

The Rubens morph of *Formica exsecta* Nylander, 1846 and its separation from *Formica fennica* Seifert, 2000 (Hymenoptera, Formicidae)

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Abstract

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cryptic species

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A study of numeric morphology-based alpha-taxonomy (NUMOBAT) considering the species *Formica exsecta* Nylander, 1846 and *F. fennica* Seifert, 2000 was performed in 166 nest samples with 485 worker individuals originating from 117 localities of the Palaearctic west of 59°E. The presence of intraspecific pilosity dimorphism is shown for *F. exsecta*. The setae-reduced phenotype, termed the Rubens morph, shows a frequency of about 25%, and the more abundant setae-rich phenotype, termed the Normal morph, one of 75%. The frequency of nests containing workers of both phenotypes is 15.5% in 58 samples from Denmark, Sweden, and Finland. Applying the DIMORPH test of Seifert (2016) on this territory, it is demonstrated that the association of Rubens and Normal phenotypes within the same nest cannot be interpreted as parabiosis of independent species ($p=0.017$) or as temporary ($p=0.0004$) and permanent ($p=0.0001$) socially parasitic association, whereas genetically mediated intraspecific dimorphism is most likely ($p=0.659$, all p data according to Fisher's exact test). The Rubens morph of *F. exsecta* is phenotypically most similar to *F. fennica* but is safely separable by four different forms of exploratory data analyses using nest centroids (NC) as input data: NC-Ward, NC-part, hclust, NC-part.kmeans, and NC-NMDS-k-means. Data on zoogeography and the narrow climate niche indicate that *F. fennica* is unlikely to occur in Norway.

Introduction

The distributional range of *Formica exsecta* Nylander, 1846 covers the Palaearctic from Iberia to Kamchatka, includes the submeridional, temperate and boreal zones in the horizontal scale, and extends from the planar to the subalpine zone in the vertical scale (Seifert 2000, 2018, Seifert and Schultz 2007). Strong pilosity and color variation has led in the past to the description of various other taxa close to *F. exsecta*: *F. exsecta rubens* Forel, 1874, *F. exsecta exsectopressilabris* Forel, 1874, *F. exsecta etrusca* Emery, 1909, *F. dalcqi* Bondroit, 1918, *F. exsecta sudetica* Scholz, 1924, *F. kontunimii* Betrem, 1954, *F. nemoralis* Dlussky, 1964, and *F. mesasiatica* Dlussky, 1965. Whereas the species status of *F. mesasiatica* was recognized by Seifert (2000), albeit with some caution,

he synonymized the seven other taxa with *F. exsecta*. This assessment is in line with the current state of information after my examination of over 1100 samples of the subgenus *Coptoformica* from the whole Palaearctic, and with 800 of these samples being investigated by Numeric Morphology-Based Alpha-Taxonomy (NUMOBAT).

Seifert (2018) stated the presence of a pilosity dimorphism in *F. exsecta*. He distinguished a setae-reduced Rubens morph and a setae-rich Normal morph and reported that the Rubens morph is very similar to *Formica fennica* Seifert, 2000. *Formica fennica* has a narrow habitat spectrum and is known so far from only four sites in southern Finland and two sites in the Caucasus whereas *F. exsecta* shows the widest habitat spectrum, largest total abundance and biggest geographical range of any *Coptoformica* species. In a study from Finland,

using microsatellite data, Hakala et al. (2018) found no genetic differences between two subjectively established morphological clusters. Within their material, they classified 38 samples as *Formica exsecta* and 33 samples as *F. "fennica"*. The failing separation by microsatellite data in the samples of Hakala et al. is easily explained by the fact that >90% of their *F. "fennica"* samples actually belonged to the Rubens morph of *F. exsecta*. Using the DIMORPH test of Seifert (2016), the first aim of this paper is to demonstrate that the Rubens and Normal morph of *F. exsecta* do not represent different species. Using NC-clustering methods (Seifert et al. 2013, Csősz and Fisher 2015), the second aim is to show that the Rubens morph is reliably separable and heterospecific from *F. fennica*. Prompted by the paper of Hakala et al. (2018), I perform here another attempt to convince morphology-based alpha-taxonomists to abandon idiosyncratic approaches and to adopt reproducible numeric character description and evaluation when aiming to investigate the real structure of biodiversity.

