Clarifying naming and identification of the outdoor species of the ant genus Tapinoma FÖRSTER, 1850 (Hymenoptera...

Article *in* Myrmecological News · January 2012

CITATIONS
12

READS
63

1 author:

Bernhard Seifert
Museum für Naturkunde - Leibniz Institute for Research on Evolution and Biodiversity
179 PUBLICATIONS **2,887** CITATIONS

SEE PROFILE

Myrmecological News	16	139-147	Vienna, January 2012

Clarifying naming and identification of the outdoor species of the ant genus *Tapinoma* FÖRSTER, 1850 (Hymenoptera: Formicidae) in Europe north of the Mediterranean region with description of a new species

Bernhard SEIFERT

Abstract

Data on four species of the ant genus *Tapinoma* FÖRSTER, 1850 are presented. Three of these maintain permanent outdoor populations in Central Europe: the autochthonous *T. subboreale* sp.n., *T. erraticum* (LATREILLE, 1798) and *T. nigerrimum* (NYLANDER, 1856) which is a recently established neozoon in Germany. All three species can be safely separated on the individual level both in the female castes and in males by principal component analysis (PCA) and discriminant analysis (DA) of multiple morphometric characters. As the lectotype of *T. ambiguum* EMERY, 1925 is heterospecific from a more northern species which had been constantly named *T. ambiguum* during the last 34 years, it was necessary to describe the latter as *T. subboreale* sp.n. The earlier synonymy of *T. ambiguum* with *T. madeirense* FOREL, 1895 was confirmed on the basis of genital characters. The neotype of *T. erraticum* was fixed from a sample collected at the type locality. *Tapinoma madeirense*, known from Madeira and southern France, and *T. subboreale* sp.n. from Central and North Europe cannot be safely distinguished in the female castes but are clearly heterospecific concluded from male genital morphology. Workers of the four considered species show a strong allometry of some shape characters: Within the average intraspecific body-size range and given in per cent of the mean, the relative depth of posterior head excavation, of the metanotal groove and of the clypeal excision grow by 66.3%, 52.1% and 14.2% while relative head length falls by 13.6%. Removal of allometric variance in all shape characters and computation of these data in a PCA and a DA showed that worker morphologies of *T. nigerrimum* and *T. erraticum* differed independently from body size and, in conclusion, should also be independent from colony maturity.

Key words: *Tapinoma*, ant taxonomy, new species, invasive species, morphometrics, allometric growth.

Myrmecol. News 16: 139-147
ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 27 November 2010; revision received 20 February 2011; accepted 28 February 2011
Subject Editor: Herbert Zettel

Bernhard Seifert, Senckenberg Museum für Naturkunde Görlitz, Am Museum 1, 02826 Görlitz, Germany. E-mail: bernhard.seifert@senckenberg.de

Introduction

It is frequent in ants that male genitalia do not show obvious morphological differences between species that are safely separable in the female castes. Typical examples for this situation are the genera *Lasius* FABRICIUS, 1804, *Formica* LINNAEUS, 1758 and *Myrmica* LATREILLE, 1804. The situation in the genus *Tapinoma* FÖRSTER, 1850 is just inverted: Interspecific differences in male genitalia appear extreme while difficulties arise to separate workers and even gynes of several species (SEIFERT 1984). The genus has three species with established and permanent outdoor populations in Europe north of the Mediterranean zone. According to the prevailing naming tradition, these are referred to as *Tapinoma ambiguum* EMERY, 1925, *T. erraticum* (LATREILLE, 1798) and *T. nigerrimum* (NYLANDER, 1856). The former two are autochthonous and live in diverse natural or semi-natural habitats, ranging from xerothermous grassland to wet peat bog, with the most northern species *T. ambiguum* having extended its range to southern Scandinavia. *Tapinoma nigerrimum*, in contrast, is an established neozoon currently known from at least three cities of Germany (HELLER in press). It was imported with soil and plant material from the Mediterranean region, forming in its urban habitats highly competitive supercolonies which survived even the very cold winters 2009 / 2010 and 2010 / 2011.

Up to the present, the taxonomical interpretation of any of these species is not based on clear facts. The three original descriptions do not allow a discrimination from similar species occurring sympatrically in the terrae typicae. Furthermore, name-bearing types of *Tapinoma nigerrimum* and *T. erraticum* are lost and the syntype series of *T. ambiguum* unfortunately contains more than one species without a holo- or lectotype being fixed so far (see below).

Recently, WETTERER & al. (2007) synonymised *Tapinoma ambiguum* with *T. madeirense* FOREL, 1895. According to a list presented, they have seen all available type specimens of both taxa but the complete treatment of the issue was restricted to only these two sentences: "Comparison of the subgenital plate in males, and clypeal morphology in queens and workers of material from Madeira and from diverse places in Europe, previously identified as *Tapinoma ambiguum* Emery, including the type speci-

mens showed that all these specimens were conspecific. Therefore *T. ambiguum* is here designated as a junior synonym of *T. madeirense* Forel that is revised to full specific status." No testable arguments such as presentation and analysis of morphological data or comparative pictures of male genitalia and a more detailed discussion of type material were provided in WETTERER & al. (2007). Accordingly, the synonymisation of *T. ambiguum* was not credibly shown. Furthermore, it seemed not very probable from a biological and zoogeographical point of view that just this northern *Tapinoma* species distributed in natural or semi-natural habitats in Central Europe and south Scandinavia and definitely showing no tramp species properties should have invaded an off-shore island separated from the next point of the European continent by 850 km of sea.

These uncertainties led the author to perform a revision with the following steps: (a) lectotype fixation for *Tapinoma ambiguum* EMERY, 1925 and neotype fixation for *T. erraticum* (LATREILLE, 1798) to set testable standards for future revisions of the whole genus, (b) showing that the males of the northern *T.* "*ambiguum*" differ from both the lectotype of *T. ambiguum* and males of *T. madeirense* FOREL, 1895 from Madeira, (c) describing the northern *T.* "*ambiguum*" as the new species *Tapinoma subboreale* sp.n., and (d) showing that isolated worker individuals of the three Central European species are safely separable by use of multiple characters. The latter may be important for the determination of incipient colonies of the invasive *T. nigerrimum* containing small workers or within the context of faunistic studies in which no nest samples have been collected.

Material and methods

Type material

***Tapinoma madeirense* FOREL, 1895:** Letotype gyne (published in WETTERER & al. 2007) on a pin together with two gynes (one without head) labelled "Typus" [red label], "Tapinoma erraticum Latr. var. madeirense Forel, Ribeira Brava, Madeira", "Coll A.Forel" and "Topmost gyne LECTOTYPE". Further eight pins with 12 paralectotype gynes and 16 paralectotype workers from Madeira (labelling not exactly documented, but see site data below). All material in Muséum d' Histoire Naturelle Geneve.

***Tapinoma ambiguum* EMERY, 1925:** Lectotype male by present designation, labelled "Drôme France Forel ♂", "SYNTYPUS Tapinoma erraticum subsp. ambiguum Emery, 1925", "T. erraticum ambiguum" and "Lectotype Tapinoma ambiguum Emery, 1925 design. B.Seifert 2010". Paralectotypes: 4 workers labelled "Prag Wasmann", "SYNTYPUS Tapinoma erraticum subsp. ambiguum Emery, 1925". 1 male without gaster labelled "New Forest 29.VI. 19", "SYNTYPUS Tapinoma erraticum subsp. ambiguum Emery, 1925". All above mentioned material in Museo Civico di Storia Naturale Genoa (Genova).

