Lasius nigroemarginatus Forel, 1874 is a F$_1$ Hybrid between *L. emarginatus* (Olivier, 1792) and *L. platythorax* Seifert, 1991 (Hymenoptera, Formicidae)

With 7 figures and 1 table

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Abstract

Lasius nigroemarginatus Forel, 1874, that has been synonymized in recent catalogues with *Lasius emarginatus* (Olivier, 1792), is shown to represent a F$_1$ hybrid between *L. emarginatus* and *L. platythorax* Seifert, 1991. This conclusion was firstly drawn from numeric description of 16 phenotypic characters and the placement of four type workers of *L. nigroemarginatus* within vectorial space of the three possible parental species. These were represented by 144 workers of *Lasius niger* (Linnaeus, 1758), 90 workers of *L. emarginatus* and 94 workers of *L. platythorax* – with a coverage for all species by their whole Palaearctic range. The type sample was placed intermediate between (and clearly separated from) the clusters of *L. emarginatus* and *L. platythorax* in both Nonmetric Multidimensional Scaling and when run as a wild-card in a three-class linear discriminant analysis. Comparing structural and pigmentation characters one by one, the types of *L. nigroemarginatus* were intermediate between *L. emarginatus* and *L. platythorax* in five characters, closer to *L. emarginatus* in four characters and closer to *L. platythorax* in seven characters. The conclusions derived from the position in the morphological space were supported by data on swarming time and nest habitat selection and the odor perceived by the collector Forel. *Lasius niger* could be clearly excluded to represent a parental species. It is argued that the International Code of Zoological Nomenclature (ICZN) shows logical inconsistencies and explanatory weakness regarding the treatment of truly hybridogenous species and that the Articles 1.3.3, 17.2 and 23.8 of ICZN should be amended or re-written.

Key words

morphological space, multidimensional scaling, hybrid analysis, swarming time

Zusammenfassung

Es wird gezeigt, dass der in neueren taxonomischen Katalogen als jüngeres Synonym von *Lasius emarginatus* (Olivier, 1792) gelistete *Lasius nigroemarginatus* Forel, 1874 ein F$_1$-hybrid zwischen *L. emarginatus* und *L. platythorax* Seifert, 1991 ist. Diese Schlussfolgerung ergab sich aus der Position von vier Typusexemplaren von *L. nigroemarginatus* in dem durch 16 kontinuierliche phenotypische Merkmale charakterisierten Vektorraum der drei möglichen Elternarten. Diese waren im Untersuchungsmaterial vertreten durch 144 Arbeiterinnen von *Lasius niger* (Linnaeus, 1758), 90 Arbeiterinnen von *L. emarginatus* und 94 Arbeiterinnen von *L. platythorax* – wobei das Material aus dem gesamten paläarktischen Verbreitungsgebiet der betrachteten Arten stammte. Sowohl eine Nichtmetrische Multidimensionale

Skalierung als auch ein hypothesenfreies (wild-card) Rechnen in einer linearen Diskriminanzanalyse platzierte die Typusexemplare zwischen den Clustern von *L. emarginatus* und *L. platythorax* und weit entfernt vom Cluster von *Lasius niger*. Eine gesonderte Betrachtung der Struktur- und Pigmentmerkmale zeigt, dass die Typen von *L. nigroemarginatus* in fünf Merkmalen ideal intermediär zwischen *L. emarginatus* und *L. platythorax*, in vier Merkmalen näher zu *L. emarginatus* und in sieben Merkmalen näher zu *L. platythorax* positioniert waren. Die aus der Position im morphologischen Raum abgeleiteten Schlussfolgerungen werden durch Daten zu Schwarmzeiten und Mikrohabitatwahl sowie den durch Forel beim Öffnen des Nestes wahrgenommenen Geruch bestätigt. *Lasius niger* konnte klar als Elternart ausgeschlossen werden. Es wird darauf hingewiesen, dass der Internationale Code für Zoologische Nomenklatur (ICZN) logische Inkonsistenzen und Definitionsschwächen bezüglich der Behandlung von echten hybridogenen Arten aufweist und dass die Artikel 1.3.3, 17.2 und 23.8 des ICZN geändert oder neugeschrieben werden sollten.

Schlüsselwörter

morphological space, multidimensional scaling, hybrid analysis, swarming time

1. Introduction

Lasius nigroemarginatus Forel, 1874, firstly described with the spelling "*Lasius nigro–emarginatus*", was synonymized by Wilson (1955) with *L. emarginatus* (Olivier, 1792) and this interpretation has been maintained up to the present (Bolton 2018). The type series of *L. nigroemarginatus*, containing workers and alate gynes, was collected by Auguste Forel 5 July 1871 from under the bark of a tree near Mendrisio / Switzerland. Forel (1874) wrote that the coloration of the specimens was exactly intermediate between *Lasius niger* (Linnaeus 1758) and *L. emarginatus* and that he perceived a slight odor as it is characteristic for *L. emarginatus*. He further noted that the mesosoma of gynes was less flattened than in *L. emarginatus* but flatter than in *L. niger*. From this description and the naming chosen by Forel it is obvious that he believed the specimens to represent hybrids between *L. niger* and *L. emarginatus*. It was a fashion in the late 19th century, and a habit of Forel in particular, to postulate hybrid forms and to give these a taxonomic naming. Many of the hybrid forms supposed by Forel have later turned out of not being hybrids – examples in *Lasius* are according to Seifert (1992): *L. brunneo-emarginatus* Forel, 1874 which is synonym of *L. emarginatus* or *L. alieno-brunneus* Forel, 1874 which is a synonym of *L. brunneus* (Latreille, 1798). Yet, Forel's ideas sometimes came close to reality as in the case treated here. Seifert (1992, 2018) stated that the type series of *L. nigroemarginatus* represented a hybrid between *Lasius emarginatus* and *Lasius platythorax* Seifert, 1991 but he did only present some verbal arguments instead of testable conclusive data. This paper intends to correct this failure by application of a complex numeric approach.

