forel, 1895), *H. gibbinota* (Forel, 1912) and *H. lesnei* (Bondroit, 1916) – refer to species clearly different from both *H. punctatissima* and *H. schauinslandi* (see section 3.3.).

Primary morphometric data of workers and ergatoid females specimens of 5 European species of *Hypoponera* and of the gynes of *H. punctatissima* and *H. schauinslandi* are given in Tabs 1 and 2. No conspicuous external characters such as carinae, dents, curvatures, sculptural elements, setae etc. were discovered that could allow a discrimination of the sister species *H. punctatissima* and *H. schauinslandi* by subjective visual inspection. Reliably possible was the separation of workers by discriminant functions, the details of which are given in the Appendix (section 4). The resulting discriminant scores D(10) given as arithmetic mean $\pm$ standard deviation [lower extreme, upper extreme] were:

H. punctatissima D(10) 3.068 ± 1.004 [+ 0.61, + 4.84] n = 48

H. schauinslandi D(10) -2.815 ± 0.995 [- 4.91, - 0.61] n = 45

100 % of the 93 initial classifications were confirmed by D(10) with error probabilities of $p < 0.05$ in the worst case and any of the involved type individuals was allocated to either cluster with an error probability $p < 0.006$ (Fig. 2). Hence the synonymies stated above are fully confirmed:

D(10) was 3.02, 3.21, 2.83 in the lectotype and two paratypes of *H. punctatissima* from Rauden, 2.37 and 0.77 in the syntypes of *H. tarda* from Oxford, 3.80, 4.17 and 4.29 in the lectotype and two paratypes of *H. exacta* from Al Hammamat, - 0.99 and - 1.54 in the syntypes of *H. aemula* from Kilimandjaro and - 3.21, - 4.28 and - 2.93 in the syntypes of *H. bondroiti* from Bruxelles.

A reliable separation of gynes was possible by discriminant functions, the details of which are given in the Appendix (section 4). The resulting D(9) were:

H. punctatissima D(9) 3.294 ± 0.816 [+ 1.77, + 5.15] n = 37

H. schauinslandi D(9) -4.316 ± 1.234 [- 6.38, - 1.77] n = 24

Any of the 61 initial classifications was confirmed by D(9) and any specimen including the types was allocated to either cluster with an error probability $p < 0.001$ (Fig. 3). Hence, the synonymies stated above are fully confirmed also in the gynes: D(9) was 1.77 the paratype of *H. punctatissima* from Rauden, minus 5.48 and minus 4.14 in the syntypes of *H. schauinslandi* from the Laysan Island, and minus 5.35 in the syntype of *H. bondroiti* from Bruxelles.

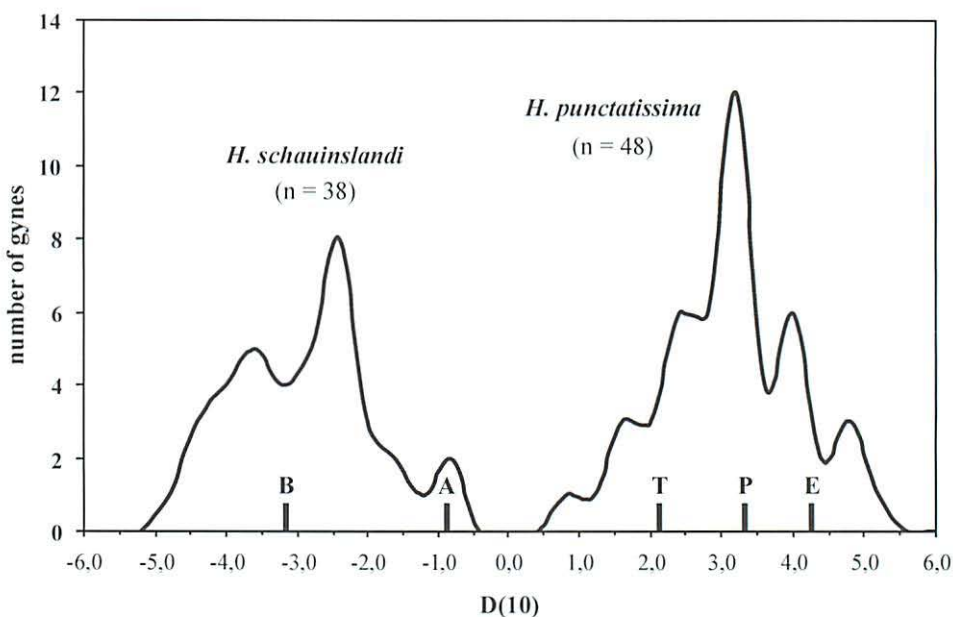


Fig. 2 Canonical discriminant values D(10) of workers of *H. schauinslandi* (Emery, 1899) and *H. punctatissima* (Roger, 1859). Position of type specimens is indicated by letters: B – *H. bondroiti* (Forel, 1911), A – *H. aemula* (Santschi, 1911), T – *H. tarda* (Charsley, 1877), P – *H. punctatissima*, and E – *H. exacta* (Santschi, 1923)