Tapinoma erraticum (LATREILLE, 1798): Neotype worker by present designation, labelled "FRA: 45.0517°N, 1.5372°E, Nespouls-Faugère, 330 m, along road, under stone, leg. Galkowski 2008.07.02" and "Neotype Tapinoma erraticum (Latreille 1798), design. B.Seifert 2010"; Senckenberg Museum für Naturkunde Görlitz.

***Tapinoma subboreale* sp.n.:** See below in the section containing the description of this species.

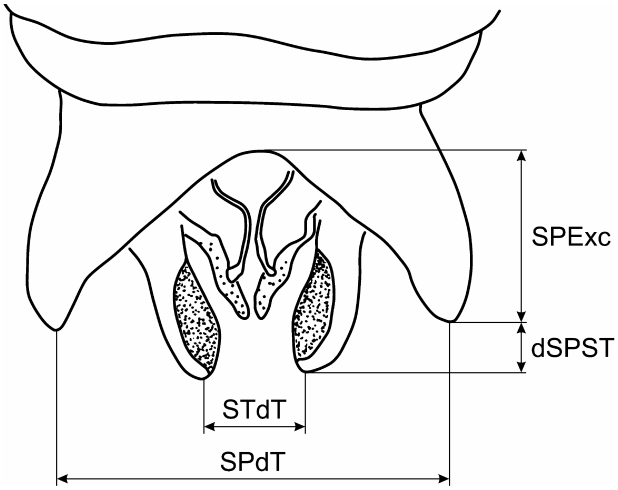

Fig. 1: Ventral aspect of male genital of *Tapinoma subboreale* sp.n. with plane of subgenital plate in visual plane, measuring schedules shown. Pilosity omitted.

Material used in numeric morphological analyses

Tapinoma erraticum (LATREILLE, 1798): 21 samples with 41 workers and 18 gynes from the following localities: Czechia: Praha (= Prague), leg. Wasmann, pre 1925 (paralectotypes of *T. ambiguum*); Praha-Prokop, 3.V.1981. France: Nespouls-Faugère, 2.VII.2008 (neotype of *T. erraticum*), leg. Galkowski; Tourettes-sur-Loup, V.1955, leg. Collingwood. Germany: Badra near Kelbra, 25.V. 1987, leg. Seifert; Gumperda, 24.VIII.1986, leg. Seifert; Mechernich, Kalenberg, VI.1990; Meisdorf, 16.V.2002, leg. Seifert; Radebeul, Belvedere, 4.VII.1998, leg. Seifert; Reichenthal / Schwarzwald, 5.V.1990, samples No 1 and 2, leg. Seifert; Schönecken near Prüm, 1.V.1990, leg. Seifert, 3.V.1990, leg. Seifert, 5.V.1990, leg. Seifert; Schönecken near Prüm, Burgberg, 3.V.1990, leg. Seifert; Steinthalleben, 24.V.1987, leg. Seifert; Sättelstädt, 5.IX.1984, leg. Seifert; Tote Täler near Freyburg, 26.VI.1991, leg. Seifert; Tübingen: Spitzberg, 9.VII.1990, leg. Seifert; Wandersleben near Gotha, 3.IX.1984, leg. Seifert; Weischlitz near Jocketa, 17.V.1986, leg. Seifert.

***Tapinoma madeirense* FOREL, 1895:** Concluded from labelling and preparation, probably eight different samples from Madeira with 23 workers, 15 gynes and four males from the following localities were investigated: Curral, leg. Schmitz, pre 1895 (paratypes); Madeira, pre 1895 (probably two samples, paratypes); Madeira, leg Schmitz, pre 1895 (paratypes); Ribeira Brava, pre 1895 (lectotype, paratypes); near Christo Rei, 29.VI.2002, leg. Espadaler; near Meio da Serra, 22.VI.2002 leg. Espadaler; near Santo da Serra, 28.III.1975 leg. Espadaler.

***Tapinoma nigerrimum* (NYLANDER, 1856):** Eight samples with 24 workers, two gynes and one male from the following localities: Germany: Edesheim / Pfalz, VI. 2009; Ingelheim / Rhein, VI.2009, VII.2009, X.2009 (sample No K2); Neustadt an der Weinstraße, 28.X.2009, samples No 1, 3 and 6; all German material leg. Heller. Spain: without locality, IV.1976, leg. Collingwood.

***Tapinoma subboreale* sp.n.:** 36 samples with 49 workers, 24 gynes and ten males from the following localities: Austria: Roppen, 5.VII.1994, leg. Seifert. Czechia: Praha (Prague), leg. Wasmann, pre 1925 (paralectotype of

T. ambiguum). G e r m a n y : Balgstädt near Freyburg, 23.VII.1980, leg. Seifert; Baruth near Bautzen, 9.V.2010, samples No 782, 915, leg. Seifert; Bilzingsleben near Kindelbrück, 10.IX.1981, leg. Seifert; Bothenheilingen near Mühlhausen, 1988, leg. Bellstedt; Brandis near Leipzig, 9.VII.1993, samples No 11 and g1, leg. Seifert; Bad Frankenhausen, 26.V.1987, leg. Seifert; Friedrichsaue near Aschersleben, 10.VI.1979, No 99, leg. Seifert; Friedrichsaue near Aschersleben, 20.VI.1979, No 114, leg. Seifert; Geesow near Gartz, 26.V.1987, leg. Seifert; Hankensbüttel, 1.IX.1991, leg. Seifert; Ichstedt, 10.VI.1998, leg. Weipert; Kosakenberg / Kyffhäuser, 10.VI.1998, leg. Burger; Oderberg, 9.V.2002, leg. Seifert; Poxdorfer Hang near Graitschen, 24.VII.1986, leg. Seifert; Rohrdorf near Isny, 8.V. 1993, leg. Seifert; Schwarza near Rudolstadt 19.IX.1987, leg. Sander; Schönecken near Prüm, 3.V.1990, leg. Seifert; Singen, 23.V.1991, leg. Seifert; Günstedt near Sömmerda, 1992, leg. Bellstedt; Tübingen: Spitzberg, 9.VII.1990, leg. Seifert; Waldhausen near Aalen, 13.X.2005, leg. Seifert; Wandersleben near Gotha, 3.IX.1984, leg. Seifert; Weischütz near Freyburg, 14.VI.2002, leg. Seifert (holotype sample); Ziemendorf near Arendsee, 13.X.2008, leg. Lange. H u n g a r y : Bugac near Kiskunfelgyhaza, 1978, 14.VI. 1979, leg. Gallé, 3.VI.1981, leg. Seifert 30.VII.1981, leg. Gallé; Harkany, V.1983, leg. Sieber. S l o v a k i a : Zemplinska Sirava near Kosice, 30.VIII.1983, leg. Seifert. S w e d e n : Öland: Borgholm, 16.VI.1992, samples No 7 and 75, leg. Seifert; Öland: Kastlösa, 12.VI.1992, leg. Seifert.