Numeric description of any form of phenotypical characters provides the input data of a discipline that Seifert (2009) has named Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT). Both this naming and its acronym have not been used by other taxonomists so far but I suggest that we must have a name for a stringent working philosophy which contrasts with the idiosyncratic approaches unfortunately predominating so far in fundamental research of morphology-based alpha-taxonomy. NUMOBAT procedures which include advanced forms of exploratory and hypothesis-driven data analyses (Seifert et al. 2013, Csösz & Fisher 2015), a clear species concept (Seifert 2014, 2018) and a test system for intraspecific dimorphism (Seifert 2016) reduce the error rate of alpha-taxonomic decisions considerably.

Hybrid identification by advanced methods of NUMOBAT is most effectively done within the vectorial space. The most powerful method are here discriminant functions in which clearly defined samples of parental species form the basal vector-defining hypothesis whereas suspicious samples are run as wild-cards – i.e., without imposing a hypothesis. This approach has been successfully used in the genera *Formica* (Seifert 1999; Kulmuni et al. 2010; Seifert et al. 2010), *Myrmica* (Bagherian et al. 2012), *Lasius* (Seifert 2006), and *Camponotus* (Seifert 2019) as well as in unpublished hybrid studies of the author in *Temnothorax*.

2. Material

A detailed account of the samples is given below in the following sequence and format: site, date in the format yyyy.mm.dd, sample No [latitude in decimal format, longitude in decimal format, altitude in meters]. The accuracy of coordinates is proportional to the number of decimal points and "xx" in the sampling date sequence mean missing data. In some samples without any direct or derived information on date, the collector is given to allow an approximate conclusion on the time period of collection. Sample numbers are missing in many samples.

Lasius niger (Linnaeus, 1758)

A total of 67 nest samples, all stored in SMN Görlitz, originated from the following countries: Algeria 1, China 1, Bulgaria 1, Denmark 2, Finland 1, France 6, Great Britain 3, Germany 9, Italy 2, Kazakhstan 9, Kyrghystan 6, Mongolia 2, Poland 3, Russia 13, Spain 3, Sweden 1 and Turkey 1. A total of 144 workers were subjected to NUMOBAT.