Material and methods

To have an improved separation between the *Formica exsecta* morphs and between the Rubens morph of *F. exsecta* from *F. fennica*, the materials of this study were restricted to the Palaearctic west of 59°E, that is, west of the Ural Mountains. NUMOBAT data were recorded in 166 nest samples and 485 worker individuals, the majority of which is deposited in the collection of Senckenberg Museum of Natural History Görlitz. This material listed below in the following sequence and format: site, date in the yyyy.mm.dd format, field sample number "field No" which is found on the mounted specimens [latitude and longitude in decimal format, meters above sea level]. 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 of date, the assumed period is given and the collector is named if known.

Formica exsecta Nylander, 1846

A total of 152 nest samples with 431 workers were investigated.

Austria: Brunau, 2001.09.xx [47.23, 10.85, 700]; Fernpass, 1994.07.04, no. 20 [47.40, 10.90, 1420]; Gilmert, Lafaster-Alm, 1995.10.22 [47.26, 11.76, 1758]; Großglockner, Franz-Josephs-Höhe, 1968.xx.xx [47.075, 12.751, 2369]; Großglockner, Glocknerhaus, 1994.06.20 [47.070, 12.769, 2200]; Gschnitz, Sandertal, 1995.09.24 [47.00, 11.40, 1700]; Gschnitz, Schatthang, 1995.09.24 [47.00, 11.40, 1900]; Gschnitz, Blockfeld, 1995.09.24 [47.00, 11.40, 1900]; Kitzbühel, Bischof, 1994.08.22 [47.405, 12.512, 2000]; Kleiner Gamsstein, 1995.10.22 [47.733, 14.467, 1100]; National Park Kalkalpen, 2011.08.05 [47.750, 14.438, 990]; Pottenbrunn-3 km SSW, 1994.05.12, no. 043 [48.215, 15.718, 330]; Roßan,

