

Inconvenient hyperdiversity – the traditional concept of “*Pheidole pallidula*” includes four cryptic species (Hymenoptera: Formicidae)

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Abstract

Results of a pilot study are presented suggesting that Edward Wilson’s guess of some 1500 species in the hyperdiverse genus *Pheidole* Westwood, 1839 is likely to turn out as rather moderate estimate. Investigation of 112 nest samples containing 287 major workers of Westpalaeartic ants currently named *Pheidole pallidula* (Nylander, 1849) was performed by the explorative data analyses NC-Ward and NC-k-means clustering in combination with cross-validated linear discriminant analysis. Seventeen primary morphometric data were recorded by high-resolution stereomicroscopy. Allometric variance of shape variables was removed. Four cryptic species, forming the *Ph. pallidula* complex, were resolved: *Ph. pallidula*, *Ph. balcanica* nov. sp., *Ph. koshewnikovi* Ruzsky, 1905 and *Ph. cicatricosa* Stitz, 1917. The classification error varied between 0 and 2.8% in NC clustering of nest samples and between 1.6 and 3.7% in cross-validated linear discriminant analysis of individuals. *Ph. cicatricosa* has a North African distribution whereas *Ph. pallidula*, *Ph. balcanica* nov. sp. and *Ph. koshewnikovi* are Eurasian species with large sympatric ranges in the Balkans and Asia Minor. Colonization of urban regions north of the Alps and of offshore islands in the Mediterranean Sea indicates an invasive potential of the supercolonial social type of *Ph. pallidula*. There are no indications that any of these four taxa might represent an intraspecific polymorphism and signals for putative interspecific hybridization are not significant. The following synonymies were established: *Ph. subdentata* Mayr, 1853, *Ph. pallidula* var. *obscura* Santschi, 1936 and *Xenoaphaenogaster inquilina* Baroni Urbani, 1964 are junior synonyms of *Ph. pallidula*, *Ph. pallidula* var. *arenarum* Ruzsky, 1905 and *Ph. pallidula* ssp. *orientalis* Müller, 1923 are junior synonyms of *Ph. koshewnikovi* and *Ph. pallidula* var. *recticeps* Menozzi, 1932 is a junior synonym of *Ph. cicatricosa*. The senior synonymy of the following seven Westpalaeartic taxa with any member of the *Ph. pallidula* complex was excluded by type investigation and diagnostic statements in the original descriptions: *Ph. sinaitica* Mayr, 1862, *Ph. jordanica* Saulcy, 1874, *Ph. teneriffana* Forel, 1893, *Ph. laticeps* Mayr, 1904, *Ph. schmitzi* Forel, 1911, *Ph. obtusa* Stitz, 1917 and *Ph. pallidula selenia* Özdikmen, 2010. Species delimitation in the less differentiated caste of minor workers was not tested but seems possible when accessory morphological characters are included.

Keywords numeric morphology-based alpha-taxonomy | NC clustering | species delimitation | invasive species

1. Introduction

'*Pheidole* is among the largest of all genera of plants and animals. The number of its known species worldwide is now close to 900, and the actual number worldwide, with undescribed species added, could easily be 1500' – these are the first two sentences in Edward O. Wilson's Opus Magnum, his revision of the New World species of ant genus *Pheidole* Westwood, 1839 (Wilson 2003). He also stated that *Pheidole* rivals in species number the cosmopolitan formicine ant genus *Camponotus* Mayr, 1861. Using diagnostic characters that can be recognized by subjective eye inspection and a very simple morphometrics, Wilson increased the number of the New World *Pheidole* species from 287 previously named to 624. He noted that undescribed species were still pouring in to the Harvard collections when his monograph went to press. One may ask which species number would result if a taxonomic study of *Pheidole* also included species not separable by simple eye inspection of a trained expert. The number of cryptic species in ants is enormous (Seifert 2009). This inconvenient truth is likely to deter young scientists from doing ant taxonomy or biodiversity studies with ants. Yet, time-consuming research on cryptic species may be a fascinating detective story and is rewarding. It opens the eyes to the understanding of hidden species-specific biologies and of previously unknown interspecific relations. The example presented here is a first attempt in the genus *Pheidole* of an in-depth analysis by numeric morphology-based alpha-taxonomy (NUMOBAT).

The taxonomic concepts of the last 45 years (and the faunal lists accordingly) assumed the presence of only a single autochthonous species of *Pheidole* in the Mediterranean region of Europe and Asia Minor and then east to the former Soviet Middle Asia. This ant was constantly named *Pheidole pallidula* (Nylander, 1849). Yet, subjective inspection of several samples originating from SW Europe east to Asia Minor raised doubts on homospecificity of these socially polymorphic ants which were a focal object of numerous investigations of European myrmecologists on caste differentiation, kinship relations, social structure, intra- and interspecific behaviour or physiology (e.g., Delage-Darchen 1974; Passera 1974, 1977; Lachaud et al. 1992; Cammaerts & Cammaerts 1998; Fournier et al. 2003; Lecat et al. 2008; Sempo & Detrain 2010). I frequently asked myself if all these authors have really studied the same ant. The deciding impetus to launch this study was the recent discovery of a supercolonial *Pheidole* species that became established as a permanent outdoor species in two settlement areas of southwest Germany (Heller 2011). It was deemed to represent *Ph. pallidula* and survived mean January temperatures of minus 2°C without being affected in any way. The small revision presented

here considers all 17 Westpalaeartic taxa possibly being related to *Ph. pallidula*. The paper shows the power of NUMOBAT to uncover unexpected species numbers beyond the level of subjective recognition. The example indicates that Wilson's guess of some 1500 species in the hyperdiverse genus *Pheidole* is likely to turn out as rather moderate estimate.

2. Material

2.1. Material used in the exploratory and supervised data analyses

A detailed account of the samples is given below in the sequence site, date in the format yyyy.mm.dd, sample No [latitude in decimal format, longitude in decimal format, altitude in meters].

Pheidole balcanica sp. nov.

A total of 34 nest samples originated from the following countries: Bosnia 2, Bulgaria 8, Croatia 4, Greece 5, Montenegro 5 and Turkey 12 samples. A total of 95 major workers was subject to NUMOBAT investigation.

BULGARIA: Arkutino, 1978.08.01 [42.319, 27.742, 23]; Arkutino-1 km N, 1982.09.17, No 424 [42.328, 27.742, 23]; Chernomorec, 2006.07.22, No 1 and No 2 [42.44, 27.64, 5]; Melnik, 1982.09.01, No 387 [41.530, 23.392, 400]; Nessebar, 1974.07.20 [42.660, 27.710, 10]; Sozopol, 1982.09.20, No 362 [42.411, 27.694, 30]; Sozopol-15 km WNW, 1982.09.16, No 373 [42.433, 27.529, 12]. **CROATIA:** Pula, 2013.06.06, No 35 [44.874, 13.854, 50]; Rab-3.5 km W, 2014.08.09, No 103 [44.762, 14.717, 1]; Smokvitzka Krmpotska-0.4 km W, 2014.07.29, holotype *balcanica* [45.08710, 14.84735, 8]; Split, 2013.08.16, No x [43.512, 16.414, 50]. **GREECE:** Agia Triada, 2001.06.03, No 102 [40.498, 22.881, 5]; Kalamata-8 km E, 1996.07.23 [37.078, 22.165, 500]; Palaeokastritza-1 km NW, 1996.10.06, No 234 [39.678, 19.694, 180]; Peloponnisos, without date [assumed 37.5, 22.0, 300]; Valta-1.2 km W, Mt. Panachaiko, 2014.07.13 [38.117, 22.053, 934]. **MONTENEGRO:** Herceg Novi, 2013.05.11, No 16 [42.453, 18.552, 107]; Podgorica-12 km NE, 2014.06.04, No 7 [42.546, 19.367, 131]; Skadar, Komarno-4.8 km N, 2014.06.03, No 5 and No 8 [42.330, 19.071, 129]; Skadar, Virpasar, 2014.06.02, No 11 [42.244, 19.094, 33]. **TURKEY:** Beldibi, 2010.06.27, No 1 and No 2 [36.730, 30.560, 10]; Yahyali-Cubuklu village, 2010.06.08, No 1187 [38.102, 35.252, 1387]; Edirne, 2007.09.04, No 0006 [41.667, 26.550, 41]; Göynük, 2010.06.28 [36.670, 30.550, 144]; Ilgin-Digrak Köyü, 2011.06.16, No 0653 [38.029, 31.755, 1463]; Kirklareli-Alpullu, 2013.04.23, No 0126c [41.367, 27.133, 41]; Kirklareli-Vize, 2011.05.25, No 0244 [41.584, 27.710, 348]; Kiyiköy, 2011.05.22, No 0137 [41.657, 28.086, 33]; Lake Göltaşı, 2010.07.04 [36.570, 29.950, 1019]; Sahinyurdu village, 1998.08.12, No 0595 [40.467, 29.216, 950]; Sancak-Tepesi, 2003.09.12, No 0202a [41.067, 30.150, 330].

Pheidole koshewnikovi Ruzsky, 1905

A total of 38 nest samples originated from the following countries: Azerbaijan 1, Cyprus 1, Greece 12, Kazakhstan 3, Kyrgyzstan 6, Montenegro 1, Turkey 13 and Uzbekistan 1 sample. A total of 99 major workers was subject to NUMOBAT investigation.