The type gyne of *H. jugata* from Imerina, in which both scapes are missing, could not be included in the analysis above. The primary data of this type gyne were CS 677, CL/CW 1.145, MW/CS 0.770, PEW/CS 0.493, PEL/CS 0.385, ML/CS 1.654, NOH/CS 0.376, FODG 13.5. To objectively assess the position of this taxon, a separate analysis calculating a discriminant D(8) was run, the details of which are given in the Appendix (section 4).

The exclusion of the powerful character SL from the analysis did not decrease the discriminative performance dramatically: 100 % of the initial classifications still were confirmed, 98.4 % of individuals were classified with error probabilities of $p < 0.01$, and any of the involved type individuals was allocated to either cluster with an error probability $p < 0.001$. The type of *H. jugata* showed a $D(8)$ of 1.70 with a probability to belong to *H. punctatissima* of $p > 0.999$. The overall $D(8)$ for 62 gyne specimens were:

H. punctatissima $D(8)$ 2.481 ± 0.816 $[+ 0.65, + 3.78]$ $n = 38$

H. schauinslandi $D(8)$ $- 3.124 \pm 1.240$ $[- 5.11, - 0.65]$ $n = 24$

Comparative statements on the character combination of ergatoid males are not possible here because only one specimen plus one head of one *H. schauinslandi* male was available. However, with CS given in mm, the size-corrected scape length index

$$SL/CS_{cor} = SL/CS / (-0.3589 CS + 0.8741)$$

of these two individuals was clearly lower than in all 11 *H. punctatissima* males: 0.857 and 0.885 against 1.000 ± 0.018 $[0.968, 1.028]$. These data promise a clear separation of both sister species when more specimens with complete character sets would be available.

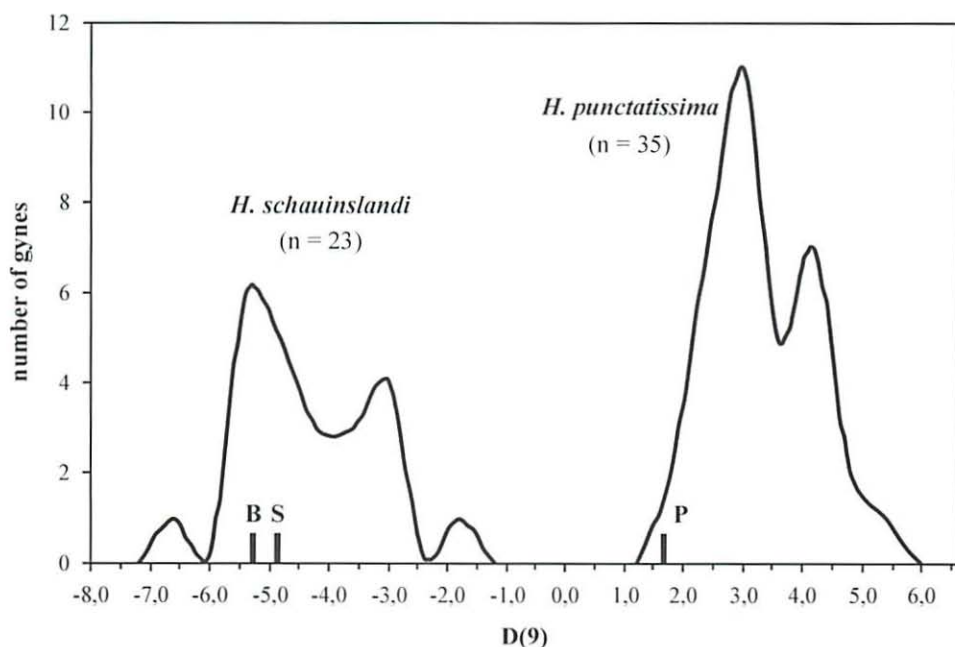


Fig. 3 Canonical discriminant values $D(9)$ of gynes of *H. schauinslandi* (Emery, 1899) and *H. punctatissima* (Roger, 1859). Position of type specimens is indicated by letters: **B** – *H. bondroiti* (Forel, 1911), **S** – *H. schauinslandi*, and **P** – *H. punctatissima*

Tab. 1 Morphometry of worker and ergatoid female individuals of 6 species of *Hypoponera* occurring in Europe given as arithmetic mean $\pm$ standard deviation [minimum, maximum]. Characters in heavy type are most diagnostic