1994.07.07, no. g23 [47.45, 11.78, 2000]; Seetaler Alp, Zirbitzkogel, 1971.09.04 [47.06, 14.55, 2000]; Spitz-15 km W, Jauerling, 1990.07.05 [48.353, 15.332, 700]; Vikartal, 1995.10.08 [47.20, 11.45, 1500]. **Bulgaria:** Rhodopes: "Betova" [site not identifiable], 1985.07.03 [42?, 24.5?, 1300]; Rhodopes: Pamporovo, 1975.07.20 [41.61, 24.67, 1400]; Rila: Borovec, 1977.08.01 [42.26, 23.61, 1300]; Rila: Borovec, 1988.06.16 [42.26, 23.61, 1900]. **Denmark:** Jutland, Rye, 1986.08.xx [56.08, 9.73, 77]. **Finland:** Broända, 1996.07.07, no. 27, no. 130 [60.11, 24.27, 30]; Jyväskylä, Kypärämäki, 1998.06.01 [62.24, 25.70, 140]; Järäjävi-S, 2002.07.23 no. 039 [69.641, 29.046, 102]; Järäjävi-S, 2002.07.23 no. 040 [69.641, 29.045, 101]; Järäjävi-S, 2002.07.23 no. 041 [69.642, 29.045, 101]; Järäjävi-S, 2002.07.23 no. 042, no. 044 [69.642, 29.046, 100]; Kiannanniemi, 2002.07.19, no. 018 [65.165, 29.105, 207]; Kiiminki-26 km ENE, 1996.07.15, no. 146 [65.208, 26.325, 120]; Käylä-2 km NE, 1996.07.17, no. 147 [66.320, 29.170, 250]; Käylä-3 km E, no. 113, no. 159 [66.310, 29.203, 250]; Köyliö, 1999.06.25 [61.117, 22.300, 70]; Puhos-6.5 km WNW, 1996.07.13, no. 114 [62.107, 29.793, 97]; Renko-13 km WSW, 1996.07.11, no. 19 [60.836, 24.067, 136]; Sodankylä-26 km NNE, 1996.07.18, no. 55 [67.64, 26.74, 205]; Sodankylä-33 km N, 2002.07.21, no. 029, no. 031 [67.707, 26.749, 208]; Tammela-9 km ENE, 1996.07.11 [60.83, 23.93, 120]; Tronsbøle-0.2 km NE, Oby, 2015.05.07, no. A, no. B [59.940, 23.198, 20]; Utajärvi-2 km NE, no. 120 [64.728, 24.426, 80]. **France:** Mt. Canigou, pre 1918, type *F. dalcqi* [42.51, 2.45, 2000]; Mt. Canigou, pre 1930 (leg. Weiss) [42.51, 2.45, 2200]; Refuge des Besines, 1998.09.17, no. 016 [42.604, 1.868, 2100]. **Germany:** Althütten-dorf, 1985.05.07 [52.96, 13.80, 71]; Canthnitz-0.7 km E, 1997.08.23, no. 220 [53.376, 13.394, 103]; Dabelow, 1982.06.01 [53.248, 13.198, 64]; Dallgow-S, 1996.08.03 [52.52, 13.06, 41]; Eberswalde, 1987.06.12 [52.83, 13.79, 31]; Eberswalde-2.4 km E, 1997.08.21 [52.82, 13.85, 66]; Eberswalde-5 km N, 1995.07.10 [52.89, 13.88, 38]; Eberswalde-Buchholz, 1985.05.07 [52.88, 13.76, 70]; Eberswalde-Finow, 1987.04.12 [52.84, 13.73, 35]; Federsee: Wildes Ried, 1990.09.xx [48.045, 9.648, 583]; Federsee: Wildes Ried, 1991.05.xx [48.045, 9.648, 583]; Geesow, 1987.08.03 [53.239, 14.388, 25]; Meseberg, 1982.08.30 [52.95, 13.10, 50]; Müritzhof, 1988.07.27 [53.45, 12.74, 70]; Carwitz, NSG Hauptmannsberg, 2000.04.22, no. 014, no. 016, no. 017, no. 019, no. 024 [53.31, 13.455, 115]; Neulöwenberg 1982.06.xx [52.90, 13.19, 67]; Oberhershof-2 km ENE, 1991.09.04 [50.180, 6.542, 580]; Ödenwaldstetten, 1991.05.19, no. 19 [48.35, 9.39, 750]. **Italy:** Abetone, pre. 1920 [44.143, 10.666, 1400]; Abetone, Seletta, 1960.07.15 [44.132, 10.644, 1700]; Apennino Modenese: Le Pozze, 1941.07.26, [44, 11, 1000, guess]; Bosco di Corniglio, 1985.08. xx [44.44, 10.04, 880]; Corvara: Colfosco, 1993.08.22 [45.56, 11.86, 1900]; Monte Cimone, Lago Ninfä, 1959. xx.xx, no. 55–57 [44.21, 10.72, 1500]; Praccia, 1890.07. xx, type *F. etrusca* [44.061, 10.911, 750]; Pejo-6 km N, Stelvio NP, 2004.06.16, no. 18 [46.411, 10.688, 2400];