AZERBAIJDSHAN: Atschinour, 2006.05, No 054c [assumed: 40.0, 49.0, 9]. **CYPRUS:** Nikokleia, Paphos, 2012.05.06 [34.728, 32.565, 62]. **GREECE:** Andros: Arni, 2006.04/05, No ADphryg5 [37.866, 24.845, 410]; Argolida: Scotini, 2013.08.27, No PEL119 [37.790, 22.430, 910]; Attiki: Panepistimioupoli, 2014.09.06 [37.966, 23.786, 262]; Crete: Damnoni, 2007.09, No 001b [35.174, 24.416, 9]; Dodecanese: Asfendiou-0.6 km SE, 2006.07 [36.848, 27.215, 380]; Korinthos, 2013.09.04, No PEL142A [39.930, 22.930, 37]; Koronisia-1.2 km SE, 2014.03.23 [39.007, 20.926, 2]; Mytilini: Achladeri, 2011.11.21, No 005/009 [39.155, 26.276, 6]; Panepistimioupolis, 2009.05.10, No 022 [37.966, 23.786, 263]; Peloponnisos, pre 1915 lectotype *orientalis* [assumed: 37.5, 22.0, 300]; Rhodes: Apolakia, 2004.04.29, No 008/018 [36.066, 27.794, 74]; Spartia-0.6 km NE, 2014.06.23, No KEF164 [38.115, 20.567, 140]. **KAZAKHSTAN:** Aksu-Canyon, 1998.07.30, No 006 and No 008 [42.332, 70.375, 1400]; Lake Balkhash, 1903.08.20, lectotype *koshewnikovi* [46.300, 73.800, 350]. **KYRGHYZTAN:** Ala-Buka, Terek-Sai, 1998.07.29, No 099 [41.392, 71.308, 1250]; Ferghansky Chrebet: Yassy river, 1965.05.29, No 62 and No 63 [40.77, 73.30, 1000]; Fergana: Papan reservoir, 1999.07.27, No 151 and No 152 [40.359, 72.920, 1300]; Turkestansky Chrebet: near Lajljik, 1963.06.24 [40.2, 72.1, 1000]. **MONTENEGRO:** Skadar, Komarno-2.5 km NW, 2014.06.03, No 19 [42.304, 19.048, 152]; Afsar village, 2009.10.21, No 0929b [39.774, 32.136, 1188]. **TURKEY:** Antalya-Lara, 2011.08.27, No 0104 [38.867, 30.767, 52]; Asiliarmut village, 2010.06.15, No 1531 [40.439, 35.549, 897]; Bagrikurt village, 2011.06.16, No 1080 [38.125, 32.469, 1509]; Cankiri-Korgun, 2010.06.01, No 0700b [40.768, 33.544, 1041]; Corum-Ugurludag, 2010.06.15, No 1518a [40.386, 35.465, 1385]; Delice village, 2010.06.13, No 1440a [39.579, 34.536, 1029]; Ilgin-Cavuscugöl, 2011.06.15, No 0999 [38.358, 31.844, 1074]; Kabakcevligi, 2010.08.10, No 2175 [39.283, 37.719, 1629]; Karabük-Safranbolu, 2005.06.30, No 0015 [41.233, 32.667, 287]; Manavgat: Sorgun, 2001.05.e [36.783, 31.417, 1]; Osmaniye: Bahce, 1966.04.21 [37.220, 36.160, 400]; Yesilyurt village, 2011.06.21, No 1424 [37.776, 33.754, 1301]. **UZBEKISTAN:** Kysyl-Kum, pre 1905 (coll. Ruzsky) [assumed: 41.0, 65.0, 230]

Pheidole pallidula (Nylander, 1849)

A total of 38 nest samples originated from the following countries: Bosnia 1, Bulgaria 6, France 3, Germany 2, Greece 1, Italy 17, Montenegro 2, Portugal 1, Spain 2, Switzerland 2 and Turkey 1 sample. A total of 89 major workers was subject to NUMOBAT investigation. In detail:

BOSNIA: Boracko Lake, 2012.08.07, No 1 [43.559, 18.025, 400]; **BULGARIA:** Melnik-2 km N, 1982.08.31, No 407 [41.538, 23.406, 465]; Nessebar 1964.10 [42.66, 27.71, 10]; Obsor 1979.08.01 [42.82, 27.88, 30]; Obsor, 1980.08.01 [42.82, 27.88, 30]; Rozen-2 km SW 1982.08.27, No 372 [41.516, 23.424, 439]; Valley of Melnik river, 1982.08.30, No 381 [41.530, 23.400, 430]. **FRANCE:** Breil sur Royal, 2002.05.08, No 018 [43.945, 7.519, 293]; Digne les Bains, Cathedral, 1999.08, No 006 [44.092, 6.236, 597]; Remoulins, Pont du Gard, after 1980 [43.947, 4.535, 45]. **GERMANY:** Heilbronn, 2003.07.30, [49.140, 9.210, 165]; Neustadt a.d. Weinstrasse, 2009.08 [49.350, 8.150, 135]. **GREECE:** Platanon, 1999.05.17, No 003 [38.169, 22.272, 20]. **ITALY:** Copiani Marina, 2004.07.01, No 05 [38.922, 16.810, 18]; Isola San Domino, 1992.03.15, No PH10 [42.117, 15.490, 50]; Klausen-0.4 km N, 2013.09.08 [46.642, 11.568, 579]; Lampedusa, Albero Sole, 2013.11.08, No 4 [35.526, 12.540, 122]; Lampedusa, Congli beach, 2013.11.07, No 2 [36.515, 12.561, 75]; Latina: Sperlonga 1986.04.19, No PH11 [41.260, 13.430, 30]; Sicily: Messina, Mortelle, 2013.11.04, No 1 [38.274, 15.608, 4]; Sicily: Isola Favignana, 1991.04.27, No PH3 and No PH14 [37.93, 12.33, 15]; Sicily: Isola Levanzo 1990.04.04, No PH6 [37.99, 12.34, 80]; Sicily: Isola Marettimo, 1991.05.04, No PH5 [37.97, 12.06, 200]; Sicily: Isola Filicudi, 1990.04.06, No PH8 [38.570, 14.560, 300]; Riva (G.Mayr), pre 1853, type *subdentata* [45.889, 10.843, 80]; Rufe: Torre Ruffa, 1999.05.22, No 081 [38.646, 15.843, 50]; San Giorgio Morgeto, 1990.08.02, No PH9 [36.816; 11.990; 6]; Segreta-4 km N, Etna park, 2013.11.06, No 3 [37.666,

14.986, 1243]; Sila Grande, Cupone, 1999.05.20, No 048 [39.390, 16.547, 1200]. **MONTENEGRO:** Podgorica-12 km NE, 2014.06.04, No 4 [42.546, 19.367, 131]; Slano-0.5 km N, 2014.06.01, No 9 [42.791, 17.886, 35]. **PORTUGAL:** Aljesur west, 2002.03.16, No 027 [37.317, -8.869, 57]. **SPAIN:** Mallorca: Ermita de Betlem, 2009.05.12 [39.737, 3.311, 278]; Mallorca: Talais d'Alcudia, 2004.03.08, No 025 [39.869, 3.175, 307]. **SWITZERLAND:** Monte Caslone, 1996.04/06, No St.2 [45.960, 8.880, 300]; Monte Caslone, 1996.06/07, No St.10 [45.961, 8.880, 400]. **TURKEY:** Kirkklareli-Vize, 2011.05.25, No 0235a [41.584, 27.710, 348].

Pheidole cicatricosa Stitz, 1917

Four major workers of the type samples of *Ph. cicatricosa* and *Ph. recticeps* Menozzi, 1932.

ALGERIA: Temassinin, 1914.01.30 [28.120, 6.819, 379]. **LIBYA:** Ghadames, coll. Forel, 1889/1893 [30.133, 9.500, 335].

2.2. Type material

Pheidole subdentata (Mayr, 1853)

One type worker, a major, labelled 'Riva Coll. G. Mayr', 'Oecoph. subdentata Mayr. det G. Mayr', 'zu G. Mayr Bd. II. p. 143' and 'Type', stored in Naturhistorisches Museum Wien.

Pheidole teneriffana Forel, 1893

Lectotype major worker (by present designation) labelled 'Ph. Teneriffana Forel [major sign] type Las Palmas Canarias', 'ANTWEB CASENT 0249900' and 'Lectotype *Pheidole teneriffana* Forel 1893, des. B. Seifert 2015', stored in Muséum d' Histoire Naturelle Genève.

Note: there are two localities named Las Palmas on Tenerife - one is situated directly at the northern shore and another one in the western mountains. As Forel wrote in the original description 'Laguna Teneriffe', the type locality should refer to the northern site [28.582, -16.166, 1]. It is also possible that the finding refers to Las Palmas on the island of Gran Canaria but then we have a severe disagreement with the published type locality.

Pheidole sinaitica laticeps Mayr, 1904

One type worker, a major, labelled 'Kairo Coll. G. Mayr', 'Ph. sinaitica var. laticeps G. Mayr, Type', 'Type' and 'ANTWEB CASENT 0906620', stored in Naturhistorisches Museum Wien.

Pheidole pallidula koshewnikovi Ruzsky, 1905

Lectotype by present designation labelled 'major worker: Lectotype *Pheidole pallidula* ssp. *koshewnikovi* Ruzsky 1905, des. B. Seifert 2015', 'Pheid. pallidula koshewnikovi R. Balchasch-See.' [handwriting of Ruzsky], 'SYNTYPUS *Pheidole pallidula* var. *koshewnikovi* Ruzsky 1905' [handwriting of Emery]; stored in Museo Civico die Storia Naturale Genova.

Pheidole pallidula var. *cicatricosa* Stitz, 1917

Major worker labelled 'S.O. Algerien Temassinin. v. Geyer. 30.1.14', 'Lectotype *Pheidole pallidula cicatricosa* Stitz 1917 des. B. Seifert 2015', 'GBIF-D/FoCol 1293 specimen label data documented', and '*Pheidole pallidula cicatricosa*'; stored in Zoologisches Museum Berlin.

Pheidole pallidula var. *obtusa* Stitz, 1917

Major worker labelled 'Aegypten', 'Type', 'GBIF-D/FoCol 1300 specimen label data documented', 'Pheidole megacephala var. obtusa'; major worker labelled 'Type', 'Aegypten', 'GBIF-D/FoCol 1301 specimen label data documented', 'ANTWEB CASENT 0906516', 'Pheidole megacephala var. obtusa'; major worker labelled 'Aegypten', 'Type', 'GBIF-D/FoCol 1302 specimen label data documented', 'Pheidole megacephala var. obtusa'; two major workers on two pins, labelled 'Aegypten. Ehrenberg.' 'Pheidole megacephala var. obtusa'; all stored in Zoologisches Museum Berlin.