Recording of morphological data

Twelve, seven and five metric characters were recorded in workers, gynes and males. In bilaterally recorded characters, arithmetic means of both body sides were calculated. All measurements were made on mounted and dried specimens using a pin-holding stage, permitting full rotations around X, Y, and Z axes. A Wild M10 high-performance stereomicroscope equipped with a 1.6× planapochromatic objective was used at magnifications of 120 - 320×. A Schott KL 1500 cold-light source equipped with two flexible, focally mounted light-cables, providing 30°-inclined light from variable directions, allowed sufficient illumination over the full magnification range and a clear visualization of silhouette lines. A Schott KL 2500 LCD cold-light source in combination with a Leica coaxial polarized-light illuminator provided optimum resolution of tiny structures and microsculpture at highest magnifications. Simultaneous or alternative use of the cold-light sources depending upon the required illumination regime was quickly provided by regulating voltage up and down. A Leica cross-scaled ocular micrometer with 120 graduation marks ranging over 65% of the visual field was used. To avoid the parallax error, its measuring line was constantly kept vertical within the visual field. Measurements of body parts always refer to real cuticular surface and not to the diffuse pubescence surface. All measurements of male genitalia where performed in ventral view with the plane of the subgenital plate positioned within the visual plane (Fig. 1). Because of the very hairy subgenital plates, care is needed to find real cuticular surface.

CL Maximum cephalic length measured between points A and B; A is the posteromedian margin point of head capsule; B is an imagined median point situated at the same transversal level as the most anterior points of clypeus left and right of clypeal excision. Bilateral asymmetries are averaged.

CS Cephalic size; arithmetic mean of CL and CW.

CW Maximum cephalic width.

dAN Minimum distance of inner (centripetal) margins of antennal socket rings.

dSPST Longitudinal distance between transversal level of caudal tips of subgenital plate and transversal level of stipal tips. Bilateral mean. This is a measure of how much the stipes surpass the caudalmost portion of the subgenital plate.

EL Eye length; maximum diameter of compound eye; bilateral mean.

ExCly Maximum depth of anteromedian clypeal excision as it appears in frontodorsal view; bilateral asymmetries averaged.

ExOcc Depth of excavation of posterior margin of head capsule as it appears in the measuring position for CL.

F2 Median length of second funiculus segment in dorsal view (i.e., with swivelling plane of 1st funiculus segment positioned in visual plane); take care to measure median length because of unequal length of the segment's sides.

IF2 F2 divided by maximum width of second funiculus segment (excluding pubescence) in dorsal view.

MGr Depth of metanotal groove / depression in lateral view; the upper reference line extends between the highest points of mesonotum and propodeum perpendicular to which depth measuring is performed.

ML Mesosoma length from caudalmost point of lateral metapleuron to rear margin of anterior pronotal fringe (in workers) or to anteriormost point of anterior mesosomal face (in males and gynes).

MW Maximum pronotal width.

PoOc Postocular distance: distance from transversal level of posterior eye margin to hind margin of head measured in median line; bilateral asymmetries averaged.

SL Scape length excluding articulatory condyle.

SPdT Distance of caudal tips of subgenital plate.

SPExc Depth of median excision of subgenital plate (Fig. 1).

STdT Distance of the tips of the stipes.

Removal of allometric variance

In order to quantify scaling patterns of various shape characters of workers, a removal of allometric variance (RAV) was performed with the procedure described by SEIFERT (2008). RAV was calculated for the assumption of all individuals having an identical cephalic size of 0.75 mm. Overall RAV functions were applied the parameters of which were calculated as the arithmetic mean of the species-specific functions of all four species considered here, except for F2 / CS and IF2 in which only the data of *Tapinoma erraticum* and *T. nigerrimum* were used:

$CL / CW_{0.75} = CL / CW / (-0.4910 * CS + 1.4931) * 1.1249$

$SL / CS_{0.75} = SL / CS / (-0.1701 * CS + 1.1400) * 1.0120$

$EL / CS_{0.75} = EL / CS / (-0.0397 * CS + 0.3023) * 0.2725$

$ExOcc / CS_{0.75}$ [%] = ExOcc / CS / (1.429 * CS - 0.399) * 0.673

$ExCly / CS_{0.75}$ [%] = ExCly / CS / (3.033 * CS + 4.470) * 6.674

$dAN / CS_{0.75} = dAN / CS / (0.0064 * CS + 0.2894) * 0.2941$

$MW / CS_{0.75} = MW / CS / (0.0450 * CS + 0.6233) * 0.6571$
$ML / CS_{0.75} = ML / CS / (-0.0096 * CS + 1.3446) * 1.3369$
$MGr / CS_{0.75}$ [%] = MGr / CS / (6.015 * CS - 0.905) * 3.606
$F2 / CS_{0.75}$ [%] = F2 / CS / (-0.409 * CS + 14.98) * 14.68
$IF2_{0.75} = IF2 / (0.5103 * CS + 1.3202) * 1.7030$

Data analysis

All analyses were performed with the SPSS 15.0 statistical package on the basis of individuals. The selected characters were computed in a principal component analysis (PCA) and a canonical discriminant analysis (DA). All characters passed the tolerance test in a DA to the level of 0.01 as implemented by SPSS. A parallel run of an ordinary DA and of a "Leave-One-Out Cross-Validation" DA (LOOCV-DA, LACHENBRUCH & MICKEY 1968, LESAFFRE & al. 1989) was performed to realistically estimate the error rate. The data presented by SEIFERT & SCHULTZ (2009) show that the means of the pessimistic error indication by the LOOCV-DA and of the optimistic error indication by the ordinary DA are close to the true error rate.

Results and discussion

The type series of *Tapinoma ambiguum* EMERY, 1925 and the fixation of a lectotype

EMERY (1925) named three localities in his original description of *Tapinoma ambiguum*: Departement Drôme (France), New Forest (England) and Prague (Bohemia). All this material could be studied. The type series consists of three different species – among them only a single specimen, a worker from Prague, is consistent with the traditional conception of *T. ambiguum*. Unfortunately it would have been assailable to save the stability of nomenclature by fixing the lectotype in this specimen because EMERY (1925) explicitly specified "Département de la Drôme; localité typique" and because he largely based his new taxon on male genital characteristics and not on those of workers. As a consequence, I was forced to fix the lectotype of *T. ambiguum* in the male from Drôme.