Toscanian Alps: Giulia (leg. Wolf) pre 1945 [44,10,1000, guess]. **Netherlands:** Bergen, 1994.09.13 [52.670, 4.677, 11]. **Norway:** Alta-9.5 km S, 2015.07.10, no. 1, no. 2 [69.911, 23.081, 90]; Gjoktbukmyra, 2016.07.11, no. 4 [69.147, 29.207, 64]; Hedmark: Dalholen, 1993.06.28 [62.191, 9.746, 820]; Klingenberg, 2015.08.20, no. 6 [61.017, 11.855, 493]; Klingenberg-E, 2012.07.13, no. 93 [61.001, 12.060, 460]; Klingenberg-Ulva, 2012.07.13, no. 92 [61.001, 12.059, 462]; Osen: Drageid: Seter-4.8 km E, 2012.04.29 [64.392, 10.589, 45]; Osen: Drageid, 2015.08.24, no. 1–3 [64.392, 10.589, 55]; Osen: Drageid, 2016.08.23, no. 3 [64.391, 10.590, 59]; Oyermoen, 2012.06.27, no. 71 [60.248, 12.442, 300]; Tysil: Torberget, 2015.08.21, no. 4, no. 5 [61.105, 12.019, 528]; Tysil: Torberget, 2016.07.23, no. 1, no. 2 [61.105, 12.019, 528]. **Russia:** Kormovische, 2001.xx.xx, no. U79 [56.83, 57.95, 250]; Svenigorod, 1985.08.xx, no. 623 [55.70, 36.72, 150]; Voronesh Zapovednik, 1962.08.29, no. 221, type *F. nemoralis* [51.809, 39.446, 130]. **Slovenia:** Loibl Pass-5 km S, 1994.07.11, no. g10, no. 12 [46.404, 14.277, 700]. **Spain:** Camprodon-10 km NW, 1994.07.13 [42.401, 2.304, 1600]; Sierra de Guadarrama, 2009.10.16 [40.823, -3.960, 1824]. **Sweden:** Aaland, 1998.xx.xx, no. S60 [60.23, 19.95, 20]; Abisko, 1951.07.xx [68.50, 18.66, 500]; Andrarum, 1992.06.09, no. g4, no. g17 [55.708, 13.966, 115]; Ange-WSW, 2002.08.03, no. 029–032 [62.422, 15.000, 269]; Arvidsjaur-Aljeplog, 2002.07.29, no. 013, no. 014 [65.926, 18.311, 464]; Attonträsk-4 km SW, 1996.07.29, no. 109, no. 125 [64.401, 18.004, 471]; Attoträsk-6 km NE, 1996.07.28, no. 49, no. 76, no. 137, no. 141 [64.461, 18.153, 430]; Degeberga- 6 km SSW, 1992.06.09, no. g89 [55.784, 14.045, 125]; Falkenberg, 2000.xx.xx [56.92, 12.49, 32]; Kalix, 2000.xx.xx, no. S96, no. S100, no. S101 [65.84, 23.10, 7]; Orsa-45 km N, 2002.08.04, no. 036, no. 037 [61.407, 14.819, 480]; Orsa-45 km N, 2002.08.04, no. 039 [61.409, 14.821, 476]; Storuman, 2002.07.31, no. 018 [64.924, 17.034, 422]; Storuman, 2002.07.31, no. 019 [64.923, 17.033, 423]; Sweg, 2002.08.04, no. 034 [62.140, 13.984, 378]; Upland: Hallnäs, 1998.xx.xx, no. S75 [60.53, 17.87, 10]; Öland: Böda, 1992.06.14 [57.250, 17.06, 9]; Öland: Borgholm Slott, 2000.10.08, no. 008–010 [56.870, 16.640, 60]; Östernoret-3 km SW, 1996.07.29, no. 71, no. 126 [64.071, 17.290, 320]. **Switzerland:** Alp La Schera, 1998.07.26, no. 51 [47.648, 10.194, 2080]; Valle Fermanur: Apples, pre 1874, type *F. rubens* [46.550, 6.433, 622]; La Punt-3.7 km NW, no. 58, no. 106 [46.588, 9.900, 2150]; S-Scharl-0.5 km S, 1998.07.27, no. 184 [46.713, 10.336, 1900]; S-Scharl-0.8 km S, 1998.07.27, no. 243 [46.710, 10.334, 2100]; S-Scharl-0.9 km S, 1998.07.27, no. 182 [46.709, 10.333, 2215]; S-Scharl-2.6 km SSE, 1998.07.27, no. 146 [46.697, 10.350, 2140]; S-Scharl-2.6 km SSE, 1998.07.27, no. 247 [46.697, 10.347, 2175]; Stabelchod, 1998.07.28, no. 81 [46.661, 10.241, 1940]; Stabelchod, 1998.07.28, no. 174 [46.665, 10.243, 1990]; Stabelchod- 1 km W, 1998.07.28, no. 172 [46.662, 10.224, 1880]; Ticino: Piora, 1981.07.22 [46.544, 8.686, 1930]. **Turkey:** Gerede, 1976.02.27 [40.810, 32.192, 1600].