Pheidole pallidula orientalis Müller, 1923

Lectotype major worker and 1 paralectotype major worker labelled 'Pheidole pallidula arenarum v. orientalis Emery', 'Peloponesus +Iul 5' [interpretation of poorly legible handwriting of Emery], 'ANTWEB CASENT 0904193', 'SYNTYPUS *Pheidole pallidula arenarum orientalis* Emery', 'top specimen: Lectotype *Pheidole pallidula* ssp. *orientalis* Müller 1923 [Emery 1915], des. B. Seifert 2015'; stored in Museo Civico die Storia Naturale Genova. The lectotype is photographed in antweb.org under CASENT 0904193. The pin contains four majors belonging to two species. Counted from top to bottom, these are: 1st = lectotype of *Ph. koshewnikovi*, 2nd = paralectotype of *Ph. koshewnikovi*; 3rd and 4th: *Ph. balcanica* nov. sp.

Pheidole pallidula recticeps Menozzi, 1932

Lectotype (by present designation) and two paralectotype major workers on the same pin, labelled 'Typus', 'Ph. pallidula Nyl r tristis For v. recticeps type Forel Ghadame (Ali Ben Belkassem' [Forels handwriting], 'CASENT 0907791, BOTTOM' and 'Lectotype (bottom sp.) *Pheidole recticeps* Menozzi 1932, des. B. Seifert 2015', stored in Muséum d' Histoire Naturelle Genève.

Pheidole pallidula selenia Özdikmen, 2010

Replacement name for *Pheidole pallidula* var. *inermis* Stitz, 1917 [Junior primary homonym of *Pheidole inermis* Mayr, 1870].

Lectotype major worker labelled 'S.O. Algerien Qued Agelil. v. Geyer. 19.3.14', 'Lectotype *Pheidole pallidula* var. *inermis* Stitz 1917 des. B. Seifert 2015', 'GBIF-D/FoCol 1298 specimen label data documented', 'Pheidole pallidula var. *inermis*'; paralectotype major worker labelled 'S.O. Algerien Qued Agelil. v. Geyer. 19.3.14', 'GBIF-D/FoCol 1299 specimen label data documented', 'Pheidole pallidula var. *inermis*'. stored in Zoologisches Museum Berlin.

Pheidole balcanica sp. nov.

Holotype, a major worker, labelled 'Holotype *Pheidole balcanica* Seifert, des. B. Seifert 2015', 'CRO: 45.08710°N, 14.84735°E, Smokvica Krmpotska-400 m W, 8 m, Wegrund, unter Stein, Juniperus, Gras, niedriger Wald, Seifert 2014.07.29–85'. Paratypes: 2 mounted major workers, 3 mounted minor workers, 7 ethanol-stored majors and 16 ethanol-stored minors from the holotype nest with the same locality label; all material in Senckenberg Museum für Naturkunde Görlitz.

3. Methods

3.1. Equipment and measurement procedures

A pin-holding stage, permitting full rotations around X, Y, and Z axes and a Leica M165C high-performance stereomicroscope equipped with a 2.0x planapochromatic objective (resolution 1050 lines/mm) was used for spatial adjustment of specimens at magnifications of 120–360x. The mean relative measuring error over all magnifications was 0.2%. A Schott KL 1500 cold-light source equipped with two flexible, focally mounted light-cables, providing 30°-inclined light from variable directions, allowed sufficient illumination over the full magnification range and a clear visualization of silhouette lines. A Schott KL 2500 LCD cold-light source in combination with a Leica coaxial polarized-light illuminator provided optimal resolution of tiny structures and microsculpture at highest magnifications. Simultaneous or alternative use of the cold-light sources depending upon the required illumination regime was quickly provided by regulating voltage up and down. A Leica cross-scaled ocular micrometer with 120 graduation marks ranging over 52% of the visual field was used. To avoid the parallax error, its measuring line was constantly kept vertical within the visual field.

3.2. The morphometric characters

The study focussed on major workers ('soldiers') because this distinct caste shows a higher degree of morphological differentiation than the caste of minor workers (Wilson 2003). This selection increased the probability for a successful species delimitation while keeping data-recording time at an acceptable level. Another argument to favour majors is that type specimens have been selected more frequently in this caste. Sixteen morphometric characters were investigated. In bilaterally developed characters, arithmetic means of both body sides were calculated. All measurements were made on mounted and fully dried specimens. Measurements of body parts always refer to real cuticular surface and not to the diffuse pubescence surface.

APrMn – angle between integrated dorsal profile of propodeum and the straight posterior profile of mesonotum (Fig. 1).

CL – maximum cephalic length in median line; the head must be carefully tilted to the position with the true maximum. Excavations of hind vertex and/or clypeus reduce CL. Surface irregularities due to sculpture, carinae in particular, are considered by averaging between peaks and valleys of sculpture.

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

CW – maximum cephalic width.

dAN – minimum distance between margins of antennal sockets measured in almost frontal view.

EL – maximum diameter of the elliptic eye. All structurally defined ommatidia, pigmented or not, are included.

ExOcc – with maximum cephalic length in measuring plane, depth of excavation of posterior border of head. Surface irregularities due to sculpture are considered by averaging between peaks and valleys of sculpture.

Fe3L – Length of hindfemur on extensor side; measured from the distalmost point of femur to borderpoint between femur and trochantellus, equivalent measurements are possible with view on plane or edge of femur and intermediate viewing positions.

GuHL – length of longest seta on underside of head (gula) posterior of the level of anterior eye margin.

Mesosomal longitudinal axis – is defined in lateral view from centre of metapleural lobe to lowest point of anterior pronotal shield (dashed line in Fig. 1).

ML – mesosoma length from caudalmost point of propodeal lobe to transition point between anterior pronotal slope and anterior propodeal shield (preferentially measured in lateral view; if the transition point is not well defined, use dorsal view and take the centre of the dark-shaded borderline between pronotal slope and pronotal shield as anterior reference point).

MW – maximum pronotal width in dorsal view

PEH – petiole height; maximum height of section line in lateral view measured perpendicular to the linearization of ventral profile line.

PEW – maximum width of petiole.

PnHaa – pronotal height above all, measured perpendicular to longitudinal mesosomal axis from lowest point of pronotal sclerite to highest point of promesonotum (Fig. 1).

PoOc – postocular distance; using the cross-scaled ocular micrometer, the head is adjusted to the measuring

position of CL; caudal measuring point: median occipital margin as average between peaks and valleys of microsclupture; frontal measuring point: median head at the level of the posterior eye margin; average left and right postocular distance.

PPW – maximum width of postpetiole.

PrOc – preocular distance in lateral view; measured as the shortest distance between the anterior eye margin and the sharp frontal margin of the gena.

SL – maximum straight line scape length excluding the articular condyle as arithmetic mean of both scapes.

3.3. Removal of allometric variance

In major workers of *Pheidole*, morphological characters are strongly influenced by allometric growth. In order to reveal in comparative tables which shape variables do really differ between the species independent from body size, a removal of allometric variance (RAV) was performed with the procedure described by Seifert (2008). As standard for all members of the *Pheidole* group, RAV was calculated assuming all individuals to have an cephalic size of CS = 1.25 mm. RAV functions describe collective parameters calculated as the arithmetic mean of the species-specific functions of the three species with more than 80 individuals measured per species. Inspection of scatter plots indicated the use of monophasic linear RAV functions. Major-minor intermediates, leading to a sigmoid allometry curve from minor to major workers, have not been observed in the investigated material. The RAV functions of 15 shape and one seta characters are

$$\begin{aligned}
 CL/CW_{1.25} &= CL / CW / (-0.0475 * CS + 0.9985) * 0.9391 \\
 SL/CS_{1.25} &= SL / CS / (-0.3007 * CS + 0.9509) * 0.5750 \\
 Fe3L/CS_{1.25} &= Fe3L / CS / (-0.2549 * CS + 1.0601) * 0.7415 \\
 PoOc/CS_{1.25} &= PoOc / CS / (+0.1244 * CS + 0.3821) * 0.5376 \\
 PrOc/CS_{1.25} &= PrOc / CS / (-0.0075 * CS + 0.2334) * 0.2241 \\
 ExOc/CS_{1.25} &= ExOc / CS / (+0.0585 * CS + 0.0160) * 0.0892 \\
 dAN/CS_{1.25} &= dAN / CS / (-0.0462 * CS + 0.3509) * 0.2931 \\
 EL/CS_{1.25} &= EL / CS / (-0.0562 * CS + 0.2113) * 0.1411 \\
 MW/CS_{1.25} &= MW / CS / (-0.0318 * CS + 0.4965) * 0.4568 \\
 ML/CS_{1.25} &= ML / CS / (-0.2013 * CS + 1.0980) * 0.8463 \\
 PnHaa/CS_{1.25} &= PnHaa / CS / (-0.0496 * CS + 0.4023) * 0.3403 \\
 APrMn/CS_{1.25} &= APrMn / CS / (-6.77 * CS + 128.5) * 120.0 \\
 PEW/CS_{1.25} &= PEW / CS / (-0.0145 * CS + 0.1562) * 0.1381 \\
 PPW/CS_{1.25} &= PPW / CS / (+0.0064 * CS + 0.2599) * 0.2679 \\
 PEH/CS_{1.25} &= PEH / CS / (-0.0279 * CS + 0.2233) * 0.1884 \\
 GuHL/CS_{1.25} &= GuHL / CS / (-0.0899 * CS + 0.3022) * 0.1898
 \end{aligned}$$

These RAV-corrected variables were used in the exploratory and hypothesis-driven data analyses.

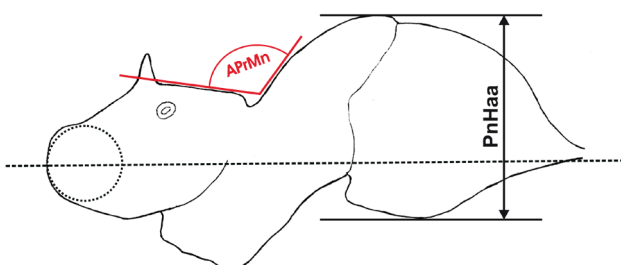


Figure 1. Morphometric characters in lateral aspect of mesosoma. The dotted line shows the level mesosomal longitudinal axis.