	<i>H. eduardi</i> (n = 10)	<i>H. punctatissima</i> (n = 48)	<i>H. schauinslandi</i> (n = 45)	<i>H. lesnei</i> (n = 1)	<i>H. abeillei</i> (n = 2)
CS	627 $\pm$ 22 [604, 669]	616 $\pm$ 17 [592, 663]	558 $\pm$ 26 [514, 625]	550	463 $\pm$ 16 [451, 474]
CL/CW	1.182 $\pm$ 0.019 [1.147, 1.208]	1.172 $\pm$ 0.015 [1.135, 1.203]	1.181 $\pm$ 0.019 [1.124, 1.212]	1.283	1.361 $\pm$ 0.007 [1.356, 1.366]
SL/CS	0.840 $\pm$ 0.014 [0.813, 0.859]	0.773 $\pm$ 0.009 [0.742, 0.787]	0.734 $\pm$ 0.009 [0.706, 0.756]	0.728	0.818 $\pm$ 0.004 [0.815, 0.821]
FR/CS	0.148 $\pm$ 0.008 [0.137, 0.160]	0.122 $\pm$ 0.008 [0.103, 0.139]	0.119 $\pm$ 0.007 [0.106, 0.138]	0.139	0.084 $\pm$ 0.005 [0.080, 0.087]
FoDG	11.69 $\pm$ 0.67 [10.8, 12.8]	12.52 $\pm$ 0.63 [10.9, 14.2]	12.53 $\pm$ 0.63 [10.7, 14.0]	13.00	11.70 $\pm$ 0.70 [11.2, 12.2]
ML/CS	1.469 $\pm$ 0.018 [1.448, 1.507]	1.490 $\pm$ 0.023 [1.449, 1.542]	1.473 $\pm$ 0.026 [1.431, 1.565]	1.518	1.512 $\pm$ 0.009 [1.505, 1.518]
MW/CS	0.683 $\pm$ 0.016 [0.646, 0.702]	0.663 $\pm$ 0.018 [0.622, 0.710]	0.659 $\pm$ 0.018 [0.621, 0.697]	0.642	0.644 $\pm$ 0.002 [0.642, 0.645]
ML/MW	2.151 $\pm$ 0.057 [2.063, 2.257]	2.248 $\pm$ 0.065 [2.118, 2.441]	2.235 $\pm$ 0.068 [2.098, 2.384]	2.364	2.348 $\pm$ 0.006 [2.344, 2.353]
PEW/CS	0.483 $\pm$ 0.019 [0.449, 0.508]	0.469 $\pm$ 0.019 [0.437, 0.533]	0.456 $\pm$ 0.026 [0.416, 0.526]	0.451	0.463 $\pm$ 0.007 [0.458, 0.468]
PEL/CS	0.343 $\pm$ 0.009 [0.327, 0.363]	0.374 $\pm$ 0.006 [0.361, 0.386]	0.363 $\pm$ 0.009 [0.349, 0.388]	0.387	0.478 $\pm$ 0.005 [0.475, 0.482]
NOH/CS	0.402 $\pm$ 0.015 [0.384, 0.420]	0.363 $\pm$ 0.014 [0.338, 0.396]	0.350 $\pm$ 0.016 [0.318, 0.391]	0.319	0.322 $\pm$ 0.004 [0.319, 0.324]
PEL/NOH	0.853 $\pm$ 0.026 [0.812, 0.888]	1.031 $\pm$ 0.038 [0.936, 1.116]	1.038 $\pm$ 0.042 [0.951, 1.118]	1.213	1.488 $\pm$ 0.032 [1.466, 1.511]

3.3. Taxa belonging neither to *H. punctatissima* nor to *H. schauinslandi*

Hypoponera abeillei (André, 1881)

The two worker syntypes from Ajaccio strikingly differ from both *H. punctatissima* and *H. schauinslandi* in many characters – e.g. much larger CL/CW, SL/CS, and PEL/CS or much smaller FR/CS (Tab. 1). The elongated head and petiole is outstanding among European *Hypoponera*. The specimens show no visible ommatidia and a very small subpetiolar corner but no suggestion of a fenestra or translucent spot. This is clearly a good species.