Formica fennica Seifert, 2000

A total of 14 nest samples with 54 workers were investigated.

Azerbaijan: Ilisu, 2006.06.03, no. 24 [41.457, 47.063, 1706]. **Finland:** Iisalmi Kotikylä, 1998.07 [63.450, 27.167, 100]; Iisalmi Kotikylä, 2009.07.24 [63.450, 27.167, 100]; Ilomantsi, Maukkula, pre 1996 (leg. Saaristo) [62.62, 30.84, 170]; Luhanpää-1.42 km NE, 1999.07.07, no. 273 [61.058, 25.050, 130]; Luhanpää-1.42 km NE, 2001.07.22, no. 1, no. 2 [61.058, 25.050, 130]; Puhos-6.5 km WNW, 1996.07.13, no. 86, no. 105, no. 119 (type *F. fennica*) [62.108, 29.800, 100]; Puhos-6.5 km WNW, 2002.07.19, no. 013–015 [62.108, 29.800, 100]. **Georgia:** Schenako, 1985.08.01 [42.732, 45.662, 1600].

Stereomicroscopic equipment and measurement procedures were as given in Seifert (2019).

NUMOBAT data were recorded in the primary characters CS, CL, CW, ClySet, ClyPub, EyeHL, F2L, F3L, nCox, nHTfl, nMet, nOce, OceD, SL, sqPDG, sqPDO, TERG, and T3f; the recording rules are explained in Seifert (2018: 399–407). It is repeated and emphasized here that the performance of species delimitation in *Coptoformica* is strongly dependent from identification of basal remains of broken-off setae by high-resolution microscopy. The standardized characters were used in the analyses as variable of absolute body size (CS), as shape variables (CL/CW, SL/CS, OceD/CS, F2L/CS, F3L/CS, F2L/F3L), as variables describing seta conditions (ClySet, ClyPub, EyeHL, nCox, nHTfl, nMet, nOce, OceD, TERG, T3f) and as variables describing pubescence conditions (ClyPub, sqPDG, sqPDO).

Hypotheses on phenotype dimorphism within the *F. exsecta* sample were formed by a Two-Step Cluster Analysis (TSCA). The TSCA was run with automatic determination of the number of clusters using the SPSS 15.0 software package. The first step of analysis is construction of a Cluster Features (CF) tree which provides a capsule summary of the data file. The second step is grouping the leaf nodes of the CF tree using an agglomerative clustering algorithm which produces a range of solutions which are then compared using Schwarz's Bayesian Criterion to determine the "best" number of clusters. The hypothesis provided by the TSCA was checked and corrected by a single run of a linear discriminant analysis (LDA). LDA, Principal Component analysis (PCA), ANOVA and χ^2 tests were run with the SPSS 15.0 software package. The DIMORPH test was performed according to Seifert (2016).

Nest samples of *F. exsecta* containing only worker individuals of the setae-reduced Rubens morph are under increased risk of being confused with *F. fennica*. In order to demonstrate a clear species separation, these samples were run together with those of *F. fennica* in different forms of expository data analyses using nest centroids as input data (NC clustering; Seifert et al. 2013). These were firstly hierarchical NC-Ward clustering, secondly and thirdly the hierarchical method NC-part.hclust and the iterative

vector-quantization method NC-part.kmeans (the latter two methods are implemented in partitioning algorithms based on recursive thresholding, Csősz and Fisher 2015), and nonmetric multidimensional scaling combined with iterative vector-quantization NC-NMDS-k-means (Seifert et al. 2013). Checking samples with controversial classifications was done by an interaction of NC clustering and a controlling linear discriminant analysis (LDA) in which these samples were run as wild-cards following the rationale described in Seifert et al. (2013). The final classification (“final species hypothesis”) was established by the LDA in an iterative procedure and there remained no undecided cases even if their posterior probabilities were close to 0.5.