ALGERIA: Alger city, 1965.07.24 [36.75, 3.06, 200]. BULGARIA: Pirin Mts., Karlanovo, 1983.07.07 [41.543, 23,420, 540]. CHINA: Boro-Horo Mountain range, 2010.07.11, No 138 [44.444, 82.041, 1040]. DENMARK: Femoller 1974.07.24, No A, No C [56.226, 10.552, 78]. FINLAND: Lilla Träskön, 1996.07.07, No 158 [59.930, 24.370, 5]. FRANCE: Azay-sur-Cher, 2007.xx.xx, No 6 [47.346, 0.844, 65]; Cerniebaud, 1990.07.12, No 157 [47.733, 6.100, 960]; Cluses / Arve, 1990.07.18, No 144 [46.056, 6.607, 495]; Corsica: Saint Florent, 2014.07.03 [42.672, 9.284, 8]; Labergement Ste. Marie, 1990.07.11 [47.774, 6.282, 870]; Narbonne-4 km NE, 1991.05.05, No 60 [43.197, 3.075, 19]. GREAT BRITAIN: Culbin / Moray, 1956.09.xx [57.632, -3.726, 5]; Portland Island, western quarries, 1990.07.22 [50.456, -3.726, 5]; Wareham, 1990.07.22, No A [50.688, -2.111, 11]. GERMANY: Ahrenshoop-4 km NE, 1989.08.16, No 65 [54.409, 12.463, 10]; Görlitz, 1989.07.24, No II, No XIII, No 37 [51.158, 14.988, 195]; Lauchhammer, Restloch 37, 1987.07. xx [51.49, 13.79, 100]; Leipzig, Messegelände, 1985. xx.xx [51.318, 12.403, 130]; Quitzdorf, 1989.07.29, No 3 [51.264, 14.788, 164]; Rommersheim, 1990.04.30 [50.194, 6.445, 475]; Gutendorf, Steinbruch, 1987.06.24 [50.913, 11.218, 405]. ITALY: La Camosciara, 2009.07.11, No 118 [41.772, 13.908, 1053]; Val Fondillo, 2009.07.07, No 026 [41.768, 13.855, 1106]. KAZAKHSTAN: Almaty, Hotel Raketa, 2001.07.12, No 220 [43.267, 76.917, 760]; Dsungar Alatao, 2001.08.08, No 50 [45.254, 80.296, 1400]; East of Lake Zaisan, 2001.07.25, No 332 [47.706, 85.300, 496]; South of Lake Zaisan, 2001.07.23, No 352 [47.636, 84.064, 685]; Manrak Mountains, 2001.07.27, No 268, No 311 [47.323, 84.621, 1168]; Southern Tarbagatai Mountains, 2001.08.04, No 289 [44.119, 82.371, 1697]; Southwestern Tarbagatai Mountains, 2001.07.20, No 299 [44.170, 80.470, 610]; Saur Mountains, 2001.07.24, No 237 [47.294, 85.617, 1486]. KYRGHYSTAN: Dzeti Oguz, 2000.07.23, No 256, No 274 [42.346, 78.228, 2030]; Karakol, 2000.07.24, No 51, No 261 [42.493, 78.398, 1800]; Karakol, Zapovednik, 2000.07.27, No 266 [42.411, 78.448, 2150]; Tschon-Aschu pass, 2000.07.24, No 191, No 258 [42.593, 78.878, 2070]. MONGOLIA: Bodonchin Gol, 1980.07.17 [45.77, 92.18, 1266]; Bodonchin Gol, 1982.07.17 [45.77, 92.18, 1266]. POLAND: Bolechovice, 1989.09.11, No 15 [50.147, 19.793, 275]; Lopuzsna, 1989.09.12, No 34 [48.485, 20.144, 680]; Lopuzsna, 1989.09.13, No 113 [48.485, 20.144, 680]. RUSSIA: Babushkin, 2002.08.26, No 3 [51.708, 105.853, 490]; Bayan village, 2002.08.17, No 1, No 2 [50.550, 105.283, 797]; Irkutsk, Ostrov Yunosť, 2005.07.28, No 2 [52.30, 104.2, 430]; Irkutsk, park, 2001.08.22, No 001 [52.287, 104.271, 460]; Irkutsk, park, 2005.07.27, No 5 [52.328, 104.243, 430]; Irkutsk, park, 2006.05.17, No 1, No 2 [52.328, 104.243, 430]; Maima-10 km S, 2000.07.20, No 5 [52.05, 85.540, 250 m]; Salair Mountains, 2007.07.16, No 2 [54.10, 85.49, 400]; St. Petersburg, city, 1995.08.xx [59.9, 30.4, 12]; Tomsk-20 km S, 2008.08.05, No 9 [56.27, 84.94, 80]; Volchikha, 2008.09.03, No N25 [51.883, 80.317, 190]. SPAIN: Ebro delta, La Cava, 1991.05.06 [40.718, 0.741, 1]; Madrid, city, 2014.04.25, No 4 [40.433, -3.679, 686]; Espot-1 km W, 1991.05.16, No 32, No XIII [42.588, 1.071, 1700]. SWEDEN: Linnaeus' Hammarby, 1996.08.01, No 190 [59.817, 17.776, 25]. TURKEY: Aksehir, 2003.05.17, No 415 [38.216, 37.249, 1021].

Lasius emarginatus (Olivier, 1792)

A total of 38 nest samples, all stored in SMN Görlitz, originated from the following countries: Austria 6, Croatia 3, Czechia 2, France 3, Germany 10, Greece 6, Italy 6, Switzerland 1 and Ukraine 1. A total of 90 workers were subjected to NUMOBAT investigation.

AUSTRIA: Praditz, Weisse Wand, 2012.08.05, No 6 [46.731, 13.269, 1395]; Wien: Hietzing, 2002.08.19, No 11131 [48.192, 16.362, 177]; Wien: Kahlenberg, 2018.04.09, No WAG2215, No WAG2217 [48.276, 16.342, 341]; Wien: Leopoldsberg 2018.04.09, No WAG2201, No WAG 2202 [48.277, 16.344, 363]. CROATIA: Jablanac-0.8 km SE, 2014.08.03, No 96 [44.701, 14.904, 11]; Punat-5 km SE, 1997.06.01, No 460 [44.970, 14.660, 120]; Rab, old city, 2014.08.09, No 103 [44.754, 14.763, 7]. CZECHIA: Praha-Prokop, 1989.07.08, No 1, No 2 [50.032, 14.364, 270]. FRANCE: Beley–12 km E, 1996.04.14 [45.758, 5.873, 250], Paris, 2010.07.07 [48.956, 2.339, 41]; Pas de l'Echelle, 1990.07.18 [46.170, 6.214, 550]. GERMANY: Dresden-Klotzsche, 1978.08.13 [51.118, 13.786, 200]; Isteiner Klotz, 47.662, 7.529, 255]; Leipzig, city, 1978.08.22 [51.332, 12.385, 116]; Lindelbach-1 km N, 1991.05.29-217 [49.737, 10.019, 300]; Questenberg, 1987.05.28 [51.493, 11.117, 275]; Singen-2 km W, 1991.05.23, No 61, No 65u [47.763, 8.819, 555]; Zittauer Gebirge, Töpfer, 1989.08.22 [50.849, 14.762, 570]; Zscheiplitz, 1989.05.19 [51.215, 11.728, 196]; Zwickau-Planitz, Kreuzberg, 1989.07.01 [50.676, 12.459, 387]. GREECE: Kalamata-20 km E, 1994.06.01, No 1345 [37.073, 22.256, 1250]; Mt. Olympus region: Litohoro-4 km W, 1996.05.13, No 191 [40.112, 22.480, 600]; Pieria: Elatochori-2.3 km N, 2012.09.03 [40.340, 22.257, 748]; Pilion, 2001.05.26, No 023 [39.342, 23.141, 780]; Sithonia: Parthenonas, 2009.09.02 [40.120, 23.812, 305]; Taigetos Oros, 1994.06.02, No 1363 [37.066, 22.107, 193]. ITALY: Castel Mancino, 2009.07.08, No 032 [41.813, 13.785, 1325]; Viletta Barea, 2009.07.06, No 004 [41.775, 13.934, 988]; Glurns, 2012.08.11, No 10 [46.671, 10.553, 917]; Klausen, 2013.09.08, No 194g,