Hypoponera indifferens (Forel, 1895)

This taxon from Madagascar originally had been described as a race of *H. punctatissima*

Tab. 2 Morphometry of *Hypoponera* gynes given as arithmetic mean $\pm$ standard deviation [minimum, maximum]. Characters in heavy type are diagnostic. Strings of asterisks are a visual indication of characters useful in separating *H. punctatissima* and *H. schauinslandi*

	<i>H. punctatissima</i> (n = 38)		<i>H. schauinslandi</i> (n = 24)	<i>H. eduardi</i> (n = 2)
CS	705 $\pm$ 22 [637, 753]	**	617 $\pm$ 21 [572, 650]	676 $\pm$ 6 [672, 681]
CL/CW	1.108 $\pm$ 0.018 [1.078, 1.145]	*	1.131 $\pm$ 0.019 [1.101, 1.168]	1.131 $\pm$ 0.007 [1.126, 1.136]
SL/CS	0.758 $\pm$ 0.015 [0.723, 0.807]	**	0.727 $\pm$ 0.010 [0.706, 0.746]	0.852 $\pm$ 0.004 [0.849, 0.854]
FoDG	12.51 $\pm$ 0.58 [11.4, 13.4]		12.12 $\pm$ 0.62 [11.0, 13.7]	12.45 $\pm$ 0.64 [12.0, 12.9]
ML/CS	1.658 $\pm$ 0.028 [1.611, 1.716]		1.654 $\pm$ 0.040 [1.562, 1.750]	1.641 $\pm$ 0.013 [1.632, 1.650]
MW/CS	0.769 $\pm$ 0.020 [0.740, 0.821]		0.753 $\pm$ 0.018 [0.719, 0.786]	0.774 $\pm$ 0.007 [0.769, 0.779]
ML/MW	2.158 $\pm$ 0.073 [1.971, 2.265]		2.197 $\pm$ 0.064 [2.034, 2.285]	2.120 $\pm$ 0.036 [2.095, 2.146]
PEW/CS	0.513 $\pm$ 0.017 [0.484, 0.568]	**	0.478 $\pm$ 0.014 [0.454, 0.509]	0.532 $\pm$ 0.016 [0.520, 0.543]
PEL/CS	0.384 $\pm$ 0.008 [0.371, 0.404]		0.379 $\pm$ 0.008 [0.363, 0.397]	0.341 $\pm$ 0.001 [0.340, 0.341]
NOH/CS	0.391 $\pm$ 0.012 [0.365, 0.419]	**	0.366 $\pm$ 0.011 [0.347, 0.386]	0.445 $\pm$ 0.025 [0.427, 0.463]
PEL/NOH	0.983 $\pm$ 0.034 [0.914, 1.040]	*	1.035 $\pm$ 0.035 [0.950, 1.094]	0.768 $\pm$ 0.047 [0.734, 0.801]

but BOLTON (1995) formally raised it to species rank. Morphometric results given here clearly confirm this view.

The two syntype gynes from Moramanga and »Mackay« show the following standard measurements: CS 634, 646; CL/CW 1.198, 1.224; SL/CS 0.788, 0.824; MW/CS 0.752, 0.763; PEW/CS 0.563, 0.640; PEL/CS 0.420, 0.394; ML/CS 1.728, 1.746; NOH/CS 0.451, 0.516; FODG 12.3, 10.6; PrOc/CL 0.278, 0.280; FL/CS 0.229 (width of rupture subtracted), 0.239; FR/CS 0.097, 0.116. There is a median rupture of clypeus and anterior vertex in the Moramanga specimen. A comparison with the data presented in Tab. 2 shows that CL/CW is completely above the known range in *H. punctatissima* and *H. schauinslandi* and that 4 other characters are significantly different. The most striking difference, however, is the much larger PrOc/CL of *H. indifferens*, which ranges between 0.147 and 0.168 in *H. punctatissima* and *H. schauinslandi*.

Characters of the two syntype workers from Moramanga correlate with those of the gynes: CS 570, 606; CL/CW 1.242, 1.232; SL/CS 0.772, 0.760; MW/CS 0.691, 0.703; PEW/CS 0.521, 0.533; PEL/CS 0.403, 0.401; ML/CS 1.522, 1.544; NOH/CS 0.416, 0.424; FODG n.m., 15.8; EyePos/CL 0.379, 0.379; FR/CS 0.093, 0.083. A comparison with the data presented in Tab. 1 shows that CL/CW, PEL/CS and NOH/CS are clearly above and FR/CS below the known range in *H. punctatissima* and *H. schauinslandi*. Again the most striking difference is the eye position: EyePos/CL ranges between 0.251 and 0.284 in *H. punctatissima* and *H. schauinslandi*. Vertex foveolae are wider and deeper in *H. indifferens* and its mandibles $\pm$ 10-dentate and rather homodont.