3.4. Explorative and supervised data analyses, classification and testing for dimorphism

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

NC-Ward clustering was run first to indicate the putative number of K main clusters. In the second step, NC-K-Means was performed with the setting of K classes suggested by NC-Ward. Classifications being coincident between the hierarchical and non-hierarchical clustering formed the hypothesis for the controlling LDA that was subsequently run. Samples with classifications disagreeing between NC-Ward and NC-K-means were run in this LDA as wild-cards. The final classification ('final species hypothesis') was established by the LDA in the iterative procedure described by Seifert et al. (2013). There remained no undecided cases also if their posterior probabilities were close to 0.5. The classification of particular type specimens was checked by a 'Leave-One-Out Cross-Validation' analysis LDA (LOOCV-LDA, Lachenbruch & Mickey 1968, Lesaffre et al. 1989). LDA, LOOCV-LDA and ANOVA tests were performed with the software package SPSS 15.0. The simulation of the dimorphism scenario within the DIMORPH test (Seifert 2016) was run with 1000 repeats. Observed and predicted distributions of intranidal phenotype compositions were compared by the χ^2 test of independence according to Sokal & Rohlf (1995) and by Fisher's exact test run with the software package R (R Development Core Team 2012)

4. Results and discussion

4.1. Diagnosis of the *Pheidole pallidula* complex based on major workers

Medium-sized: CS 1.00–1.53 mm. Head rather short: in specimens with CS = 1.25 mm, ratio of maximum median cephalic length against maximum cephalic width is 0.90–0.97. Head in dorsal aspect with convex pre- and postocular sides, its hind margin strongly excavated, depth of excavation 5–11% of maximum

median head length. Eye rather small: in specimens with CS = 1.25 mm, ratio of maximum eye diameter against cephalic size EL/CS 0.125–0.162. Frontal carinae more or less linear and diverging caudad. Anterior half of dorsal head surface longitudinally carinulate caudad to about one eye length posterior of caudal eye margin. The number of these largely parallel carinulae is 25–35 and the space between carinulae rather smooth and shining, without conspicuous microsculpture. Posterior half of dorsal head surface smooth and rather shining. Masticatory border toothless with the exception of a strong apical and subapical and a weak subbasal dent. Whole dorsal surface of head with numerous, thin suberect setae. Anterior margin of hypostoma with two dents or blunt protrusions. Scape and hind femur short: in specimens with CS = 1.25 mm, ratio of scape length against cephalic size 0.53–0.62 and the ratio of hind femur length against cephalic size 0.69–0.81. Mesosoma in lateral view with short but acute propodeal spines, being steeply erected in an angle of 75–90° relative to mesosomal longitudinal axis. An almost linear prespinal profile of dorsal propodeum falls down to a usually well-visible metanotal groove (Fig. 1). The overall profile of promesonotum is strongly convex and surmounts dorsal propodeum considerably relative to the level of longitudinal mesosomal axis. Outline of promesonotum in dorsolateral (oblique) view without very prominent lobes or protrusions but very flat, obtusely-angled corners – one on dorsolateral pronotum and one or two on dorsolateral mesonotum – are usually visible. Pronotum at small magnifications smooth and shining.

4.2. Clear clustering of cryptic species

The North African species *Ph. cicatricosa* differs from the three Eurasian species and can be clearly demonstrated by a LOOCV-LDA considering four classes and RAV-corrected shape characters (see below, Tab.1, Tab. 2). However, only two samples with one and three major workers were available in this species whereas each of the three Eurasian clusters consisted of 34 nest samples at least. This strong data deficiency caused an instable behaviour of *Ph. cicatricosa* in NC clustering. Accordingly, it was excluded from these explorative data analyses (EDA). The EDA with only the Eurasian samples were run in two steps. The first step was unselective and considered the whole material of 110 nest samples and all 17 recorded characters. Hierarchical NC-Ward clustering provided two clearly separated major clades: one largely West Mediterranean clade and one largely East Mediterranean one with the latter forming two subclades (Fig. 2). The largely western

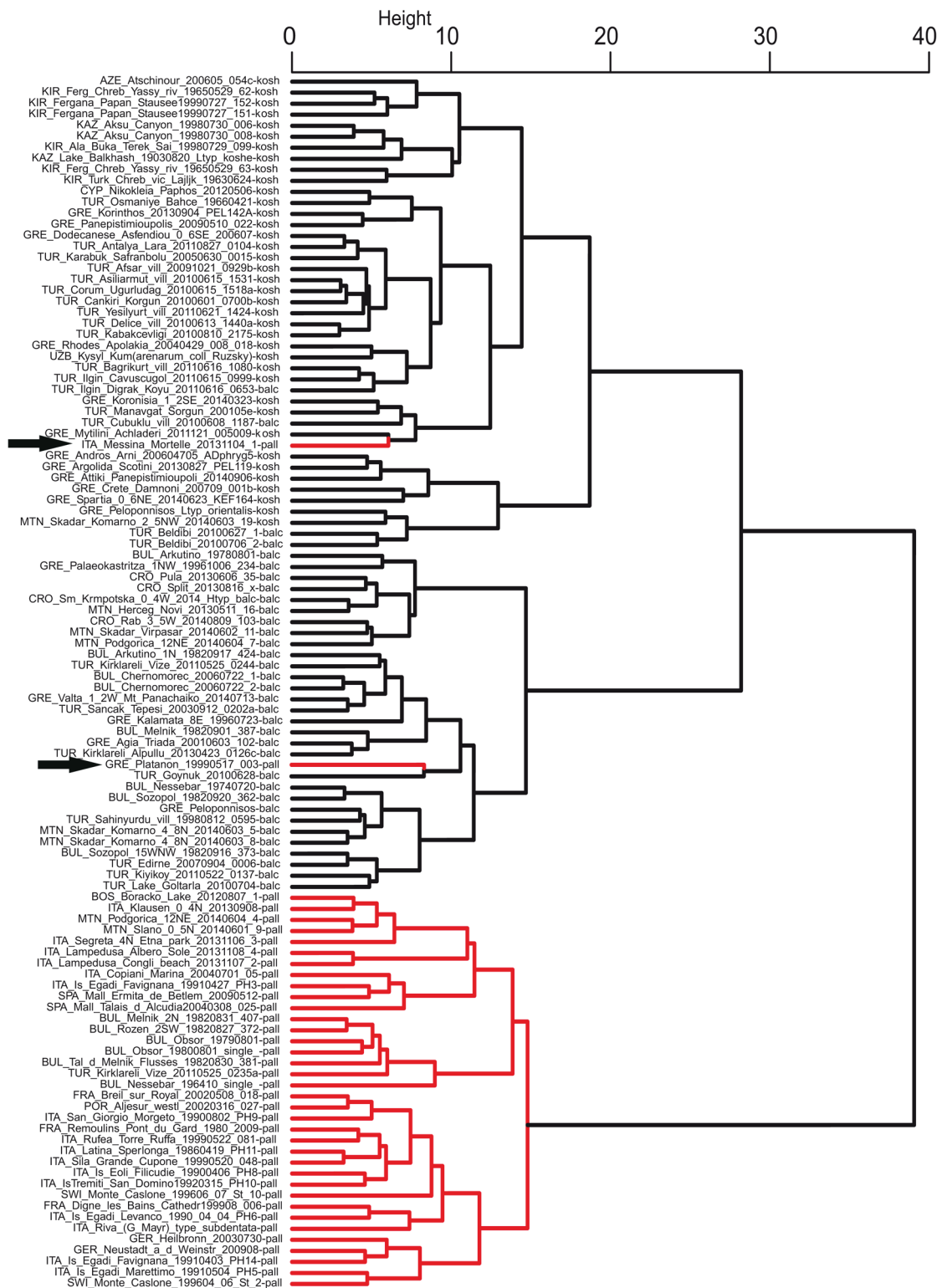


Figure 2. Hierarchical NC-Ward clustering of 110 nest samples of major workers of the three European species of the *Pheidole pallidula* species complex considering all 17 morphometric characters unselectively. The arrows mark two samples of *P. pallidula* erroneously allocated to the *P. balcanica* et *koshewnikovi* cluster. The misplacement was rectified by a wild-card run of a controlling linear discriminant function which agreed with non-hierarchical NC-K-means clustering by 100%.

clade is named herewith *Pheidole pallidula* (Nylander) based on the following argumentation. According to my own survey of the Nylander collection in Helsinki conducted in 1995, the three type workers from Messina/Sicily unfortunately do not contain majors which are required for species identification. However, according to the analysis of majors presented here, members of the two eastern subclades are completely absent from Iberia, France, Switzerland and entire Italy – in these areas *Ph. pallidula* is the only species of the *P. pallidula* species complex. Most remarkably, all eleven *Pheidole* samples found within a radius of 360 km around Messina belong to the western clade. This is a strong geographic argument

for naming the western clade *Pheidole pallidula*. A lucky message in this context is that all the biological investigations mentioned in the introduction and referred to *P. pallidula* were indeed performed in this species.