No 196b [46.642, 11.568, 580]; Procida, 2012.10.19 [40.764, 14.024, 25]. <u>SWITZERLAND</u>: Suster-2 km W, 1990.07.14, No 65 [46.228, 7.333, 614]. <u>UKRAINE</u>: Kiev, city, 2010.06.02, No 3 [50.445, 30.514, 176].

Lasius nigroemarginatus Forel, 1874

Investigated were 6 type workers labeled "Typus", "L. nigro-emarginatus W Mendrisio", "Coll. Forel.", among these one pin with 3 workers additionally labeled with "ANTWEB CASENT 0911046"; MNH Genève. NUMOBAT data were recorded in four workers.

Lasius platythorax Seifert, 1991

A total of 45 nest samples, all stored in SMN Görlitz, originated from the following countries: Bulgaria 2, Croatia 1, France 4, Great Britain 4, Germany 9, Greece 1, Ireland 1, Italy 5, Poland 1, Romania 3, Russia 13 and Sweden 1. A total of 94 workers were subjected to NUMOBAT investigation.

<u>BULGARIA</u>: Arkutino, 1978.08.01 [42.328, 27.742, 23]; Obsor, 1979.08.01 [42.820, 27.880, 30]. <u>CROATIA</u>: Krasno Polje-4.2 km NW, 2014.07.31, No 90 [44.849, 15.015, 950]. <u>FRANCE</u>: Arcachon, 2008.05.05 [44.651, -1,160, 30]; Epinasse, 2008.08.27 [46.655, 2.294, 1000]; Les Granges, 1990.07.12, No 32, No 104 [46.97, 6.38, 880]. <u>GREAT BRITAIN</u>: Hartland Moor, 1990.07.24, No C, No 57, No 103, No 143 [50.657, -2.092, 35]. <u>GERMANY</u>: Ahrenshoop-4 km NE, 1989.08.19 [54.409, 12.463, 10]; Bernsdorf-5 km NE, 1989.08.08, No 61 [51.398, 14.115, 151]; Biesig-1 km N, 1988.04.16, holotype nest of *L. platythorax*, [51.170, 14.799, 330 m]; Königshain-W, 1989.07.29, No 10 [51.19, 14.84, 300]; Königshain-Hochstein, 1989.07.26, No 47 [51.194, 14.835, 404]; Milkeler Moor, 1988.08.09 [51.334, 14.460, 137]; Sachsenberg near Särichen, 1989.07.29, No 61 [51.278, 14.866, 187]; Zittauer Gebirge, Töpfer, 1989.08.22 [50.849, 14.762, 570]; Ullersdorf, fen, 1989.07.27, No 15 [51.231, 14.822, 171]. <u>GREECE</u>: Nestos delta, floodplain forest, 2004. xx.xx [40.85, 24.80, 2]. <u>IRELAND</u>: SAC Barrigone, 2007.07.04 [52.60, -9.05, 23]. <u>ITALY</u>: Pescasseroli, 2009.07.26, No 143 [41.854, 13.777, 1297]; Pesco di Lordo, 2009.07.28, No 168 [41.788, 13.759, 1327]; Sorgente Duna, 2009.07.07, No 019, No 021 [41.887, 13.755, 1240]; San Giorgio Morgeto, 1990.08.02 [38.387, 16.107, 500]. <u>POLAND</u>: Lopuzsna, 1989.09.12, No 34 [49.491, 20.135, 680]. <u>ROMANIA</u>: Medias-Birthelm, 1987.07.22 [46.17, 24.35, 300]; Segetea, 2011.09.20, No MZEC-127 [46.626, 25.587, 770]; Semenic NP, Gabrova Breg, 2016.04.14 [45.215, 22.023, 650]. <u>RUSSIA</u>: Artybash, 2006.09.02, No N2 [51.79, 87.27, 437]; Artybash, 2006.08.30, No N9 [51.79, 87.27, 437]; Artybash, 2008.08.xx, No 54 [51.79, 87.27, 437]; Krasnij Kljuch, 2011.07.12, No 118 [51.514, 104.125, 504]; Larichikha, 1999.07.xx, No N1 [53.717, 82.967, 170]; Larichikha, 2002.07.xx, No N3, No N5 [53.70, 82.85, 170]; Odinsk-5.9 km SW, 2008.07.13, No 95 [52.439, 103.669, 480]; Odinsk-5.9 km SW, 2008.08.08, No 84 [52.426, 103.657, 480]; Razkaszikha, 2005.08. xx, No N9 [53.083, 83.850, 145]; Shtabka, 2007.07.xx, No N22 [53.250, 83.483, 181]; Svenigorod, 1985.08.24 [55.694, 36.725, 172]; Vydrino-8.8 km E, 2008.07.11, No 102 [51.444, 104.768, 480]. <u>SWEDEN</u>: Lindshammar-5 km SE, 1992.06.11, No 41 [57.193, 15.207, 300].