The taxonomic position of the lectotype was assessed by comparison with four *T. madeirense* males from two sites in Madeira and ten males from six localities in Germany and Sweden matching the conception of *Tapinoma* "*ambiguum*" as it was applied after 1976 in determination keys for Europe north of the Mediterranean zone (KUTTER 1977, ARNOLDI & DLUSSKY 1978, SEIFERT 1984, AGOSTI & COLLINGWOOD 1987, ATANASSOV & DLUSSKY 1992, CZECHOWSKI & al. 2002, SEIFERT 2007). The lectotype has a subgenital plate strongly different from those of the northern *T.* "*ambiguum*" populations but most similar to that of *T. madeirense* FOREL, 1895. There is a strong distortion of volsellae in the lectotype genital which is probably an artefact of treatment or preparation and gives it a somewhat strange overall impression. However, restricting the view to shape and position of the subgenital plate and stipes, the specimen corresponds to *T. madeirense* (Fig. 3). When plotting the morphometric character dSPST against SPdT, the lectotype of *T. ambiguum* is widely distant from northern *T.* "*ambiguum*" and close to the Madeiran males of *T. madeirense* (Fig. 2). Hence, *T. ambiguum* EMERY, 1925 should represent the continental population and is a junior synonym of *T. madeirense* FOREL, 1895. This uncomfortable finding destroys the traditional conception of northern

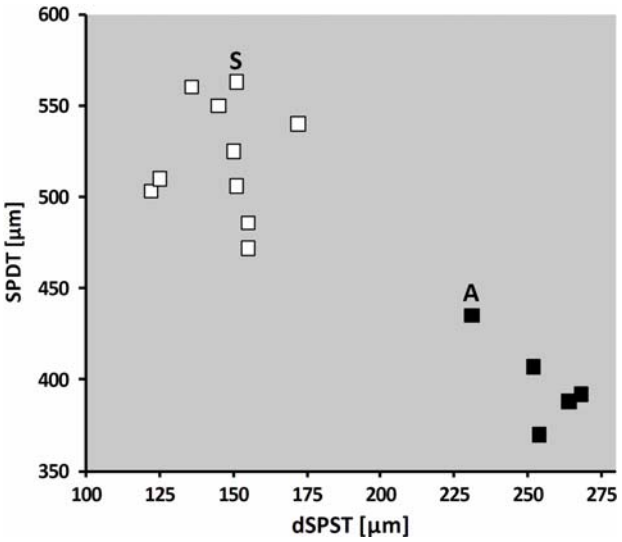

Fig. 2: Genital measurements in *Tapinoma madeirense* [black squares, lectotype of *T. ambiguum* designated with "A"] and *T. subboreale* sp.n. [white squares, holotype designated with "S"]. Distance of caudal tips of subgenital plate (SPDT) plotted against the distance of how much the stipes surpass the caudalmost portion of the subgenital plate (dSPST).

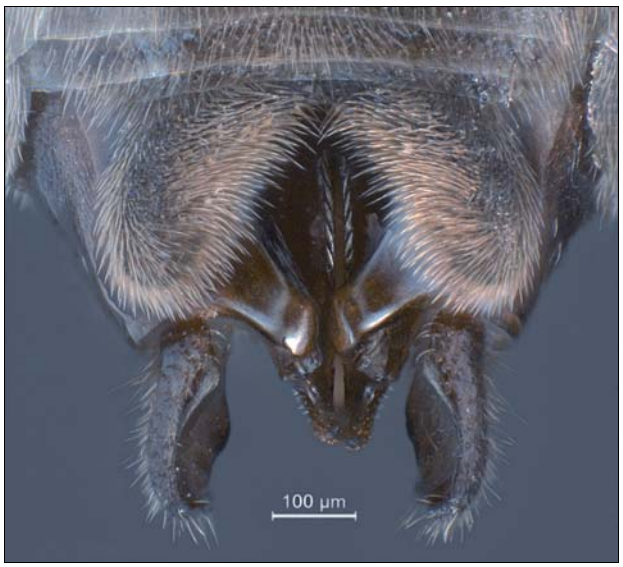

Fig. 3: Ventral aspect of male genital of *Tapinoma madeirense* with plane of subgenital plate in visual plane. Madeira: Meio da Serra, Road 203, 22.VI.2002.

T. "*ambiguum*" and forces to describe the northern population as the new species *T. subboreale* sp.n. (see below).

One specimen of the four paralectotype workers of *Tapinoma ambiguum*, labelled "Prag Wasmann" is clearly allocated to the *T. subboreale* cluster ($p > 0.9999$) while the other three paralectotype workers belong to *T. erraticum* (all with $p > 0.9999$) when clustering the three northern species *T. subboreale*, *T. erraticum* and *T. nigerrimum* in a PCA and DA. The paralectotype male with missing gaster and genitals, labelled "New Forest 29.VI.19", should belong to *Tapinoma subboreale* sp.n. as supposed by subjective assessment of head morphology and by the fact that England had only *T. erraticum* as additional species at that time.

Tab. 1: Absolute cephalic size CS and 11 RAV-corrected shape components of worker individuals of four *Tapinoma* species. All shape components are corrected for the assumption that all specimens have an equal CS = 0.75 mm. F values and significance levels of a univariate ANOVA are positioned between the species to which they refer. n.s. = nonsignificant.

	T. nigerrimum (n = 24)	**ANOVA**	***T. erraticum*** (n = 41)	**ANOVA**	***T. subboreale*** **sp.n.** (n = 49)	**ANOVA**	***T. madeirense*** (n = 23)
CS	916 ± 162 [650, 1148]	32.050 0.000	754 ± 65 [618, 866]	13.924 0.000	699 ± 70 [561, 874]	n.s.	696 ± 50 [598, 785]
CL / $CW_{0.75}$	1.146 ± 0.022 [1.112, 1.190]	10.150 0.002	1.131 ± 0.017 [1.088, 1.171]	n.s.	1.128 ± 0.020 [1.081, 1.184]	9.158 0.003	1.112 ± 0.025 [1.036, 1.165]
SL / $CS_{0.75}$	0.997 ± 0.022 [0.959, 1.043]	16.057 0.000	1.018 ± 0.019 [0.958, 1.077]	n.s.	1.010 ± 0.023 [0.959, 1.064]	n.s.	1.017 ± 0.014 [0.994, 1.045]
ExOcc / $CS_{0.75}$ [%]	0.98 ± 0.45 [0.00, 2.04]	24.398 0.000	1.57 ± 0.48 [0.59, 2.59]	80.69 0.000	0.54 ± 0.60 [0.00, 2.03]	16.760 0.000	0.02 ± 0.06 [0.00, 0.24]
ExCly / $CS_{0.75}$ [%]	7.90 ± 1.02 [5.41, 9.98]	4.528 0.037	8.35 ± 0.66 [6.97, 9.99]	400.21 0.000	5.30 ± 0.76 [3.24, 6.95]	n.s.	5.33 ± 0.56 [4.29, 6.53]
dAN / $CS_{0.75}$	0.307 ± 0.009 [0.292, 0.328]	115.31 0.000	0.285 ± 0.008 [0.270, 0.303]	45.020 0.000	0.295 ± 0.006 [0.282, 0.306]	n.s.	0.294 ± 0.007 [0.278, 0.305]
EL / $CS_{0.75}$	0.271 ± 0.009 [0.250, 0.285]	48.720 0.000	0.259 ± 0.006 [0.247, 0.270]	139.98 0.000	0.276 ± 0.008 [0.259, 0.294]	n.s.	0.277 ± 0.006 [0.267, 0.290]
MGr / $CS_{0.75}$ [%]	3.12 ± 0.46 [2.22, 4.14]	22.933 0.000	4.09 ± 0.92 [2.47, 6.32]	11.62 0.001	3.42 ± 0.95 [1.44, 5.78]	n.s.	3.38 ± 0.82 [1.13, 4.71]
MW / $CS_{0.75}$	0.636 ± 0.016 [0.609, 0.681]	20.156 0.000	0.668 ± 0.033 [0.631, 0.758]	n.s.	0.658 ± 0.020 [0.625, 0.709]	n.s.	0.662 ± 0.024 [0.621, 0.717]
ML / $CS_{0.75}$	1.297 ± 0.027 [1.248, 1.357]	87.804 0.000	1.361 ± 0.031 [1.295, 1.431]	n.s.	1.362 ± 0.033 [1.283, 1.414]	27.384 0.000	1.321 ± 0.026 [1.277, 1.373]
F2 / $CS_{0.75}$ [%]	14.77 ± 0.49 [13.58, 15.56]	12.188 0.001	14.41 ± 0.35 [13.86, 15.46]	no data	no data	no data	no data
$IF2_{0.75}$	1.753 ± 0.085 [1.589, 1.930]	60.525 0.000	1.622 ± 0.051 [1.532, 1.734]	no data	no data	no data	no data

Formal description of *Tapinoma subboreale* sp.n.