Assuming $K = 2$ (i.e., considering the western and eastern major clades only), non-hierarchical NC-K-Means clustering agreed with the classification of hierarchical NC-Ward clustering by 98.2%. Running the two disagreeing samples as wild-cards in a controlling LDA, these were classified as *Ph. pallidula* (ITA: Messina-Mortelle $p = 0.9992$, GRE: Platanon $p = 0.7538$). As result, the classification error of NC-Ward was 1.8% (Fig. 2) and of NC-K-Means 0%. A mean

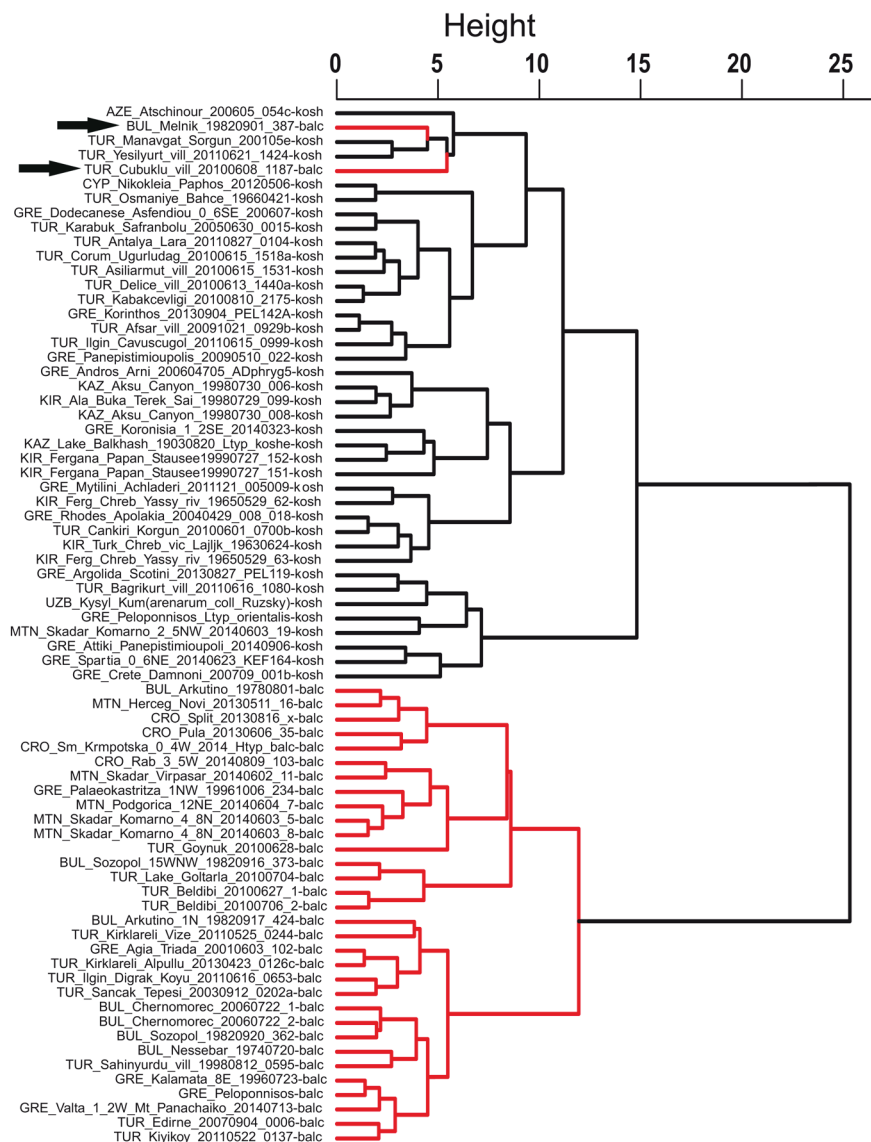


Figure 3. Hierarchical NC-Ward clustering of 72 nest samples of major workers of *Pheidole balcanica* sp.nov. and *P. koshewnikovi* after stepwise reduction to seven morphometric characters. The arrows indicate two samples of *P. balcanica* sp.nov. erroneously allocated to the *P. koshewnikovi* cluster. The misplacement was rectified by a wild-card run of a controlling linear discriminant function which agreed with non-hierarchical NC-K-means clustering by 100%.

classification error of 0.9% in 110 nest samples is clearly below the 4% threshold recommended by the Pragmatic Species Concept (Seifert 2014, Seifert & Csösz 2015) and provides a strong argument for heterospecificity of the eastern subclades and *P. pallidula*. This good separation is confirmed on the individual level: only 1.6% of 280 major workers were misclassified by the controlling LDA.

In the next step, all *P. pallidula* samples were excluded from analysis in order to improve the separation of the eastern subclades. Considering all 17 characters and assuming $K = 2$, NC-Ward and NC-K-Means disagreed in 8.3% of samples. Wild-card runs of these samples in a controlling LDA indicated a classification error of 9.7% in NC-Ward but of 1.4% only in NC-K-means. Selecting the seven characters PoOc/CS_{1,25}, PrOc/CS_{1,25}, dAN/CS_{1,25}, EL/CS_{1,25}, MW/CS_{1,25}, PnHaa/CS_{1,25}, and GuHL/CS_{1,25} by a stepwise LDA, the disagreement between the EDA methods was reduced to 2.8% while the classification errors of NC-Ward and NC-K-means decreased to 2.8 and 0% respectively (Fig. 3). A mean classification error of 1.4% in 72 nest samples is clearly below the threshold recommended by the Pragmatic Species Concept. Accordingly, the eastern subclusters are likely to represent different species. This good separation is confirmed on the individual level: only 3.7% of 191 major workers were misclassified by the controlling LDA.

4. 3. The taxonomic naming of the three clades and synonymies

It was stated above that the western clade should be named *Pheidole pallidula* (Nylander, 1849) based on a strong geographic argument. We assess now the position of type series of several taxa within an LDA considering all 17 characters and assuming four classes. These type series contained the type major worker of *Pheidole subdentata* (Mayr, 1853), the lectotype major worker of *Pheidole pallidula* ssp. *koshewnikovi* Ruzsky, 1905, the lectotype of *Pheidole pallidula* var. *cicatricosa* Stitz, 1917, the lectotype and a paralectotype of *Pheidole pallidula* ssp. *orientalis* Müller, 1923, the lectotype and two paralectotypes of *Pheidole pallidula* var. *recticeps* Menozzi, 1932 and the holotype plus two paratypes of *Pheidole balcanica* sp. nov. The exclusion of synonymies of less similar Westpalaeartic taxa is explained in a separate section below. Type material of *Pheidole pallidula* ssp. *arenarum* Ruzsky, 1905 was not available in both the collection of St. Petersburg and Genova. *P. koshewnikovi* and *P. arenarum* were described from Middle Asia and all 10 samples available from this area – collected in Uzbekistan, Kygystan, Kazakhstan – belonged to a single species. A synonymy of *P. koshewnikovi* and *P. arenarum*

is therefore most likely and herewith I determine *P. koshewnikovi* to have priority if conspecificity should be proven after unexpected discovery of *Ph. arenarum* types. *Pheidole cicatricosa* Stitz, 1917 belongs to the *Ph. pallidula* species complex and is raised herewith to species rank. This North African species differs from any of the three Eurasian clusters delimited above. Yet, there are affinities to *Ph. koshewnikovi* from which it is separable by clearly larger head size, hind femur length and postpetiolar width and smaller seta length on underside of head (Tab. 2). Much comparison material from North Africa and the Middle East is needed for a more reliable assessment of the taxonomic position of *Ph. cicatricosa* relative to *Ph. koshewnikovi*.

The morphometric allocation of type specimens to either cluster is provided by Tab. 1. *Ph. pallidula* ssp. *orientalis* Müller, 1923 is clearly a junior synonym of *Ph. koshewnikovi* Ruzsky, 1905. However, the two specimens in position 3 and 4 on the same needle with the types of *Ph. pallidula* ssp. *orientalis* belong to *Ph. balcanica* sp. nov. – this pin from ‘Peloponesus’ does obviously not represent a nest sample. Morphology indicates a junior synonymy of *Ph. subdentata* (Mayr, 1853) with *Ph. pallidula* ($p = 0.662$) but there is also some probability ($p = 0.338$) for a senior synonymy with *Ph. koshewnikovi*. The latter interpretation, however, is strongly rejected by geography: the type locality of *Ph. subdentata* in the southern Alps, Riva del Garda, is deeply within the exclusive range of *Ph. pallidula* and the next known site of *Ph. koshewnikovi* is 800 km southeast in Montenegro. *Pheidole pallidula* var. *recticeps* Menozzi, 1932 is a junior synonym of *Pheidole cicatricosa* Stitz, 1917. Fig. 4 shows the position of the type series within the species clusters provided by an LDA.

4.4. The interspecific differences

The Eurasian species *Ph. pallidula*, *balcanica* and *koshewnikovi* are hardly separable by simple eye inspection. There is a number of RAV-corrected shape variables with highly significant differences but also a very large overlap (Tab. 2). *Ph. pallidula* differs from the two eastern species by shorter scape, shorter hind femur, higher petiole and broader mesosoma. *Ph. balcanica* differs from *koshewnikovi* by smaller eye length and smaller minimum distance between the margin of antennal sockets. The larger postocular and preocular distances of *Ph. balcanica* are a consequence of the smaller eye length. With all characters expressed as absolute measurements in millimeter, *Ph. pallidula* can be separated from the two eastern species by the discriminant:

$$D_{\text{PBK}} = 13.921 + 19.038 * \text{PoOc} - 4.581 * \text{ExOcc} \\ - 39.321 * \text{CL} + 4.478 * \text{CW} + 16.902 * \text{dAN} - 17.701 * \text{SL} \\ + 21.869 * \text{MW} + 14.712 * \text{PEW} - 13.948 * \text{PPW} - 0.689 * \text{PnHaa} \\ + 69.968 * \text{PEH} + 46.064 * \text{PrOc} \\ + 24.301 * \text{EL} + 9.049 * \text{GuHL} - 10.011 * \text{ML} - 14.540 * \text{Fe3L}.$$

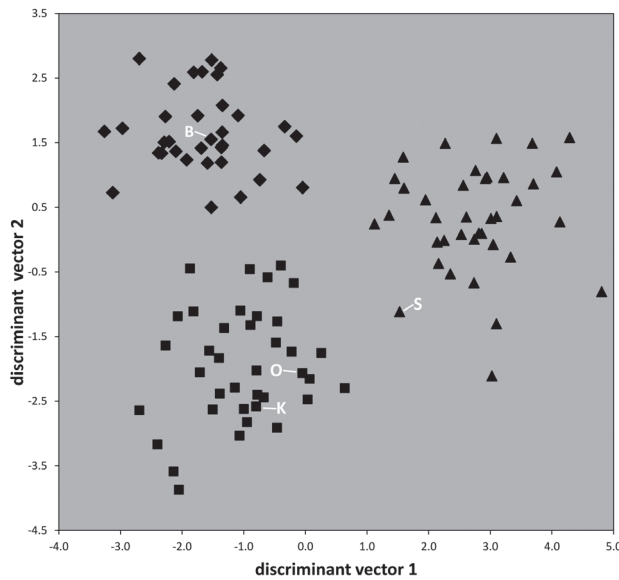


Figure 4. linear discriminant analysis of *Pheidole balcanica* nov. sp. (rhombs), *Ph. koshewnikovi* (squares) and *Ph. pallidula* (triangles). The position of types is indicated by letters: B – *Ph. balcanica*, K – *Ph. koshewnikovi*, O – *Ph. orientalis*, S – *Ph. subdentata*.