3. Methods

3.1. Recording of NUMOBAT characters

Equipment and recording procedures are as given in Seifert & Galkowski (2016).

Seventeen morphometric characters (six shape, eight seta and two pubescence characters as well as absolute size) are defined below – figures assisting the definition of these characters are given in Seifert (2018).

CL – maximum cephalic length in median line; the head must be carefully tilted to the position with the true maximum. Excavations of posterior head and/or clypeus reduce CL.

CS – arithmetic mean of CL and CW as less variable indicator of body size.

CW – maximum cephalic width; this is either across, behind, or before the eyes.

dClAn – shortest distance from posterior clypeal suture (PCS) to *upper inner* margin of antennal sockets. If no surface structure indicates the position of PCS, the center of the dark line is taken as the anterior measuring point.

EYE – eye-size: the arithmetic mean of the large (EL) and small diameter (EW) of the elliptic compound eye under consideration of all structurally visible ommatidia - i.e., including also unpigmented ones.

GuHL – maximum length of setae on underside of head ("gula").

MP6 – length of the sixth (terminal) segment of maxillary palps.

nGu – number of setae on underside of head ("gula") as seen in full profile. The bilateral sum is halved.

nHT – setae number on extensor profile of hind tibia under exclusion of the very apical setae. The bilateral sum is halved.

nOcc – setae number projecting from hind margin of vertex frontad to caudal end of eye. Counting is done with head in full face view and by rotating the head within visual plane to avoid a parallax error in estimating the 20 μm projecting distance. Keep care to avoid the parallax error when determining the anterior end of the counting line that is at level of posterior eye margin. The bilateral sum is halved.

nSc – setae number on dorsal plane of scape under exclusion of the most apical setae, counted with view on the small scape diameter. The bilateral sum is halved.

nSt – setae number on lateral and caudolateral surface of metapleuron. The upper margin of the counting area is an imagined line parallel to the lower straight margin of metapleuron and crossing the lower margin of the cuticular ring of propodeal spiracle. Protective setae fringing the orifice of the metapleural gland are excluded. The bilateral sum is halved.

PLF – mean length of pubescence hairs on head between the frontal carinae. Seven measurements in each individual are averaged.

PnHL – length of the longest hair on pronotum.

PoOc – postocular distance. Use a cross-scaled ocular micrometer and adjust the head to the measuring posi-

tion of CL. Caudal measuring point: median occipital margin; frontal measuring point: median head at the level of the posterior eye margin. Note that many heads are asymmetric and average the left and right postocular distance.

SL – maximum straight line scape length excluding the articular condyle.

sqPDCL – square root of pubescence distance PDCL on clypeus. The number of pubescence hairs crossing or just touching a census line from caudomedian clypeus to lateral clypeal depression is counted. Hairs crossing / touching the census line are counted as 1 / 0.5. Erroneous zero counts in surface areas with torn-off pubescence can

Tab. 1: RAV-corrected morphometric data of individual workers of *Lasius niger*, *L. emarginatus*, *L. emarginatus* x *platythorax* and *L. platythorax*; i = number of individuals; arrangement of data: arithmetic mean ± standard deviation [minimum, maximum]. The columns with ANOVA data are placed between the columns of compared entities.