Tapinoma ambiguum (nec sensu EMERY, 1925!): KUTTER (1977), ARNOLDI & DLUSSKY (1978), SEIFERT (1984), AGOSTI & COLLINGWOOD (1987), ATANASSOV & DLUSSKY (1992), DOUWES (1995), GALLÉ & al. (1998), WERNER & BEZDĚČKA (2001), CZECHOWSKI & al. (2002), BOER & al. (2003), NEUMEYER & SEIFERT (2005), SCHLICK-STEINER & al. (2003), GLASER (2005), SEIFERT (2007).

Tapinoma madeirense (nec sensu FOREL, 1895!): CSŐSZ & al. (2011).

Etymology. The species epithet is an adjective derived from Latin, meaning "below northern" – referring to the fact that the most northern Scandinavian populations are found south of the boreal zone.

Type material. Holotype male labelled "GER: 51.2294 °N, 11.7329°E, Weischütz-Kirche 1.7 km NE, limestone grassland, 215 m, Seifert 2002.06.14-542", "Holotype *Tapinoma subboreale* Seifert"; five paratype males and five paratype workers with the same locality label and "Paratype *Tapinoma subboreale* Seifert" on a separate pin (1 male, 2 workers) and in ethanol (4 males, 3 workers); all material from the same nest sample; five paratype gynes labelled "GER: 50.879°N, 10.840°E, 300 m, Wanderlebener Gleiche, B. Seifert 1984.09.03" and "Paratype *Tapinoma subboreale* Seifert"; all material in Senckenberg Museum für Naturkunde Görlitz.

Description and differential diagnosis. Worker (Tab. 1): All data primary ratios (without RAV correction). Rather small, mean CS 699 µm. Depth of anteromedian clypeal excision 5.2% of cephalic size, much lower than in *Tapinoma erraticum* or *T. nigerrimum* but equal to *T. madeirense.* In general most similar to *T. madeirense* but the following three characters show statistically significant differences: With maximum cephalic length in visual plane, excavation of hind vertex just notable, being ± 0.43% of CS (in *T. madeirense* almost zero). Head and mesosoma more elongated than in *T. madeirense*, CL / CW 1.153, ML / CS 1.362. Using the seven characters, presented in Table 1, there was no clear clustering of workers in a PCA while a DA and LOOCV-DA resulted in error rates of 12.5 and 18.7% in 62 workers (data not shown). The univariate analysis of variance (ANOVA) confirmed as highly significant difference to *T. madeirense* a smaller CL / $CW_{0.75}$, ExOcc / $CS_{0.75}$ and ML / $CS_{0.75}$ (Tab. 1). For differences to *T. erraticum* and *T. nigerrimum* see below and Table 1.

Gyne (Tab. 2): Rather small, CS 836 - 930 µm. Depth of anteromedian clypeal excision much lower than in *Tapinoma erraticum* or *T. nigerrimum* but equal to *T. madeirense.* In all studied characters most similar to *T. madeirense* but statistically significant differences are the more elongated head, the larger distance of the inner margins of antennal fossae and the larger eye length (Tab. 2). Using the seven characters presented in Table 2, there was no clear

Tab. 2: Absolute cephalic size CS and six shape components of gyne individuals of four *Tapinoma* species. F values and significance levels of a univariate ANOVA refer to *T. ambiguum* and *T. madeirense*. n.s. = nonsignificant.

	T. nigerrimum (n = 2)	***T. erraticum*** (n = 18)	***T. subboreale* sp.n.** (n = 24)	**ANOVA**	***T. madeirense*** (n = 14)
CS	1238 ± 1 [1237, 1239]	960 ± 23 [918, 1006]	877 ± 23 [836, 930]	8.041 0.007	897 ± 19 [855, 917]
CL / CW	0.865 ± 0.024 [0.848, 0.882]	0.948 ± 0.031 [0.869, 1.003]	0.982 ± 0.016 [0.941, 1.006]	9.583 0.004	0.966 ± 0.013 [0.938, 0.989]
SL / CS	0.848 ± 0.003 [0.846, 0.850]	0.919 ± 0.027 [0.855, 0.952]	0.909 ± 0.018 [0.878, 0.942]	n.s.	0.905 ± 0.020 [0.870, 0.934]
ExCly / CS [%]	8.05 ± 0.51 [7.69, 8.41]	8.31 ± 1.19 [6.45, 11.12]	4.69 ± 0.50 [3.82, 5.65]	n.s.	4.47 ± 0.62 [3.50, 5.55]
dAN / CS	no data	no data	0.303 ± 0.008 [0.286, 0.321]	8.821 0.005	0.296 ± 0.007 [0.281, 0.304]
EL / CS	no data	no data	0.324 ± 0.009 [0.311, 0.346]	9.447 0.004	0.315 ± 0.010 [0.305, 0.337]
PoOC / CL	no data	no data	0.376 ± 0.012 [0.351, 0.392]	n.s.	0.374 ± 0.007 [0.362, 0.390]

clustering of gynes of *T. subboreale* sp.n. and *T. madeirense* in a PCA while a DA and LOOCV-DA resulted in error rates 5.1 and 15.4% in 38 gynes (data not shown). For differences to *T. erraticum* and *T. nigerrimum* see below and Table 2.

Male (Fig. 4, Tab. 3): Absolute body size equal to *Tapinoma madeirense*, ML 1310 - 1630 µm. Anteromedian clypeal incision shallow, clearly wider than deep. With the genital in ventral view and the subgenital plate positioned in visual plane, stipal tips much less surpassing the caudal tips of the subgenital plate than in *T. madeirense* (dSPST 122 - 172 vs. 252 - 268 µm), the divergence of the caudal tips of the subgenital plate is much larger (SPdT 472 - 563 vs. 370 - 435 µm, compare also Figs. 3 and 4). As a result, the ratio SPdT / dSPST is much larger than in *T. madeirense* – 3.04 - 4.12 vs. 1.46 - 1.88. Due to extreme elongation and strong divergence of the tips of subgenital plate these are clearly visible also in dorsal aspect of the genital – there is no other *Tapinoma* species in Europe with a comparable morphology of the subgenital plate.

Neotype fixation in *Tapinoma erraticum* (LATREILLE, 1798) and discrimination of female castes from *T. subboreale* sp.n.