Standard air temperature (TAS) in °C of sampling sites 2 m above ground can be used as a rough approximation of the thermal niche component (Steiner et al. 2010, Seifert et al. 2014). Following Seifert and Pannier (2007), TAS was calculated as mean air temperature from 1 May to 31 August of the nearest three meteorological

stations of the years 1961 to 1990 provided by Klimaabteilung der Zentralanstalt für Meteorologie und Geodynamik (1996). Values were corrected for an altitudinal temperature decrease of 0.661 °C per 100 m: $TAS = -0.694 * LAT + 0.078 * LON - 0.00661 * ALT + 52.20$.

Results and discussion

Existence of pilosity and pubescence dimorphism in *Formica exsecta*

The analysis of phenotype variance was restricted to the characters CS, CL/CW, SL/CS, ClySet, ClyPub, nOce, Oced/CS, EyeHL, sqPDO, sqPDG, TERG, nCox, nHTFL, and nMet because the full set of characters was not available for all Western Palaearctic samples. Yet, three of the four excluded characters (F2L/CS, F3L/CS, and F2L/F3L) did not contribute to morph separation (Table 1). Within 431 worker individuals investigated,

Table 1. Morphometrics of worker individuals of *Formica fennica* and the two pilosity morphs of *F. exsecta*. Data are given as arithmetic mean $\pm$ standard deviation [lower extreme, upper extreme]; n = number of individuals. The columns with data of an univariate ANOVA test (F values, significance levels p , and degrees of freedom $df/2$) are placed between the columns of the compared entities. F values of most discriminative characters are given in heavy type.

	<i>F. exsecta</i> Normal morph ($n=288$)	ANOVA $F, p, df/2$	<i>F. exsecta</i> Rubens morph ($n=143$)	ANOVA $F, p, df/2$	<i>F. fennica</i> ($n=54$)
CS [μ m]	1390 $\pm$ 81 [1143,1586]	1.66, 0.198 429	1397 $\pm$ 83 [1145,1608]	65.03 , 0.000 195	1287 $\pm$ 93 [1050,1468]
CL/CW	1.045 $\pm$ 0.023 [0.983,1.119]	15.50, 0.000 429	1.054 $\pm$ 0.020 [1.009,1.105]	18.52, 0.000 195	1.068 $\pm$ 0.021 [1.019,1.118]
SL/CS	1.028 $\pm$ 0.022 [0.966,1.085]	9.91, 0.002 429	1.020 $\pm$ 0.023 [0.965,1.071]	0.09, 0.762 195	1.022 $\pm$ 0.026 [0.962,1.084]
EyeHL	27.2 $\pm$ 6.9 [0.0,60.3]	0.89, 0.347 429	26.5 $\pm$ 8.0 [16.1,44.8]	5.17, 0.024 195	23.9 $\pm$ 2.3 [20.7,27.0]
TERG	1.03 $\pm$ 0.16 [1.0,2.0]	227.18 , 0.000 429	1.92 $\pm$ 0.98 [1.00,4.00]	117.02 , 0.000 195	3.48 $\pm$ 0.64 [3.0,6.0]
nCOX	9.63 $\pm$ 2.99 [2.5,18.5]	399.87 , 0.000 429	4.00 $\pm$ 2.26 [0.5,13.0]	97.07 , 0.000 195	0.89 $\pm$ 0.88 [0.0,3.0]
nHTFL	9.45 $\pm$ 1.89 [5.1,15.5]	69.28, 0.000 429	7.93 $\pm$ 1.65 [3.8,13.1]	6.69, 0.010 195	7.22 $\pm$ 1.93 [4.2,13.9]
nMET	2.26 $\pm$ 2.15 [0.0,10.0]	100.89 , 0.000 429	0.37 $\pm$ 0.75 [0.0,3.7]	13.09, 0.000 195	0.00 $\pm$ 0.00 [0.0,0]
sqPDO	5.38 $\pm$ 0.98 [3.21,8.91]	79.53 , 0.000 429	6.43 $\pm$ 1.44 [3.74,13.40]	2.51, 0.115 195	6.77 $\pm$ 1.04 [4.52,9.92]
sqPDG	6.87 $\pm$ 1.20 [3.93,9.84]	12.64, 0.000 429	7.31 $\pm$ 1.36 [4.33,10.73]	2.35, 0.127 195	7.61 $\pm$ 0.56 [6.58,8.71]
ClySet	4.09 $\pm$ 0.56 [2.0,5.0]	1206.1 , 0.000 429	2.17 $\pm$ 0.48 [1.0,3.0]	32.46, 0.000 195	1.72 $\pm$ 0.53 [1.0,3.0]
ClyPub	3.13 $\pm$ 1.04 [0.8,6.5]	0.70, 0.404 429	3.01 $\pm$ 1.25 [0.5,6.5]	26.23, 0.000 195	2.07 $\pm$ 0.82 [0.5,4.3]
nOce	2.16 $\pm$ 0.56 [0.7,6.0]	95.59 , 0.000 429	1.57 $\pm$ 0.65 [0.0,4.0]	195.10 , 0.000 195	0.24 $\pm$ 0.42 [0.0,1.7]
OCED /CS	0.188 $\pm$ 0.010 [0.155,0.210]	0.00, 0.97 429	0.188 $\pm$ 0.011 [0.161,0.217]	20.27, 0.000 195	0.180 $\pm$ 0.010 [0.156,0.198]
T3f	0.97 $\pm$ 0.15 [0.00,1.00]	34.46, 0.000 301	0.77 $\pm$ 0.41 [0.00,1.00]	144.19 , 0.000 182	0.06 $\pm$ 0.22 [0.00,1.00]
FL2/FL3	0.987 $\pm$ 0.040 [0.896,1.077]	3.03, 0.084 142	0.979 $\pm$ 0.040 [0.885,1.085]	20.60, 0.000 144	1.004 $\pm$ 0.033 [0.938,1.094]
FL2/CS	13.57 $\pm$ 0.59 [12.43,14.77]	4.57, 0.034 142	13.37 $\pm$ 0.53 [12.08,14.63]	0.30, 0.586 144	13.31 $\pm$ 0.68 [11.98,15.21]