Positive D_{PBK} values indicate *Ph. pallidula*, negative ones the two eastern species. The classification error is 1.4% in 280 individuals. The two eastern species *Ph. balcanica* and *koshewnikovi* can be separated by the discriminant:

$$D_{\text{BK}} = 4.071 + 29.323 * \text{PoOc} + 4.580 * \text{ExOcc} \\ - 23.743 * \text{CL} + 5.688 * \text{CW} - 29.598 * \text{dAN} + 12.788 * \text{SL} \\ - 16.049 * \text{MW} - 24.383 * \text{PEW} + 11.550 * \text{PPW} \\ + 13.556 * \text{PnHaa} + 2.336 * \text{PEH} + 52.893 * \text{PrOc} \\ - 81.249 * \text{EL} + 12.055 * \text{GuHL} + 7.378 * \text{ML} - 9.450 * \text{Fe3L}.$$

Positive D_{BK} values indicate *Ph. balcanica*, negative ones *Ph. koshewnikovi*. The classification error is 3.1% in 191 individuals. Attempts to find a simpler species identification by use of a smaller number of characters unfortunately did not result in acceptable classification errors. Users may run their own analyses using the primary measurement data of all 280 individuals provided as an Excell file in the electronic supplement (www.soil-organisms.org).

4.5. Comments on geographic distribution

The North African material available for this study consisted of seven samples with four species. Two samples belonged to *Ph. cicatricosa* which suggests that it might be a common species from Algeria to Libya. Three introductions of *Pheidole pallidula* to Germany north of the

Table 1. Classification probabilities in a linear discriminant function (LDA) of type and type-associated major workers of the four *Pheidole pallidula* complex species. Acronyms: balc = *balcanica*, kosh = *koshewnikovi*, pall = *pallidula*, cica = *cicatricosa*. LOOCV = leave-one-out cross-validation.

specimens	LOOCV-LDA				LDA accepting prior classification by LOOCV-LDA			
	balc	kosh	pall	cica	balc	kosh	pall	cica
<i>Ph. balcanica</i> nov. sp., holotype, specimen 1	0.9986	0.0014	0.0000	0.0000	0.9988	0.0011	0.0000	0.0000
<i>Ph. balcanica</i> nov. sp., paratype, specimen 2	0.9701	0.0277	0.0021	0.0000	0.9802	0.0186	0.0012	0.0000
<i>Ph. balcanica</i> nov. sp., paratype, specimen 3	0.9984	0.0016	0.0000	0.0000	0.9986	0.0014	0.0000	0.0000
<i>Ph. balcanica</i> nov. sp., no type, specimen 3 (coll. Emery)	0.9977	0.0022	0.0002	0.0000	0.9981	0.0018	0.0001	0.0000
<i>Ph. balcanica</i> nov. sp., no type, specimen 4 (coll. Emery)	0.9433	0.0567	0.0000	0.0000	0.9525	0.0475	0.0000	0.0000
<i>Ph. orientalis</i> , lectotype, specimen 1 (coll. Emery)	0.0478	0.9480	0.0043	0.0000	0.0353	0.9616	0.0031	0.0000
<i>Ph. orientalis</i> , paralectotype, specimen 2 (coll. Emery)	0.0000	0.9985	0.0013	0.0002	0.0000	0.9992	0.0007	0.0000
<i>Ph. koshewnikovi</i> , lectotype	0.0001	0.9999	0.0000	0.0000	0.0001	0.9999	0.0000	0.0000
<i>Ph. subdentata</i> , type	0.0009	0.3375	0.6616	0.0000	0.0006	0.1782	0.8211	0.0000
<i>Ph. cicatricosa</i> , lectotype	0.0000	0.0000	0.0000	1.0000	0.0000	0.0000	0.0000	1.0000
<i>Ph. recticeps</i> , paralectotype, specimen 1	0.0000	0.0000	0.0000	1.0000	0.0000	0.0000	0.0000	1.0000
<i>Ph. recticeps</i> , paralectotype, specimen 2	0.0000	0.0000	0.0005	0.9995	0.0000	0.0000	0.0000	1.0000
<i>Ph. recticeps</i> , lectotype, specimen 3	0.0000	0.0000	0.0000	1.0000	0.0000	0.0000	0.0000	1.0000

Alps and occurrence on the offshore islands Mallorca and Pantelleria indicate significant tramp species properties in the supercolonial social type of this species. This makes an assessment of autochthonous distribution problematic. The natural range of *Ph. pallidula* seems to extend from Iberia east to the European part of Turkey and E Bulgaria and there are no findings in Asia Minor so far. The rather limited geographic range of *Ph. balcanica* extends over 2000 km from northwest Croatia (Pula, 44.874°N, 13.854°E) southeast to Central Anatolia (Yahyali, 38.102°N, 35.252°E). Compared to *Ph. koshewnikovi*, *Ph. balcanica* has apparently a lower potency for long range dispersal. It is not found on islands farther than 10 km from the mainland whereas *Ph. koshewnikovi* occurs on Crete and Cyprus. The geographic range of

Ph. koshewnikovi is large and extends over 4400 km from Montenegro (Skadar, 42.304°N, 19.048°E) to Kazakhstan (Lake Balkhash, 46.3°N, 73.8°E). There is a broad sympatric zone with *Ph. balcanica* extending from 19°E to 35.3°E. In Europe and Asia Minor, *Ph. koshewnikovi* occurs at significantly lower latitudes – 28 sites were situated at 38.54 ± 1.77 °N against 40.946 ± 2.521 °N in 30 sites of *Ph. balcanica* (ANOVA, $F = 17.52$, $p = 0.000$).

4.6. The situation within the sympatric zone of *P. balcanica* and *P. koshewnikovi*

Ph. balcanica and *Ph. koshewnikovi* are closely related, show a broad sympatric zone extending over some

Table 2. Absolute cephalic size, fifteen RAV-corrected shape and one RAV-corrected seta character in major workers of *Pheidole pallidula*, *P. balcanica* sp. nov., *P. koshewnikovi* and *P. cicatricosa*. Removal of allometric variance is performed for the assumption that all individuals have the same head size of 1250 µm. Columns with ANOVA values refer to comparisons of the species' columns where they are placed between. The most separating characters are indicated by F values in bold type.

	<i>pallidula</i> (n = 89)	ANOVA F, p	<i>balcanica</i> (n = 92)	ANOVA F, p	<i>koshewnikovi</i> (n = 99)	ANOVA F, p	<i>cicatricosa</i> (n = 4)
CS [µm]	1241 ± 72 [992,1416]	69.36 0.000	1329 ± 69 [1106,1457]	26.11 0.000	1271 ± 85 [1020,1462]	15.16 0.000	1440 ± 71 [1380,1523]
CL/CW [1.25]	0.927 ± 0.019 [0.880,0.962]	29.17 0.000	0.942 ± 0.018 [0.897,0.968]	4.52 0.035	0.947 ± 0.021 [0.896,0.998]	0.34 n.s.	0.941 ± 0.022 [0.914,0.968]
SL/CS [1.25]	0.562 ± 0.017 [0.523,0.606]	70.25 0.000	0.580 ± 0.012 [0.548,0.612]	9.09 0.003	0.586 ± 0.016 [0.551,0.629]	1.64 n.s.	0.597 ± 0.011 [0.582,0.606]
Fe3L/CS [1.25]	0.726 ± 0.018 [0.675,0.767]	42.68 0.000	0.743 ± 0.016 [0.708,0.786]	37.59 0.000	0.757 ± 0.018 [0.716,0.801]	26.74 0.000	0.805 ± 0.005 [0.795,0.813]
PoOc/CL [1.25]	0.540 ± 0.011 [0.506,0.571]	2.23 n.s.	0.542 ± 0.011 [0.513,0.570]	41.51 0.000	0.531 ± 0.012 [0.499,0.558]	3.02 n.s.	0.520 ± 0.010 [0.508,0.531]
ExOcc/CL [1.25]	0.087 ± 0.013 [0.059,0.122]	10.59 0.001	0.094 ± 0.010 [0.066,0.119]	18.62 0.000	0.086 ± 0.013 [0.037,0.120]	5.47 0.021	0.103 ± 0.005 [0.098,0.105]
EL/CS [1.25]	0.143 ± 0.005 [0.132,0.159]	174.09 0.000	0.132 ± 0.006 [0.118,0.148]	307.05 0.000	0.148 ± 0.007 [0.135,0.165]	1.14 n.s.	0.153 ± 0.003 [0.149,0.156]
PrOc/CS [1.25]	0.228 ± 0.009 [0.195,0.245]	5.98 0.015	0.225 ± 0.008 [0.208,0.244]	41.46 0.000	0.218 ± 0.007 [0.203,0.248]	0.94 n.s.	0.221 ± 0.002 [0.219,0.223]
dAN/CS [1.25]	0.295 ± 0.008 [0.273,0.312]	50.99 0.000	0.286 ± 0.010 [0.260,0.309]	70.00 0.000	0.296 ± 0.008 [0.278,0.321]	2.00 n.s.	0.291 ± 0.007 [0.280,0.296]
MW/CS [1.25]	0.468 ± 0.014 [0.432,0.507]	117.42 0.000	0.446 ± 0.014 [0.422,0.487]	29.07 0.000	0.457 ± 0.014 [0.420,0.514]	0.01 n.s.	0.458 ± 0.004 [0.453,0.464]
PnHaa/CS [1.25]	0.345 ± 0.017 [0.310,0.390]	10.65 0.001	0.338 ± 0.017 [0.303,0.397]	0.12 n.s.	0.338 ± 0.015 [0.306,0.373]	0.30 n.s.	0.345 ± 0.010 [0.330,0.354]
PEW/CS [1.25]	0.140 ± 0.007 [0.125,0.159]	7.76 0.006	0.138 ± 0.006 [0.127,0.154]	0.24 n.s.	0.137 ± 0.007 [0.124,0.159]	3.44 n.s.	0.144 ± 0.011 [0.130,0.156]
PPW/CS [1.25]	0.266 ± 0.019 [0.204,0.324]	5.81 0.017	0.272 ± 0.015 [0.233,0.306]	3.99 0.047	0.267 ± 0.015 [0.233,0.307]	23.23 0.000	0.304 ± 0.014 [0.290,0.318]
PEH/CS [1.25]	0.196 ± 0.007 [0.179,0.214]	214.54 0.000	0.182 ± 0.006 [0.168,0.196]	17.96 0.000	0.186 ± 0.007 [0.166,0.205]	11.29 0.001	0.200 ± 0.013 [0.188,0.218]
ML/CS [1.25]	0.836 ± 0.022 [0.775,0.926]	4.54 0.034	0.845 ± 0.022 [0.796,0.910]	23.48 0.000	0.860 ± 0.024 [0.788,0.936]	0.37 n.s.	0.870 ± 0.019 [0.841,0.882]
APrMn [1.25]	120.9 ± 9.4 [90,140]	6.46 0.012	117.7 ± 7.0 [93,138]	19.03 0.000	121.8 ± 5.9 [108,137]	1.85 n.s.	126.0 ± 4.7 [120.0,131.0]
GuHL/CS [1.25]	0.198 ± 0.024 [0.128,0.235]	5.54 0.020	0.190 ± 0.021 [0.130,0.226]	14.96 0.000	0.178 ± 0.022 [0.115,0.213]	24.40 0.000	0.122 ± 0.022 [0.102,0.152]