A recent search conducted by J. Casevitz-Weulersse showed that there were no *Tapinoma* specimens in the Latreille collection of Muséum National d'Histoire Naturelle Paris (J. Casevitz-Weulersse, pers. comm. 13 June 2008). There is also no information that any of the taxonomists of the 20th century has ever seen an original specimen of *Tapinoma erraticum*. Hence, a complete loss of original material is highly probable or, at least, a reliable identification is impossible due to the useless original description and missing labelling of specimens. The presence of a minimum of seven *Tapinoma* species in Europe (SEIFERT 1984) and the fact that a safe identification of some species cannot be guaranteed for all future by descriptive statements and published information induces the need to fix a neotype. As the description of Latreille contains no diagnostic information, the neotype designation can only follow the rationale that (a) it should belong to the species widely considered as *T. erraticum* in Europe and (b) that the neotype comes as nearly as practicable from the original type locality. The locus typicus of *T. erraticum* is Brive-la-Gaillarde (France). I selected a neotype worker from a nest sample kindly collected by Christophe Galkowski about 11 km south from the city centre of Brive. The neotype is labelled "FRA: 45.0517°N, 1.5372°E, Nespouls-Faugère, 330 m, along road, under stone, leg. Galkowski 2008.07.02" and "Neotype *Tapinoma erraticum* (Latreille, 1798), design. B.Seifert 2010". It is stored in the collection of the Senckenberg Museum für Naturkunde Görlitz and has the following data: CS 836 µm, CL / CW 1.100, SL / CS 1.024, EL / CS 0.259, dAN / CS 0.279, ExCly / CS 8.87%, ExOcc / CS 1.42%, MGr / CS 3.58%, MW / CS 0.646 and ML / CS 1.347. Digital files with detailed z-stack photographs of the neotype in different positions are available on request from SMN Görlitz. There are 19 nestmate workers from the neotype nest in the collection of SMN Görlitz either mounted or stored in undenatured 99.8% ethanol.

In addition to the morphometric data presented in Tables 1 - 2, the following verbal redescription of *Tapinoma erraticum* is given here:

Worker: Head, mesosoma and gaster covered by a rather dense pubescence. With maximum head length and width in visual plane, posterior margin of head in medium-sized and large specimens slightly excavated. Anteromedian clypeal excision usually at least as deep a wide. Eye contours deviating from ideally elliptic form, showing linear sections on median margin. Anterior margin of clypeus with a few standing setae, the two longest based near to the anterolateral margin of clypeal excision. Remaining surface of head capsule and dorsal mesosoma without standing setae, such are present on mandibles, coxae and ventral surface of gaster. Head, mesosoma and gaster dark blackish brown. Antennae, femora and tibiae dark brown. Tarsi and distal end of tibiae light yellowish brown.

Male (see fig. 3 in SEIFERT 1984 for genital in ventral view): excision of the subgenital plate much shallower than in *T. subboreale* sp.n. The caudal tips of subgenital plate

Fig. 4: Ventral aspect of male genital of *Tapinoma subboreale* sp.n. with plane of subgenital plate in visual plane. Germany: Kosakenberg near Bad Frankenhausen, 26.VI. 1999.

Tab. 3: Morphometric data of *Tapinoma subboreale* sp.n. and *T. madeirense* males. The 1st factor of PCA was extracted from the five absolute measurements given in the table in µm. n.s. = nonsignificant.

	***T. subboreale* sp.n.** (n = 10)	**ANOVA**	***T. madeirense*** (n = 4)
ML	1483 ± 104 [1314, 1627]	n.s.	1455 ± 119 [1307, 1563]
SPExc	306 ± 18 [268, 334]	103.67 0.000	210 ± 7 [204, 219]
SPdT	522 ± 18 [472, 563]	63.18 0.000	389 ± 15 [370, 407]
STdT	210 ± 58 [149, 341]	n.s.	272 ± 30 [241, 313]
dSPST	146 ± 15 [122, 172]	200.00 0.000	260 ± 8 [252, 268]
SPdT / dSPST	3.601 ± 0.426 [3.045, 4.123]	91.58 0.000	1.501 ± 0.076 [1.457, 1.615]
1st factor PCA	0.574 ± 0.397 [-0.12, 1.15]	95.72 0.000	-1.436 ± 0.103 [-1.54, -1.32]

rounded, much shorter and much less distant than in *T. subboreale* sp.n. Stipal tips, in contrast, widely separate and caudally strongly surpassing the tips of subgenital plate which is completely invisible in dorsal aspect.

A simple method to separate *Tapinoma erraticum* and *T. subboreale* sp.n. workers using only 2 - 4 diagnostic characters was already given elsewhere (SEIFERT 1984, 2007). This method, however, is only safe when samples of two or three workers per nest are considered – it fails in some 3% of individual workers. No error in separation of 90 *T. erraticum* and *T. subboreale* sp.n. workers occurred under use of the characters CS, CL / CW, SL / CS, dAN / CS, EL / CS, ExCly / CS, ExOcc / CS, MW / CS, ML / CS, and MGr / CS. This was given in both an explorative and hypothesis-driven analysis: The 1st and 2nd factor of a PCA and a DA led to a complete separation of both clusters (Figs. 5 and 6) and the error rate in both the DA and

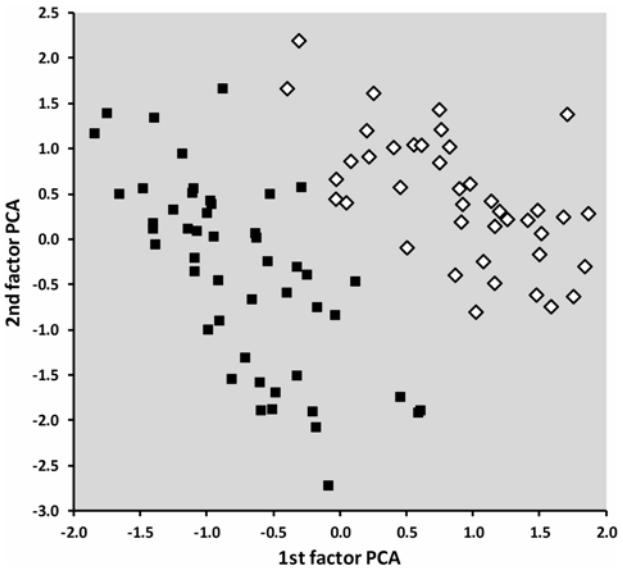

Fig. 5: Principal component analysis of worker individuals of *Tapinoma subboreale* sp.n. [black squares] and of *T. erraticum* [white rhombs] considering 10 morphometric characters.

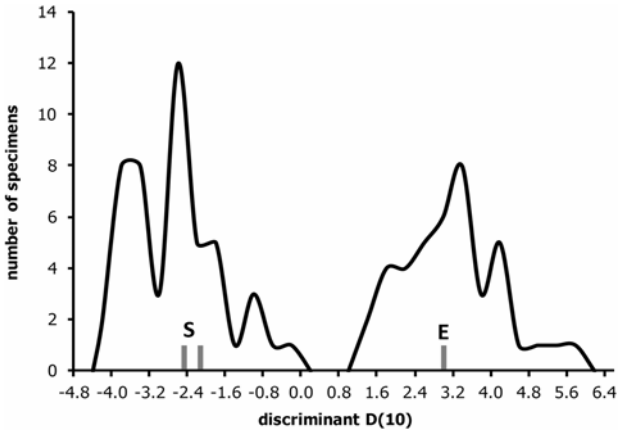

Fig. 6: Histogram of values of a discriminant analysis of worker individuals of *Tapinoma subboreale* sp.n. and *T. erraticum* considering 10 morphometric characters. The grey bars indicate the position of workers from the holotype nest of *T. subboreale* sp.n. (designated with "S") and of the neotype of *T. erraticum* (designated with "E").