|	*L. niger* (i=144)	*L. emarginatus* (i=90)	ANOVA $F_{1,92}$ p	*L. emarginatus* x *platythorax* (i=4)	ANOVA $F_{1,96}$ p	*L. platythorax* (i=94)
CS	983 ± 76 [769,1140]	946 ± 94 [740,1382]	2.90 n.s.	1026 ± 58 [968,1097]	2.18 n.s.	968 ± 79 [721,1089]
CL/CW_{900}	1.073 ± 0.014 [1.042,1.109]	1.083 ± 0.016 [1.040,1.119]	3.86 n.s.	1.067 ± 0.018 [1.050,1.090]	3.57 n.s.	1.052 ± 0.015 [1.021,1.094]
SL/CS_{900}	0.978 ± 0.019 [0.909,1.038]	1.062 ± 0.019 [1.019,1.103]	25.77 0.000	1.012 ± 0.012 [0.999,1.024]	13.10 0.000	0.980 ± 0.018 [0.940,1.027]
$MP6/CS_{900}$	0.179 ± 0.009 [0.150,0.202]	0.220 ± 0.009 [0.200,0.247]	15.02 0.000	0.202 ± 0.004 [0.196,0.206]	49.39 0.000	0.175 ± 0.008 [0.154,0.189]
$PoOc/CL_{900}$	0.235 ± 0.009 [0.206,0.258]	0.217 ± 0.008 [0.194,0.233]	26.64 0.000	0.237 ± 0.003 [0.234,0.240]	9.23 0.003	0.248 ± 0.007 [0.231,0.269]
EYE/CS_{900}	0.245 ± 0.006 [0.233,0.261]	0.254 ± 0.005 [0.242,0.266]	8.11 0.005	0.246 ± 0.003 [0.243,0.249]	13.14 0.000	0.237 ± 0.005 [0.224,0.250]
$dClAn/CS_{900}$ [%]	4.65 ± 0.38 [3.69,5.90]	5.36 ± 0.46 [3.79,6.55]	7.68 0.007	4.72 ± 0.38 [4.38,5.12]	0.28 n.s.	4.60 ± 0.46 [3.60,5.95]
$sqPDCL_{900}$	3.50 ± 0.21 [3.13,4.07]	5.23 ± 0.63 [4.06,6.90]	1.51 n.s.	5.62 ± 0.59 [4.84,6.15]	7.29 0.008	4.86 ± 0.55 [3.68,6.28]
PLF_{900}	34.2 ± 2.0 [30.7,36.8]	24.8 ± 2.6 [19.6,28.1]	4.64 0.036	27.7 ± 2.4 [24.3,29.7]	11.24 0.003	32.2 ± 2.7 [28.3,36.7]
$GuHL/CS_{900}$	0.096 ± 0.010 [0.076,0.121]	0.126 ± 0.010 [0.104,0.152]	2.38 n.s.	0.134 ± 0.015 [0.113,0.147]	0.39 n.s	0.138 ± 0.012 [0.107,0.168]
$PnHL/CS_{900}$	0.125 ± 0.010 [0.102,0.151]	0.139 ± 0.012 [0.110,0.171]	14.51 0.000	0.163 ± 0.006 [0.155,0.170]	0.0. n.s.	0.164 ± 0.009 [0.143,0.187]
$nOcc_{900}$	14.39 ± 2.73 [8.5,23.0]	11.5 ± 2.9 [5.2,18.4]	14.84 0.000	17.2 ± 1.8 [15.1,19.5]	1.03 n.s.	15.7 ± 2.9 [9.6,23.5]
nGu_{900}	8.24 ± 2.36 [3.1,15.0]	6.8 ± 2.2 [2.2,13.2]	22.47 0.000	12.2 ± 0.8 [11.4,12.9]	0.04 n.s.	11.8 ± 3.7 [4.6,22.5]
nSc_{900}	14.95 ± 3.08 [7.8,23.2]	10.0 ± 6.2 [1.0,32.7]	12.60 0.001	21.1 ± 2.3 [18.6,24.2]	0.07 n.s.	20.6 ± 4.1 [11.5,30.3]
nHT_{900}	15.02 ± 2.99 [6.8,23.0]	17.9 ± 4.3 [7.3,30.3]	2.86 n.s.	21.6± 1.7 [20.0,23.7]	1.52 n.s.	19.7 ± 2.9 [13.9,25.3]
nSt_{900}	4.64 ± 1.08 [2.2,7.9]	3.7 ± 1.0 [1.8,5.8]	0.24 n.s.	4.0 ± 0.6 [3.4,4.7]	0.22 n.s.	3.7 ± 1.0 [0.8,6.5]
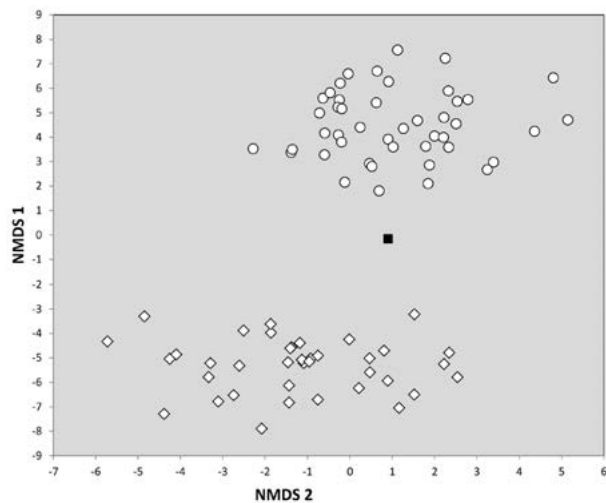
Fig. 1: Nonmetric Multidimensional Scaling plot of nest sample means of *Lasius platythorax* (white dots), *L. emarginatus* (white rhombs) and the type series of *L. nigroemarginatus* (black square).
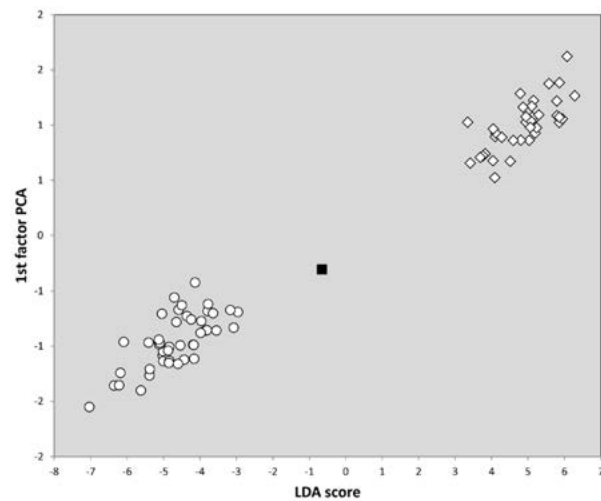

Fig. 2: Compound plot of the 1st factor of a Principal Component Analysis (PCA) and the score of a Linear Discriminant Analysis (LDA) of nest sample means of *Lasius platythorax* (white dots), *L. emarginatus* (white rhombs) and the type series of *L. nigroemarginatus* (black square). The type series was run in the LDA as wild-card.

be avoided when the basal points of the missing hairs can be visualized by adequate illumination and high-resolution optics and when average pubescence hairs length is considered. Square root data transformation is applied to normalize positively skewed distributions.

scaling (NMDS) was performed according to Seifert et al. (2013) using a script written in R and freely available under the GNU / GPL license from the following website: https://sourceforge.net/projects/agnesclustering/.