1450 km and they may occur in close neighborhood. This raises the question if there is interspecific hybridization. If so, the interspecific morphological distance in the sympatric range should be reduced compared to that from the allopatric range. The allopatric range of *Ph. balcanica* includes all areas west of 19°E and entire Bulgaria whereas *Ph. koshewnikovi* is allopatric in all areas east of 35.3°E. The sympatric range of both species includes all areas between 19°E and 35.3°E with the exception of Bulgaria. Interspecific distance is measured here as distance along the LDA vector considering all 17 characters.

There is no reduction of the distance from the zero point of the discriminant vector in the sympatric zone in *Ph. balcanica* and a weak but insignificant reduction in *Ph. koshewnikovi* (Tab. 3). This may suggest occasional hybridization with introgression into the *Ph. koshewnikovi* genome but may also represent a clinal trend from Middle Asia to Europe independent from hybridization.

The ratio of samples putatively containing workers of both species is 2.3% within 44 samples from the sympatric zone. This sample from TUR: Kirklareli-Alpullu contains only two major workers which are classified in a wild-card run of a LDA as *Ph. balcanica* ($p = 1.0000$)

and *Ph. koshewnikovi* ($p = 0.9922$). Yet, there was no confirmation by the collectors that the two specimens were really taken from the same nest. The rarity of putatively mixed nests in the sympatric zone contradicts the idea that *Ph. balcanica* and *Ph. koshewnikovi* could represent an intraspecific dimorphism. Running the DIMORPH test (Tab. 4), the observed distribution of pure and mixed samples only matches the prediction for parabiosis ($X^2 0.31$, $p = 0.691$) whereas the predictions for intraspecific dimorphism ($X^2 8.32$, $p = 0.016$), temporary social parasitism ($X^2 23.21$, $p = 0.001$) permanent social parasitism ($X^2 28.00$, $p = 0.001$) are clearly rejected. Accordingly, heterospecificity is strongly supported and the mixed sample has to be interpreted either as an exceptional parabioc association, a determination error or a sampling artefact. If one criticizes that probability values provided by the Chi-squared test become doubtful if the number of cases in a cell is below 5, I remind the fact that the X^2 values provide a correct indication which of a range of possible predictions/hypotheses best fits the observation data (Seifert 2016). The robustness of the Chi-squared test is indicated by similar probability data provided by Fisher's exact test: $p = 1.00$ for parabiosis, $p = 0.017$ for intraspecific dimorphism and $p = 0.00001$ both for temporary and permanent social parasitism.

Table 3. Distance of major worker individuals of *Pheidole balcanica* nov.sp. and *Ph. koshewnikovi* from the zero point of the interspecific discriminant vector. The ANOVA data are placed in the line between the compared data sets.

	discriminant D(17)
<i>P. balcanica</i> in allopatric zone (n = 34)	1.8992 ± 0.8106 [-0.023,3.199]
ANOVA [F, p]	0.01, 0.932
<i>P. balcanica</i> in sympatric zone (n = 58)	1.8813 ± 1.0514 [-0.912,3.730]
<i>P. koshewnikovi</i> in allopatric zone (n = 34)	-1.9300 ± 0.9950 [-3.8514,0.828]
ANOVA [F, p]	1.51, 0.222
<i>P. koshewnikovi</i> in sympatric zone (n = 65)	-1.6626 ± 1.0461 [-4.217,0.394]

Table 4. Comparison of observed and predicted occurrence of pure nests of *Pheidole balcanica* (pure balc), of pure nests of *Ph. koshewnikovi* (pure kosh) and of mixed nests of both phenotypes in the sympatric zone according to the DIMORPH test of Seifert (2016). The recognition rate on the $p > 0.95$ level was 0.829 and the mean within-nest sample size 2.8. X^2 is the test statistic of a Chi-squared test of independence according to Sokal & Rohlf (1995). X^2 data correctly show the ranking of similarity between observation and prediction with lowest values indicating which prediction is the most probable. Probability values of Fisher's exact test are given.

	observed	prediction heterospecificity			prediction intraspecific dimorphism
		parabiosis	temporary social parasitism	permanent social parasitism	
pure balc	21	21.31	1.57	0	16.60
mixed	1	0.36	0.06	0.70	10.11
pure kosh	22	22.32	42.37	43.29	18.28
X^2 , p		0.31, 0.691	23.21, 0.001	28.00, 0.001	8.32, 0.016
Fisher's exact test		1.0	0.000	0.000	0.017

4.7. List of species belonging to the *Pheidole pallidula* complex and their synonyms

The reasons for identification and synonymisation of the taxa are given in square brackets behind the heading names.

(1) *Pheidole pallidula* (Nylander, 1849)

Myrmica pallidula Nylander, 1849 [identification by geography]. The reasons for allocating this name to the western clade were given above.

Oecophthora subdentata Mayr, 1853 [synonymy by type investigation and geography]. The reasons for synonymization were explained above.

Pheidole pallidula var. *obscura* Santschi, 1936 [synonymy by geography] [replacement name for the junior homonym *Pheidole pallidula* var. *emeryi* Krausse 1912] Types of Krausse are lost (if they existed at all) and the original description is useless. A synonymy with *P. pallidula* is strongly suggested by the type locality (Sardinia). A specimen from Var /France (depicted in antweb.org under CASENT0913388) and labelled as ‘Type’ in the Santschi collection in Basel has no type status and should also not be fixed as neotype.

Xenoaphaenogaster inquilina Baroni Urbani, 1964 [synonymy by description and geography] [unresolved junior secondary homonym of *Epipheidole inquilina* Wheeler, 1903]. The type of a single specimen discovered by Baroni Urbani in Sicily in a nest of *Aphaenogaster pallida* (Nylander, 1849) is lost. According to Bolton (1987), the description suggests that it is a minor worker of *Pheidole pallidula*.

(2) *Pheidole koshewnikovi* Ruzsky, 1905

Pheidole pallidula ssp. *koshewnikovi* Ruzsky, 1905 [type investigation] The Lectotype was fixed due to agreement of Ruzsky’s original label (‘Balchasch See’) written in German with the statement in the original description (‘na zapadnom berege ozera Balkhasha’- ‘at western shore of Lake Balkhash’).

Pheidole pallidula var. *arenarum* Ruzsky, 1905 [synonymy by geography] The reasons for synonymization were explained above.

Pheidole pallidula ssp. *orientalis* Müller, 1923 [type investigation] [first available use of *Pheidole pallidula* ssp. *arenarum* var. *orientalis* Emery, 1915]

(3) *Pheidole cicatricosa* Stitz, 1917

Pheidole pallidula var. *cicatricosa* Stitz, 1917 [type investigation]

Pheidole pallidula var. *recticeps* Menozzi, 1932 [type investigation] [First available use of *Pheidole pallidula tristis recticeps* Forel, 1909].

(4) *Pheidole balcanica* nov.sp.

4.8. Westpalaeartic taxa excluded from synonymy with any *P. pallidula* complex species

It is sufficient for the purpose of this paper to exclude a synonymy of the members of the *Ph. pallidula* complex with the taxa listed below. Beyond that, the taxonomic status of most of the latter taxa cannot be determined by subjective approaches on the basis of few specimens and will remain open here. The relations between the taxa *Ph. sinaitica* Mayr, 1862, *Ph. jordanica* Saulcy, 1874, *Ph. laticeps* Mayr, 1904 and *Ph. schmitzi* Forel, 1911 in particular should be checked by a methodology comparable to that presented in this paper. These four taxa are similar and have their type localities in Egypt and Israel. Fixation of primary type specimens and multivariate analyses of big data sets are needed. Extreme interpretations of this case may vary between a single and four species.

Pheidole sinaitica Mayr, 1862

This taxon has been described from Sinai and is definitely no synonym of any member of the *P. pallidula* complex. The original description states the presence of much longer and stronger longitudinal carinulae on dorsal head with notably microreticulate-corrugate interspaces and the presence of a transverse roof-like structure on posterior mesonotum.

Mayr description fits to a non-type specimen depicted in antweb.org under CASENT0263723. This specimen has a much longer scape and femur than seen in any member of the *P. pallidula* complex.

Pheidole jordanica Saulcy, 1874

P. jordanica has been described from Jericho, Israel. The morphological description states the eyes to have twice the size and the segments of antennal club to have 1.5 fold the length observed in *P. pallidula* and the carinulae on head extending to hind vertex. This excludes a synonymy with any member of the *P. pallidula* complex. Future revisers should check a synonymy with *Ph. sinaitica*.

***Pheidole teneriffana* Forel, 1893**

It was described from Tenerife. The lectotype shows strong differences in morphometry, mesosomal shape and sculpture to any member of the *P. pallidula* complex. The description of Wilson (2003) was not based on type material but is fully consistent with the characters of the lectotype.