LOOCV-DA was 0% with 98.9% of specimens determined with posterior probabilities of $p > 0.98$. The neotype of *T. erraticum* and the two paratypes of *T. subboreale* sp.n. from the holotype nest were allocated to either cluster with both $p > 0.9999$. Gynes of *T. erraticum* and *T. subboreale* sp.n. can be fully separated by the depth of clypeal excision alone and cephalic size is a weakly overlapping accessory discriminator (Tab. 2).

Heterospecificity of *Tapinoma nigerrimum* (NYLANDER, 1856) and separation of female castes from *T. erraticum* (LATREILLE, 1798)

Considering its very diagnostic genital morphology (SEIFERT 1984) and its characteristic formation of large supercolonies containing very large workers in addition to smaller ones, it is not easily intelligible why *Tapinoma niger-*

rimum is currently listed up as junior synonym of *T. erraticum* (see BOLTON & al. 2007). A partial explanation of this is perhaps that all the synonymising authors based their conclusions on worker material only. Many somatic morphological characters in *Tapinoma* workers are obviously under stabilising selection and separate species may evolve without substantial morphological changes – the pair *T. madeirense* and *T. subboreale* sp.n. is the best example. Another part of the explanation could be strong allometries in some shape characters. Large workers of *T. nigerrimum* differ from *T. erraticum* not only in absolute size but also in several shape ratios such as much lower cephalic length index (CL / CW), shorter scape length indices (SL / CS) or much more elongated second funiculus segments (larger IF2). Unfortunately, these differences are lost or strongly reduced in small *T. nigerrimum* workers which illustrates the problem to separate workers of incipient colonies of this species from *T. erraticum*.

An impression of the strength of average allometries in the four considered *Tapinoma* species is received by the RAV functions presented above. Given that the average intraspecific cephalic size range from the smallest to the largest worker is 312 µm, the following shape ratios in per cent of the mean change as follows: ExOcc / CS grows by 66.3%, MGr / CS grows by 52.1%, ExCly / CS grows by 14.2%, CL / CW falls by 13.6%, IF2 grows by 9.3% and SL / CS decreases by 5.2%. These figures show the problem of using such shape ratios without reference to body size in determination keys for species with a large size variation as it is observed in *T. nigerrimum*. The situation is further complicated by the high overlap of data between *T. nigerrimum* and *T. erraticum* even in the most discriminative characters dAN / CS, ML / CS and IF2 (Tab. 1). The way out of this dilemma, however, was better than expected. Using head size and all eleven RAV-corrected shape ratios presented in Table 1, a full separation of 24 *T. nigerrimum* and 41 *T. erraticum* workers was given by the 1st and 4th factor of a PCA (Fig. 7). This clear separation already in an explorative data analysis was fully confirmed by a cross-validated hypothesis-driven approach: A LOOCV-DA separated all workers with posterior probabilities of $p > 0.9999$ and error rates of 0%. Hence, we have a clear indication that worker morphologies of both species differ independently from body size and, in conclusion, should also be independent from colony size. As the two available gynes of *T. nigerrimum* are radically different from those of *T. erraticum*, we can state clear interspecific differences in all three castes.

All these things being surprisingly clear, it should be noted that the naming of the ant called here *Tapinoma nigerrimum* has no other basis than following a diffuse tradition. Firstly, there are no types of *Formica nigerrima* NYLANDER, 1856 present in the collection in Helsinki according to my own search in 1996 and a later information of the keeper Anders Albrecht. Secondly, the original description of NYLANDER (1856) gives very little diagnostic information (own translation): "... lower clypeal margin narrowly, sinuously exsected … head frequently as large as gaster, subcordate … 3-4 millimetres long." This certainly excludes the smaller *Tapinoma* species but does not indicate which of the two large and supercolonial Mediterranean species could be meant. The other large species is called, again only by a diffuse tradition, *T. simrothi* KRAUSSE-HELDRUNGEN, 1911. Types of *T. simrothi* are missing and the full text of KRAUSSE-HELDRUNGEN's (1911) description allows only the conclusion that it is bigger than *erraticum*: "... klopfte ich von Wolfsmilchblüthen; sie gleicht dem *T. erraticum* Ltr., nähert sich in der Grösse aber dem *T. erraticum nigerrimum*." Future revisers of Mediterranean *Tapinoma* are recommended to fix a neotype for *T. nigerrimum* from a nest sample collected near to Montpellier containing males with broad shovel-like stipes and for *T. simrothi* from a Sardinian nest sample containing males with the typical gripper-like stipes.

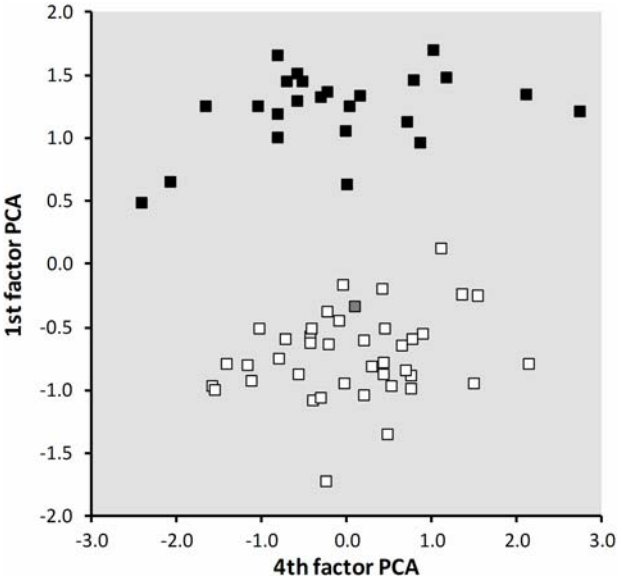

Fig. 7: Clustering of *Tapinoma nigerrimum* workers [black squares] and of *T. erraticum* workers [white squares, neotype grey square] by the 1st and 4th principal component of a PCA.

A simple key for determination of workers of the Central European *Tapinoma* species

As the complex determination procedures presented above will not readily be used by practitioners, I present here a more simple key. With exception of incipient nests of *Tapinoma nigerrimum*, the key allows a safe determination of all three species when nest samples and a good optical equipment are available.