Hypoponera gibbinota (Forel, 1912)

It remains unclear from which region of the world this ant had been introduced to a greenhouse in S England. The type worker of *H. gibbinota* is very distant from members of the *H. punctatissima* group and differs in having the anteromedian clypeal margin clearly notched, a much stronger microsculpture, a well-developed microreticulum on the gaster tergites (obscuring foveolae!), a much longer scape, a much lower PEL/NOH and a clearly larger EyePos/CL. By morphometry, the most similar European species is *H. eduardi* but *H. gibbinota* differs by notched clypeus, longer scape and stronger microreticulum on gaster tergites. Data of the *H. gibbinota* type worker: CS 678, CL/CW 1.200, SL/CS 0.884, MW/CS 0.664, PEW/CS 0.500, PEL/CS 0.337, ML/CS 1.427, NOH/CS 0.405, FODG immeasurable, EyePos/CL 0.246, FR/CS 0.157, FL/CS 0.259, PEL/NOH 0.832.

Hypoponera lesnei (Bondroit, 1916)

H. lesnei, described from Seine-et-Oise: Bois de Colombes near Paris, has been listed by BERNARD (1967) as a synonym of *H. ragusai* (Emery 1894) that was described from Sicily. I cannot comment on Bernard's unexplained speculation because types of the latter taxon were not seen. For the problems considered here, it is important to state that the *H. lesnei* type worker definitely belongs to *Hypoponera* and that it is clearly heterospecific from both *H. punctatissima* and *H. schauinslandi* or any other species described in this paper. There is no species within this study combining a large CL/CW, FR/CS, and PEL/NOH with small SL/CS. The character combination of the type worker is: CS 550, CL/CW 1.283, SL/CS 0.728, MW/CS 0.642, PEW/CS 0.451, PEL/CS 0.387, ML/CS 1.518, NOH/CS 0.319, FODG 13.0, FR/CS 0.139, PEL/NOH 1.213, 4 ommatidia per eye.

3.4. Habitat selection of *H. punctatissima* and *H. schauinslandi*

Significant differences in the nesting sites of *Hypoponera schauinslandi* and *Hypoponera punctatissima* are exposed when the consideration is restricted to localities in Europe north of 48° northern latitude.

H. schauinslandi was exclusively found in greenhouses or other heated buildings with air temperatures constantly above 19 °C (usually between 22 and 27 °C). No nest sites outside houses are known (Tab. 3). 94 % of the *H. schauinslandi* sites were greenhouses with tropical or subtropical plants situated in zoological and botanical gardens, in butterfly parks, plant stores, museums etc. The only exception, a home for old aged, most probably had a room with a lot of potted plants. This type of habitat selection indicates *H. schauins-*

landi to be a true tropical species, the anthropogenic introduction of which into the north temperate zone began no earlier than in the 1860s, when tropical plants and animals were imported in higher numbers and could be kept in greenhouses with stable heating conditions throughout the year.

In *H. punctatissima*, only 22 % of nests were found in heated houses but 78 % under open-air conditions. Among these outdoor nests, 62 % were found in heaps of decomposing organic material such as saw dust, hay, flotsam deposited on the sea shore, or manure from cow or horse stables. Many of these heaps, especially when consisting of wet and fine-grained material, may show an enormous heat production, which may force the ants in summer to construct their brood chambers 1–2 cm below the surface (Klaus Lippold pers. comm.) but prevents deeper layers from freezing even in the coldest winters.

SEIFERT (1982) has doubted permanent establishment of nests and successful overwintering of *H. punctatissima* in outdoor habitats without endogenous heat production (ONHP sites), but this idea is no longer acceptable in the context of rising global temperatures. In continental Europe north of 48° N, there is an apparent trend to increase nesting in ONHP habitats during the 20th century. The chronological sequence of six recordings from such habitats is: a xerothermous meadow in the Passendorfer Wiesen near Halle in 1953, a park lane in the city of Leipzig in 1978, a xerothermous grassland near Mainz-Finthen in 1990, a xerothermous orchard near Mainz-Finthen in 1990, a *Molinia* stand in a peat bog (!) near Hütschenhausen in 1993, and a xerothermous granite rock near Görlitz in 1994. It is noteworthy that there is no clear record exists from ONHP habitats, but 15 records from other habitats prior to 1950, while there are 6 records from ONHP habitats and 18 from other habitats after 1950. This weakly significant trend (χ^2 2.72, $p < 0.10$) is also confirmed by literature data of »*H. punctatissima*« in which the species identity is unclear: only one record from a garden in England (DONISTHORPE 1927) could possibly be attributed to an ONHP nest site before 1950.