3.2 Removal of allometric variance

There is a strong intraspecific variance of body size in *Lasius* ants which is determined by age and social structure of the colonies and by nutrition. In order to reveal in comparative tables which shape variables differ between the species independent of body size, a removal of allometric variance (RAV) was performed following the basic procedure described by Seifert (2008). Evaluation of scatter plots suggested a use of linear monophasic allometry functions. RAV was calculated assuming all individuals to have a cephalic size of CS = 900 μm. RAV functions were calculated as the arithmetic mean of the species-specific functions of 47 Palaearctic *Lasius* s. str. species with sufficient sample size. RAV functions of six shape, eight seta and two pubescence characters are as given in Seifert & Galkowski (2016) except a modification in one character:

$MP6/ CS_{900} = MP6/CS / (-0.0806*CS +0.2512)*0.1886$

3.3. Data analysis

Linear discriminant analysis (LDA), principal component analysis (PCA) and ANOVA tests were performed with the software package SPSS 15.0. Samples suspected to be hybrids were run in the LDA as wild-cards – i.e., without imposing an hypothesis. Nonmetric multidimensional

4. Results and discussion

The first indication of a hybrid identity of the type sample of *Lasius nigroemarginatus* is provided by a number NMDS plots that place the type sample clearly between the clusters of the supposed parental species *L. emarginatus* and *L. platythorax*. An example, showing the NMDS axes 2 and 5, is given by Fig. 1. A clearly intermediate and isolated position is also achieved when the type sample is run as wild-card in a LDA (Fig. 2) whereas the PCA placed the sample close to the margin of the *L. platythorax* cluster (Fig. 2). All these analyses were based on sample means of on average 2.2 worker individuals per nest. Analyses performed on individual level do also place the four individual type workers of *Lasius nigroemarginatus* outside the clusters of *L. emarginatus* and *L. platythorax* – albeit rather close to the latter (Fig. 3).

A comparison of the characters one by one (Table 1) shows that the type workers of *Lasius nigroemarginatus* are intermediate between *L. emarginatus* and *L. platythorax* in four characters (CL/CW_{900}, SL/CS_{900}, EYE/CS_{900}, PLF_{900}), closer to *L. emarginatus* in three characters ($MP6/CS_{900}$, $sqPDCL_{900}$, PLF_{900}) but closer to *L. platythorax* in seven characters ($PoOc/CL_{900}$, $dClAn/CS_{900}$, $GuHL/CS_{900}$, $PnHL/CS_{900}$, $nOcc_{900}$, nGu_{900}, nSc_{900}). Furthermore, a subjective inspection of the type workers shows that coloration of head and mesosoma is intermediate between the *L. emarginatus* and *L. platythorax* condition
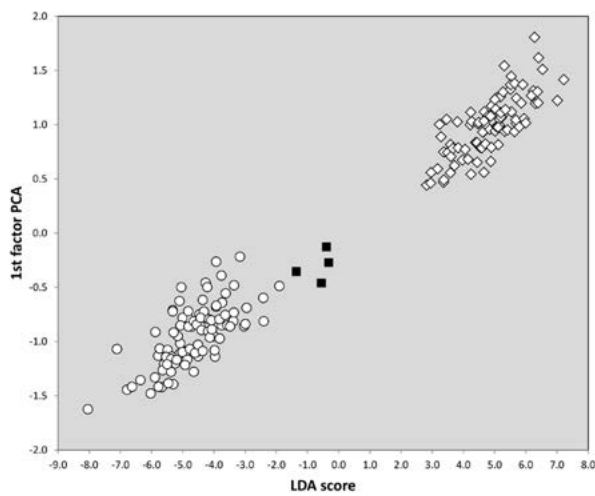
Fig. 3: Compound plot of the 1st factor of a Principal Component Analysis (PCA) and the score of a Linear Discriminant Analysis (LDA) of individual workers of *Lasius platythorax* (white dots), *L. emarginatus* (white rhombs) and the type series of *L. nigroemarginatus* (black squares). The type series workers were run in the LDA as wild-cards.
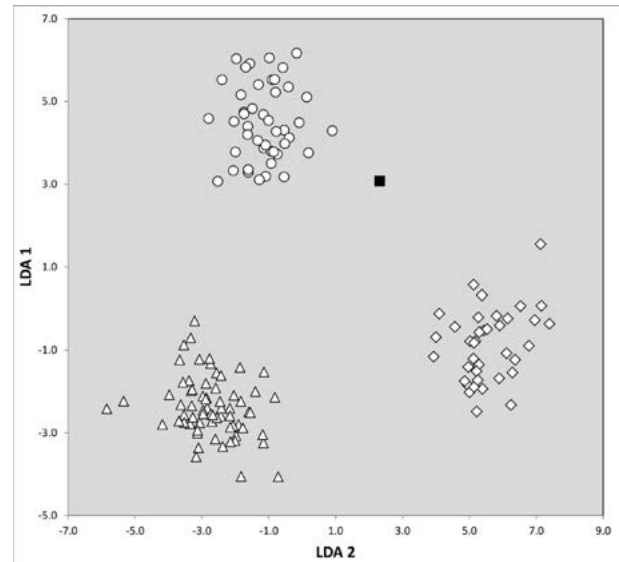

Fig. 4: Linear Discriminant Analysis (LDA) scores of nest sample means of *Lasius platythorax* (white dots), *L emarginatus* (white rhombs), *L. niger* (white triangles) and the type series of *L. nigroemarginatus* (black square). The type series was run in the LDA as wild-card.