***Pheidole laticeps* Mayr, 1904**

It was described from Cairo, Egypt. RAV-corrected scape, femur, mesosoma and eye length data of the type are above the upper extremes known for the four species of the *P. pallidula* complex (SL/CS_{1.25} 0.635, Fe3L/CS_{1.25} 0.820, ML/CS_{1.25} 0.935, EL/CS_{1.25} 0.200 – compare with Tab. 2). The presence of a transverse roof-like structure on posterior mesonotum and a much wider metanotal groove provide other diagnostic differences. The type is depicted in antweb.org under the specimen code CASENT0906620.

***Pheidole schmitzi* Forel, 1911**

This taxon was described from Jerusalem. The description of Forel shows that it differs from any species of species of the *P. pallidula* complex by strongly elongated scape and funiculus segments.

***Pheidole obtusa* Stitz, 1917**

Investigation of the type series and of those of *Pheidole pallidula selenia* Özdikmen, 2010 showed that this species strongly differs from the *Ph. pallidula* group members. *Ph. obtusa* shows strikingly larger RAV-corrected scape length, femur length and eye length data (SL/CS_{1.25} 0.677, Fe3L/CS_{1.25} 0.880, EL/CS_{1.25} 0.184 – compare with Tab. 2). Furthermore, the postpetiole is much narrower (PPW/CS_{1.25} 0.223) with the sides appearing in dorsal view convex to obtusely angled even in large specimens. Further diagnostic differences to the *Ph. pallidula* group members are provided by the following characters. The propodeal spines are thinner, longer and much less erect – they deviate by 45–65° from longitudinal mesosomal axis and are often suggestively curved caudad. The interspaces between carinulae on frontolateral vertex are somewhat shining but are much stronger microreticulate. In fully lateral view, the mesosoma shows no metanotal depression which, however, becomes visible in dorsolateral view. The mesonotum shows well marked but very blunt-angled lateral corners which may be connected by a slightly concave ridge. Mesopleuron, metapleuron and propodeum are strongly microreticulate with few largely longitudinal rugae and carinae.

***Pheidole pallidula selenia* Özdikmen, 2010**

Pheidole pallidula selenia Özdikmen, 2010 was established as replacement name for *Pheidole pallidula inermis* Stitz, 1917 that is a junior primary homonym of *Pheidole inermis* Mayr, 1870. Lectotype and paralectotype are consistent with the type series of *Pheidole obtusa* Stitz, 1917 both in RAV-corrected shape variables and subjectively described characters. The synonymy is obvious.

4.9. Problematic Taxa***Myrmica trinodis* Losana, 1834 [Incertae Sedis]**

This taxon was described as an ‘indigenous ant species of Piemonte’, Italy and to occur there in gardens. Losana’s morphological description of a very slender ant is contradictory and puzzling (three waist segments are given both in the verbal description and are also depicted in the drawing!). Types are unknown and presumed of being lost. It is unintelligible on which basis this name could be considered by Roger (1863) and Bolton (2015) as a junior synonym of the holotropical tramp species *Pheidole megacephala* (Fabricius 1793) that differs considerably and should not occur in Piemonte. Without types, the only reasonable decision is allocation to Incertae Sedis.

***Pheidole pallidula* subsp. *tristior* Schmitz, 1950.**

This name was listed for Portugal without description and is a Nomen Nudum.

***Pheidole pallidula tasdalenia* Özdikmen, 2010**

Replacement name for *Pheidole tristis* Forel, 1907 [Junior secondary homonym of *Pheidole tristis* Smith, 1858].

It was described from Kairouan, Tunisia on the basis of a single specimen considered by Forel as a microgyne (2.6–2.8 mm total length). The status of this problematic specimen cannot be cleared up without very extensive investigations of the Tunisian *Pheidole* populations.

4.10. Conclusions

The Westpalaeartic ants collected so far under the name *Pheidole pallidula* (Nylander, 1849) consist of four cryptic species which are convincingly separable by high-resolution stereomicroscopy and the explorative

data analyses NC-Ward and NC-k-means clustering in combination with cross-validated linear discriminant analysis. The *Ph. pallidula* complex consists of *Ph. pallidula*, *Ph. balcanica* nov. sp., *Ph. koshewnikovi* Ruzsky, 1905 and *Ph. cicatricosa* Stitz, 1917. The classification error varied between 0 and 2.8% in NC clustering of nest samples and between 1.6 and 3.7% in cross-validated linear discriminant analysis of individuals. *Ph. cicatricosa* has a North African distribution whereas *Ph. pallidula*, *Ph. balcanica* nov. sp. and *Ph. koshewnikovi* are Eurasian species with large sympatric ranges in the Balkans and Asia Minor. Colonization of urban regions north of the Alps and of offshore islands in the Mediterranean Sea indicates an invasive potential of the supercolonial social type of *Ph. pallidula*.

There are no indications that any of these four taxa might represent an intraspecific polymorphism and signals for putative interspecific hybridization are not significant. Examining the status of 13 other taxa appearing as possible synonyms due to morphological description and zoogeography, the senior synonymy of the four above mentioned names was established. Six taxa were recognized as junior synonyms of either *Ph. pallidula*, *Ph. koshewnikovi* or *Ph. cicatricosa* and seven taxa were excluded from synonymy with any member of the *Ph. pallidula* complex by type investigation and diagnostic statements in the original descriptions.

Future research should investigate the special zoology and autecology of these interesting species and study

interspecific relations under syntopic or sympatric occurrence in contact zones. We have no basic knowledge of the biologies of the three Eurasian and African species. There is insufficient knowledge of the mating scenarios of each species, on the relation between intranidal mating and swarming flight, inbreeding and outbreeding, on the frequency of single-queen (flight) dispersal and colony foundation relative to dispersal by colony fission. The time-consuming species identification by NUMOBAT methods is a real challenge but could represent the starting point for developing reliable species delimitation methods based on nuclear DNA markers.

5. Description of *Pheidole balcanica* sp.n.

Etymology. The name is given because large parts of the distributional range are in the Balkans.

Type material: See in section 2.2. ‘Type Material’.

Description of the major caste Figs 5–7. All data of shape variables given in the following description refer to specimens with a cephalic size CS of 1.25 mm.

Medium-sized, on the average larger than *Ph. pallidula*: CS 1.106–1.457 mm. Head rather short: ratio of maximum median cephalic length against maximum cephalic width 0.90–0.97. Outlines of head in dorsal aspect without linear components: pre- and postocular head sides and occipital corners convex, the hind margin is strongly concavely excavated, depth of excavation 7–12% of maximum median head length. The eye is the smallest within the *Ph. pallidula* species complex: ratio of maximum eye diameter against cephalic size 0.118–0.148. Frontal carinae diverging caudad. Anterior half of dorsal head surface longitudinally carinate caudad to about one eye length posterior of caudal eye margin (Fig. 5). The space between carinae rather smooth and shining, without conspicuous microsculpture. Posterior half of dorsal head surface smooth and shining. Frontal triangle smooth and shining. Clypeus with exception of a median carinula and several paramedian or lateral ones smooth and shining. Masticatory border of mandibles toothless with the exception of a very strong apical, strong subapical and a weak subbasal dent. Anterior margin of hypostoma with two dents or blunt protrusions. Scape and hind femur short: ratio of scape length against cephalic size 0.55–0.61 and ratio of hind femur length against cephalic size 0.71–0.79. Whole surface of head, scapes, femora, tibiae, promesonotum, waist and gaster with numerous, thin suberect setae. Mesosoma in lateral view (Fig. 6) with short but sharp and steeply erected propodeal spines, a linear dorsum of propodeum and a well developed metanotal



Figure 5. Dorsal aspect of head of the holotype major worker of *Pheidole balcanica* sp. nov.

groove. The overall profile of promesonotum is strongly convex and surmounts dorsal propodeum considerably relative to the level of longitudinal mesosomal axis. Outline of promesonotum in dorsolateral (oblique) view without very prominent lobes or protrusions but very flat, obtusely-angled corners – one on dorsolateral pronotum and one or two on dorsolateral mesonotum – are usually visible. Pronotum at small magnifications smooth and shining. Petiole in lateral aspect distinctly longer than high, with a rather straight anterior profile and a small semicircular dorsal crest that appears in dorsal view much wider than long (Fig. 7). Whole surface of head, scape, femora, tibiae, promesonotum, waist and gaster with numerous, thin suberect setae.

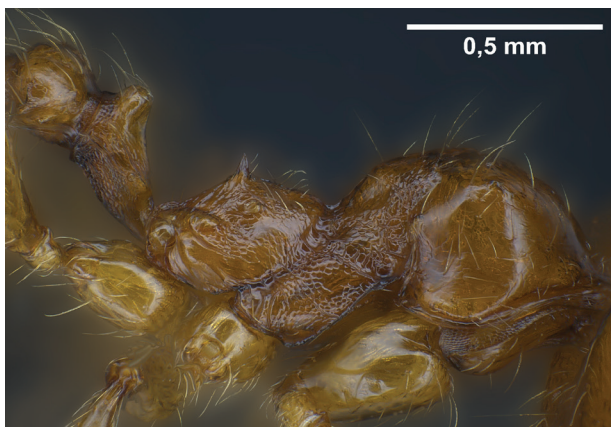


Figure 6. lateral aspect of mesosoma of the holotype major worker of *Pheidole balcanica* sp. nov.

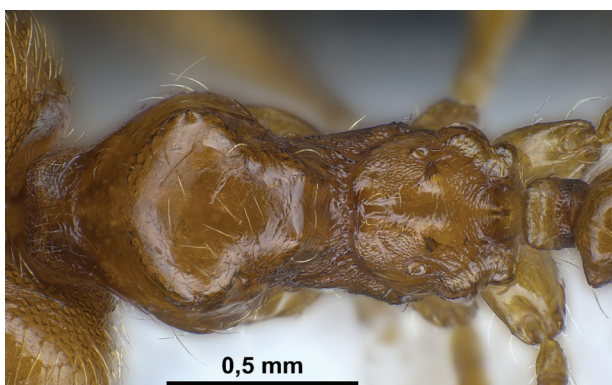


Figure 7. Dorsal aspect of mesosoma of the holotype major worker of *Pheidole balcanica* sp. nov.

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