The clear interspecific nest site differences allow a most probable allocation of the following literature records on outdoor nesting to *H. punctatissima* without having seen voucher specimens: a bone heap in Queenborough/E Kent (DONISTHORPE 1915), a coffee waste heap in a quarry near Ashbourne/Derbyshire (STRADLING 1965), four horse dung heaps at Exeter/Devon, Trescott/Staffordshire and Hopwood/Warwickshire (TIMMINGS & STRADLING 1993), a compost heap in Comberton/Worcestershire and a pile of wood chippings in a large coppice wood near Pershore/Worcestershire (WHITEHEAD 1994) and mounds of mowed grass in Belgium (several cases, DESSART & CAMMAERTS 1995). Summer temperatures in the coffee waste heap were 35 °C at 25 cm depth and there was a high abundance of *Collembola* near to surface. The preferred temperature range of *Hypoponera* within the horse dung heaps was 22–32 °C.

Confirmation by skilled determiners is urgently needed for some spectacular statements of RESSL (1995) on nesting in several natural sites in Austria, mainly xerothermous grasslands, in the years 1956–1966. Repeated occurrence of workers in winter nests of small mammals (in particular *Talpa*), as stated by Ressler, would add a really new trait to the biology of *H. punctatissima*. However, the few specimens of Ressler found in the collection of NHM Vienna turned out as *Ponera* (Schlick-Steiner und Steiner in litt.) and it remains to be studied if the many missing specimens possibly stored in the collection of Walter Faber were also misidentified.

Tab. 3 Nesting sites verified by examined voucher specimens. GH = greenhouses, HHD = heated human dwellings, ODHP = outdoor habitats with endogenous (decompository) heat production, ONHP = outdoor habitats with no endogenous heat production

	GH	HHD	ODHP	ONHP	total
<i>H. schauinslandi</i>	17	1			18
<i>H. punctatissima</i>	3	1	8	6	18

Head capsules from a sewer beneath a heated Roman bath house in Yorkshire, older than 1500 years b.p. were once determined by Chris O'Toole as *Hypoconera punctatissima* (O'Toole, pers. comm. 2003.02.26). The whereabouts of voucher specimens of this archaeological sample investigated in the 1970s are unknown, but a correct naming is supported by the circumstances of finding that speak against *Ponera*, by the most certain absence of *H. schauinslandi* from England before 1850, and by a significant probability of *H. punctatissima* to occur in Roman England. The large potency for long-range flight-dispersal (see section 3.5) and the good chance to survive temperate winters indicate that *H. punctatissima* should have reached north temperate Europe independent of anthropogenic transport and might have invaded these areas already during warmer climatic periods beginning with the Atlantic. Only the British Isles with their mild winters should have provided conditions for early invasion.

3.5. Swarming and dispersal of *H. punctatissima* and *H. schauinslandi*

Observations throughout the year of alate gynes of the two sibling species in Europe north of 48° N significantly differ (Tab. 4). In *H. punctatissima*, 19 observations were made between 28 May and 16 August (= 95 %) but only one outside this period (5 November, referring to an intranidal observation). This pronounced summer peak is obviously both a consequence of a real production maximum in the many outdoor nests and of favourable flight temperatures from late June to mid August. In fact 14 out of 18 summer observations refer to catches of alate gynes in dispersal and only 5 to intranidal collecting. Take-off of alate gynes from a nest in a xerothermous rock area was once directly observed near the town of Görlitz: the gynes flew off on 9 August 1994, 18.00 – 18.15 h local time when air temperatures were 22 °C (after a daily maximum of 25 °C). Very high flight temperatures and much sunshine are obviously not necessary. The mean and maximum of daily air temperatures were 18.7 ± 2.3 [15.0, 21.5] °C and 24.1 ± 3.2 [19, 28] °C during eight flight days with weather recordings available – these means are only 1.5 – 2.5 K higher than average seasonal values.

In *H. schauinslandi*, 8 observations (= 80 %) fall into the period from 9 November to 25 February but only two were made on 10 and 13 July (in both cases referring to an alate gyne caught at window panes in a building). These data suggest *H. schauinslandi* alates mainly to develop in winter and rarely in summer which appears unintelligible in view of rather constant temperature, and humidity conditions provided in greenhouses throughout the year. However the data are significant – when weighted against the overall frequency of greenhouse collecting: within 23 greenhouse collecting days of different investigators

from October to March recorded in the author's files, 8 yielded alate gynes and 15 not while all 20 collections from April to September yielded no alates (X^2 6.40, $p < 0.02$). A possible explanation might be that development of alates is depressed by the long-day light regime of the summer period.

The mode of dispersal of both sibling species in temperate Europe N of 48° N is most different. There is no suggestion that *H. schauinslandi* gynes are capable of long-range flight-dispersal in climates with July isotherms below 20 °C. No alate gynes in dispersal were caught outside buildings. In two cases they were caught on a window pane inside a building in Frankfurt City and in another one in an electrocution trap in a butcher's shop in London City. If outdoor flight-dispersal should ever occur in *H. schauinslandi*, it should not end in finding a suitable nesting site. Hence, dispersal of *H. schauinslandi* undoubtedly depends upon passive anthropogenic transport to heated houses with living soil. A zoogeographic characteristics of this species is: tropical, cosmopolitan, tramp species.