1a Largest workers within a mature nest with CW > 900 µm. Inner margins of antennal sockets more distant, dAN / CS 0.309 ± 0.009; 2nd funiculus segment slender, IF2 frequently > 1.7; mesosoma relatively shorter, ML / CS 1.289 ± 0.027. Passively introduced neozoon in urban areas of Germany. Frequently supercolonial. ... . ***T. nigerrimum***

1b Largest workers within a mature nest with CW < 850 µm. Inner margins of antennal sockets more approached, dAN / CS 0.290 ± 0.009; 2nd funiculus segment thicker, IF2 frequently < 1.7; mesosoma relatively longer, ML / CS 1.363 ± 0.032. Usually not in urban areas, polygynous but not supercolonial. **2**

2a Maximum depth T of median clypeal excavation smaller than its width B; nest means of T

< 6.8% CW (use three workers per nest). Maximum eye length larger: EL / CW 0.260 ± 0.008 [0.246, 0.278]. Posterior margin of head in adjustment to measure CL straight or with suggested median excavation. Pubescence on head thinner and more appressed. .... ***T. subboreale* sp.n.**

2b T at least as large as B; nest means of T > 7.2% CW (use three workers per nest). Maximum eye length smaller: EL / CW 0.243 ± 0.005 [0.233, 0.254]. Posterior margin of head in adjustment to measure CL with a shallow but wide excavation. Pubescence on head denser and less strongly appressed. ..... ***T. erraticum***

Acknowledgements

I wish to thank Christophe Galkowski (St. Aubin de Medoc) for kindly collecting a neotype at the type locality of *Tapinoma erraticum*, Gerhard Heller (Ingelheim) for providing samples of *T. nigerrimum* from each German site, Roland Schultz (Görlitz) for providing z-stack photos of the male genitals, Eckehart Mättig (Görlitz) for help in picture processing, Xavier Espadaler (Barcelona) for providing material of *T. madeirense* from Madeira, and the curators Bernhard Merz (Muséum d'Histoire Naturelle Geneve) and Fabio Penati (Museo Civico di Storia Naturale Genova) for providing types of Forel and Emery.

References

AGOSTI, D. & COLLINGWOOD, C.A. 1987: A provisional list of the Balkan ants (Hym., Formicidae) and a key to the worker caste. II Key to the worker caste, including the European species without the Iberian. – Mitteilungen der Schweizerischen Entomologischen Gesellschaft 60: 261-293.

ARNOLDI, K. & DLUSSKY, G. 1978: Nadsem. Formicoidea. 1. Sem. Formicidae – muravi. In: MEDVEDJEV, G.S. (Ed.): Opredelitel' nasekomykh evropejskoj chasti SSSR. Tom 3. Pereponchatokrylye, pervaya chast. – Opredeliteli k Faune SSSR 119: 519-556.

ATANASSOV, N. & DLUSSKY, G.M. 1992: Fauna na Bulgariya 22. Hymenoptera: Formicidae. – Izdatelstvo na Bulgarskata Akademia na Naukite, Sofia, 310 pp.

BOER, P., DEKONINCK, W., VAN LOON, A.J. & VANKERKHOVEN, F. 2003: Lijst van mieren (Hymenoptera: Formicidae) van België en Nederland, hun Nederlandse namen en hun voorkomen. – Entomologische Berichten Amsterdam 63: 54-58.

BOLTON, B., ALPERT, G., WARD, P.S. & NASKRECKI, P. 2007: Bolton's catalogue of ants of the world 1758-2005. – Harvard University Press, Cambridge, MA, CD-ROM.

CSŐSZ, S., MARKÓ, B. & GALLÉ, L. 2011: The myrmecofauna (Hymenoptera: Formicidae) of Hungary: an updated checklist. – North-Western Journal of Zoology 7: 55-62.

CZECHOWSKI, W., RADCHENKO, A. & CZECHOWSKA, W. 2002: The ants (Hymenoptera, Formicidae) of Poland. – Museum and Institute of Zoology PAS, Warszawa, 200 pp.

DOUWES, P. 1995: Sveriges myror. – Entomologisk Tidskrift 116: 83-99.

EMERY, C. 1925: Revision des espèces paléarctiques du genre *Tapinoma*. – Revue Suisse de Zoologie 32: 45-64.

GALLÉ, L., CSŐSZ, S., TARTALLY, A. & KOVÁCS, É. 1998: A checklist of Hungarian ants. – Folia entomologica hungarica 59: 213-220.

GLASER, F. 2005: Rote Liste gefährdeter Ameisen Vorarlbergs. – Vorarlberger Naturschau – Rote Listen 3: 1-128.

HELLER, G. in press: *Pheidole pallidula* (NYLANDER, 1849) und *Tapinoma nigerrimum* (NYLANDER, 1856) (Hymenoptera: Formicidae), etablierte Neozoa in Rheinland-Pfalz. – Mainzer Naturwissenschaftliches Archiv.

KRAUSSE-HELDRUNGEN, A.H. 1911: Über *Messor structor* LTR. und einige andere Ameisen auf Sardinien. – Bollettino della Societa Entomologica Italiana 41: 14-18.

KUTTER, H. 1977: Hymenoptera, Formicidae. – Fauna Insecta Helvetica 6: 1-298.

LACHENBRUCH, P. & MICKEY, M. 1968: Estimation of error rates in discriminant analysis. – Technometrics 10: 1-11.

LESAFFRE, E., WILLEMS, J.L. & ALBERT, A. 1989: Estimation of error rate in multiple group logistic discrimination. The approximate leaving-one-out method. – Communication in Statistics: Theory and Methods 18: 2989-3007.

NEUMEYER, R. & SEIFERT, B. 2005: Kommentierte Liste der frei lebenden Ameisen (Hymenoptera: Formicidae) in der Schweiz. – Mitteilungen der Schweizerischen Entomologischen Gesellschaft 78: 1-17.

NYLANDER, W. 1856: Synopsis des formicides de France et d'Algérie. – Annales des Sciences Naturelles (Zoologie) (4)5: 51-109.

SCHLICK-STEINER, B., STEINER, F. & SCHÖDL, S. 2003: Rote Listen ausgewählter Tiergruppen Niederösterreichs – Ameisen (Hymenoptera: Formicidae), 1. Fassung 2002. – Amt der NÖ Landesregierung, Abteilung Naturschutz, St. Pölten, 75 pp.

SEIFERT, B. 1984: A method for differentiation of the female castes of *Tapinoma ambiguum* EMERY and *Tapinoma erraticum* (LATR.) and remarks on their distribution in Europe north of the Mediterranean Region. – Faunistische Abhandlungen des Museums für Tierkunde Dresden 11: 151-155.

SEIFERT, B. 2007: Die Ameisen Mittel- und Nordeuropas. – lutra Verlags- und Vertriebsgesellschaft, Tauer, 368 pp.

SEIFERT, B. 2008: Removal of allometric variance improves species separation in multi-character discriminant functions when species are strongly allometric and exposes diagnostic characters. – Myrmecological News 11: 91-105.

SEIFERT, B. & SCHULTZ, R. 2009: A taxonomic revision of the *Formica subpilosa* RUZSKY, 1902 group (Hymenoptera: Formicidae). – Myrmecological News 12: 67-83.

WERNER, P. & BEZDĚČKA, P. 2001: Checklist of ants of the Czech Republic. – Journal of the Society for Natural Sience, Uherske Hradiste 6: 174-183.

WETTERER, J.K., ESPADALER, X., WETTERER, A.L., AGUIN-POMBO, D. & FRANQUINHO-AGUIAR, A.M. 2007: Ants (Hymenoptera: Formicidae) of the Madeiran Archipelago. – Sociobiology 49: 265-297.