Fig. 5: Lateral view of a worker of *Lasius platythorax*, showing a dark brown mesosoma and head and a low propodeal dome.

but that propodeal shape is similar to the *L. emarginatus* condition (Figs 5-7). Table 1 also shows that *Lasius niger*, with its very low pubescence distance (sqPDCL$_{900}$) and setae length data (GuHL/CS$_{900}$, PnHL/CS$_{900}$), is no candi-

date of a parental species in this hybridization case. This exclusion of *Lasius niger* is confirmed when the type workers of *L. nigroemarginatus* are run as wild-card in a 3-class LDA (Fig. 4).

Fig. 6: Lateral view of a type worker of *Lasius nigroemarginatus*, showing a reddish brown mesosoma and head (a condition intermediate between *L. platythorax* and *L. emarginatus*) and a high propodeal dome (a condition similar to *L. emarginatus*).

Which biological data can support the hybrid indication provided by morphology? According to SEIFERT (2018) the swarming season of *Lasius emarginatus* and *L. platythorax* in Europe is almost completely overlapping: 57 observations of *L. emarginatus* occurred 24 July ± 19 days [10 June, 4 September] and 24 observations of *L. platythorax* 27 July ± 17 days [21 June, 29 August]. However, the daily hours of swarming are strongly separated: five observed swarms of *Lasius platythorax* took place 15:55 ± 1:46 [13:36, 18:00] hours solar time (ST) but 11 observations in *L. emarginatus* 20:32 ± 1:05 [18:50, 23:00] hours ST. These data show that direct encounters of the two species during swarming should be rare but there remains a fair probability that the first swarming *L. emarginatus* males could meet the last swarming *L. platythorax* gynes between 18 and 19 h ST. The idea of a *L. platythorax* gyne mated by a *L. emarginatus* male is in line with the nest habitat reported by Forel. The *L. platythorax* gyne founded the colony under the bark of a tree which is typical for this species but rarely seen in *L. emarginatus*. I conclude that the whole body of presented data provides sufficient evidence for the hybrid identity of *Lasius nigroemarginatus* with just those parental species supposed by SEIFERT (1992, 2018).

The taxonomic treatment of this case is problematic and ambiguously regulated by the ICZN. From an evolutionary perspective hybrids can only have a significance (and deserve a taxonomic name) if they form an independent, long-term stable population separate from the parental species – i.e., if they represent a truly hybridogenous species. The Italian Sparrow *Passer italiae* (VIEILLOT, 1817) is a classical example (HERMANSEN et al. 2011, ELGVIN et al. 2011). *Lasius nigroemarginatus*, representing a rare, accidental F_1 hybrid case, definitely does not belong to this category. What says the Code? The regulations of ICZN regarding hybrid cases (and not only regarding these) are written without considering an evolutionary context, they are in a way free to personal interpretations. Firstly, Article 1.3.3 excludes a name from the provisions of the code if proposed for "hybrid specimens as such". The term may well apply to both rare, accidental hybrid specimens as well as to individuals coming from established populations of truly hybridogenous species. Accordingly, both *Lasius nigroemarginatus* and *Passer italiae* would have to be excluded from the provisions of the Code. Article 17.2 then states that a name is available if applied to a "taxon" known, or later found, to be of hybrid origin. This means that a name excluded from the provisions of the Code in an earlier part of the text is now stated by the

Fig. 7: Lateral view of a worker of *Lasius emarginatus*, showing a light reddish mesosoma and reddish brown head and a rather high propodeal dome.

same text to be available. Reading further in the Code, Article 23.8 regulates that a species-group name established for an "animal" later found to be a hybrid must not be used as the valid name for either of the parental species, even if it is older than all other available names for them. This regulates only that *Lasius nigroemarginatus* cannot be used as a synonym of either *L. emarginatus* or *L. platythorax*. Taking all things together, we arrive at the strange logic that *Lasius nigroemarginatus* would be an available name that cannot be synonymized with either parental species under the provisions of the Code but simultaneously is excluded from the provisions of the Code. While this distorted, unlucky situation in *Lasius nigroemarginatus*, representing a rare accidental hybrid, does not really cause greater damage to taxonomy, the Code has to make amendments regarding the treatment of truly hybridogenous species. The Code should explain in Articles 1.3.3, 17.2 and 23.8 which evolutionary meaning is behind the currently used terms "hybrid specimens as such", "taxon" and "animal" or it should use other terms. The final result has to be that truly hybridogenous species do apply to Articles 17.2 and 23.8 but not to Article 1.3.3.

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