In *H. punctatissima*, as much as 86 % of dispersing alates were caught outside of buildings and as much as 50 % far away from the next human settlement (Tab. 5). In one case an alate gyne was caught in a pitfall trap in a small, isolated peat bog in the centre of a compact 36 km² forest. This clearly indicates a high potency for long-range flight-dispersal in temperate climates. This adaptation and the well-documented ability for permanent nesting in natural habitats makes it most probable that *H. punctatissima* was not depending upon passive anthropogenic introduction into areas north of 48° N – though human civilisation undoubtedly provided the basis for a considerable increase of its abundance. A zoogeographic characteristic of this species is: tropical to south temperate, cosmopolitan.

Tab. 4 Occurrence throughout the year of alate gynes verified by examined voucher specimens

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	total
<i>H. schauinslandi</i>	4	2					2				1	1	10
<i>H. punctatissima</i>					1	3	9	7			1		20

Tab. 5 Spatial occurrence of *flying* gynes verified by examined voucher specimens. inBu = within human buildings, ouBu = outside human buildings but within human settlements, open = far away from human settlements

	inBu	ouBu	open
<i>H. schauinslandi</i>	3		
<i>H. punctatissima</i>	2	5	7

3.6. Other traits of the biology of *H. punctatissima* and *H. schauinslandi*

Very little is known about other traits of the biology in *H. punctatissima*. Absence of voucher specimens also makes an interpretation of published statements difficult – e.g. it is not clear to which species the observations of HAMILTON (1979) could refer.

For *H. schauinslandi* and referring to the population on the Okinawa Islands, YAMAUCHI et al (1996) provided the following basic data:

- (1) nests are weakly polygynous and polydomous colonies occur.
- (2) there is a distinct size dimorphism in ergatoid males: CS in minors is 508 – 615 μm and in majors 695 – 808 μm .
- (3) a differential behaviour exists between males: majors fight with majors – no killings but damage of appendages was observed in 7 out of 8 cases. Majors do not attack minors because minors seem to mimic females. Minors do not fight among themselves. Both minor and major males mate with both gynomorphic and ergatoid females.
- (4) there is a distinct polymorphism of female reproductives: gynomorphic queens have large eyes, 3 ocellae, a large mesosoma and 3 + 3 ovarioles and are able to fly. Ergatoid queens are similar to workers but have a slightly larger size, larger eyes, a spermatheka (that is always inseminated) and 3 + 3 ovarioles. Workers are always without ovarioles and a spermatheka.
- (5) the arithmetic mean, standard deviation and upper and lower extremes were in 26 nest populations: 29.2 ± 34.8 [1,184] for workers, 3.7 ± 4.5 [0,20] for ergatoid queens (these found in 22 nests), 0.73 ± 1.06 [0,4] for gynomorphic queens (found in 10 nests), 0.38 ± 0.64 [0,2] for major males (found in 8 nests), 0.58 ± 1.24 [0,6] for minor males (found in 9 nests) and 5.30 ± 9.47 [0,39] for alate gynes (found in 12 nests).

In its European greenhouse habitats, *H. schauinslandi* was repeatedly observed to nest under very moist conditions in log or under bark. Collembola and other microarthropods seem to be its most preferred prey, which was also observed for *H. punctatissima* in a coffee waste heap. The obvious dependence of both *H. schauinslandi* and *H. punctatissima* upon small epigeal and hypogeal arthropods and difficulties to use other food sources prevents them from having a wider synanthropic distribution.

The following observations, where voucher specimens are available, indicate a high similarity of *H. punctatissima* with *H. schauinslandi* in a number of basic traits:

- (1) at least occasional polygyny/polydomy is suggested by observations of Klaus Lippold (pers. comm.) who stated »I found nest by nest closely together under the whole surface of a large sawdust heap. I could not really decide if it were many different societies or a single one.«
- (2) presence of size dimorphism in ergatoid males: CS was 615 – 722 μm in minors and 762 – 879 μm in majors. In size and general habitus, the latter resemble *Harpagoxenus*.
- (3) fighting between major males is indicated by traumatological findings: 3 out of 8 morphometrically investigated major males showed healed injuries as completed peroxidase reactions indicated. In two cases the funiculus was cut off after the pedicellus, in another case the tibio-femoral junction was damaged. No injuries were observed in 19 minor males and these obviously do not fight among themselves as the presence of 17 uninjured minor males within a nest sample from Doberschütz 1981.09.21 suggests.

- (4) polymorphism in female reproductives: gynomorphic and ergatoid specimens are observed. The ergatoids are most similar to workers but have larger CS, ML/CS and MW/CS. However, the only conspicuous external character to distinguish ergatoids from workers is the larger eye. The eye size index (arithmetic mean of maximum and minimum eye diameter divided by CS) is 0.044 – 0.069 in workers and 0.077 – 0.112 in ergatoid females.
- (5) As data for worker nest populations are available: 29, 30, 40, 50, 171 and 175. Production of alate gynes was 25 and 29 in two reported cases.

Singularity of ergatoid males within *H. punctatissima* nests seems to be rare. For the nest samples seen by the author and supplemented by statements of the collectors, 2, 2, 2, 3, 3, and 17 ergatoid males were recorded. Major and minor males can be found within the same nest.

4. Appendix – discriminant functions

Allometric variance was removed in *H. punctatissima* and *H. schauinslandi* by the following functions with CS given in mm:

for workers and ergatoid females:

$$CL_{cor} = CL/CW / (-0.32782 * CS + 1.3665)$$

$$SL_{cor} = SL/CS / (-0.11300 * CS + 0.8202)$$

$$FR_{cor} = FR/CS / (+0.03960 * CS + 0.0991)$$

$$MW_{cor} = MW/CS / (+0.29324 * CS + 0.4853)$$

$$PEW_{cor} = PEW/CS / (+0.51137 * CS + 0.1615)$$

$$PEL_{cor} = PEL/CS / (+0.09268 * CS + 0.3156)$$

$$NOH_{cor} = NOH/CS / (+0.33847 * CS + 0.1582)$$

$$FoDG_{cor} = FoDG / (-3.835 * CS + 14.68)$$

$$ML_{cor} = ML/CS / (+0.30388 * CS + 1.3024)$$

in gynomorphic females:

$$CL_{cor} = CL/CW / (-0.35182 * CS + 1.3615)$$

$$SL_{cor} = SL/CS / (-0.20526 * CS + 0.8840)$$

$$MW_{cor} = MW/CS / (+0.04802 * CS + 0.7426)$$

$$PEW_{cor} = PEW/CS / (+0.08920 * CS + 0.4345)$$

$$PEL_{cor} = PEL/CS / (-0.05723 * CS + 0.4254)$$

$$NOH_{cor} = NOH/CS / (+0.04261 * CS + 0.3532)$$

$$FoDG_{cor} = FoDG / (-2.335 * CS + 14.14)$$

$$ML_{cor} = ML/CS / (+0.14106 * CS + 1.5694)$$

With these size-corrected values the following canonical discriminants were calculated for workers and ergatoid females:

$$D(10) = -79.04 + 20.740 \text{ CS} + 4.429 \text{ CL}_{\text{cor}} + 78.305 \text{ SL}_{\text{cor}} + 7.143 \text{ PEW}_{\text{cor}} - 3.301 \text{ PEL}_{\text{cor}} \\ - 8.530 \text{ NOH}_{\text{cor}} + 1.088 \text{ FR}_{\text{cor}} + 4.983 \text{ ML}_{\text{cor}} - 6.797 \text{ MW}_{\text{cor}} - 0.031 \text{ FoDG}_{\text{cor}}$$

for gynomorphic females:

$$D(9) = -84.44 + 29.133 \text{ CS} - 3.999 \text{ CL}_{\text{cor}} + 46.127 \text{ SL}_{\text{cor}} + 12.373 \text{ PEW}_{\text{cor}} + 18.118 \text{ PEL}_{\text{cor}} \\ + 8.518 \text{ NOH}_{\text{cor}} - 20.687 \text{ ML}_{\text{cor}} + 1.147 \text{ MW}_{\text{cor}} + 0.595 \text{ FoDG}_{\text{cor}}$$

for gynomorphic females under exclusion of scape length:

$$D(8) = -51.924 + 37.438 \text{ CS} + 8.647 \text{ CL}_{\text{cor}} + 2.088 \text{ PEW}_{\text{cor}} + 29.229 \text{ PEL}_{\text{cor}} \\ + 13.820 \text{ NOH}_{\text{cor}} - 33.337 \text{ ML}_{\text{cor}} - 3.291 \text{ MW}_{\text{cor}} + 1.034 \text{ FoDG}_{\text{cor}}$$

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Manuscript accepted: 17 November 2003

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Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Abhandlungen und Berichte des Naturkundemuseums Görlitz](#)

Jahr/Year: 2003

Band/Volume: [75](#)

Autor(en)/Author(s): Seifert Bernhard

Artikel/Article: [Hypoponera punctatissima \(Roger\) and H. schauinslandi \(Emery\) - Two morphologically and biologically distinct species \(Hymenoptera: Formicidae\) 61-81](#)