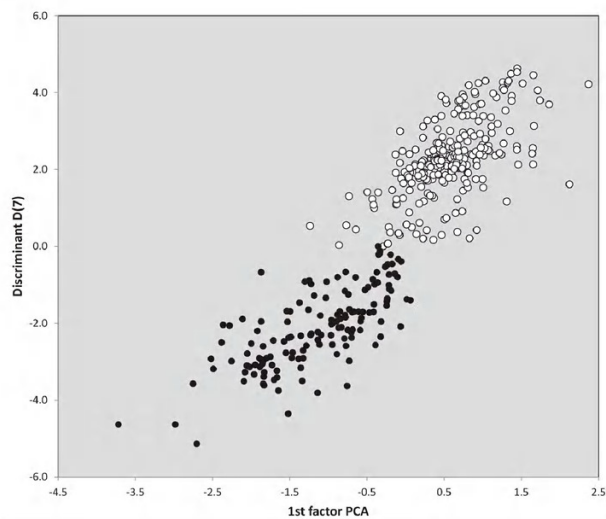


Figure 1. Discriminant value D(7) and 1st factor of a principal component analysis. Data of 288 workers of the Normal morph (white dots) and 143 workers of the Rubens morph (black dots) of *Formica exsecta*.

the Two-Step Cluster Analysis (TSCA) distinguished only two clusters: the Normal morph and the Rubens morph. The final morph hypothesis was established by a single run of an LDA which confirmed 96.3% of the TSCA classifications. Based on this hypothesis, a stepwise character-reduced LDA was run which extracted a discriminant function of seven characters with

$$D(7) = 5.098 \cdot SL/CS + 1.609 \cdot ClySet - 0.044 \cdot EyeHL - 0.191 \cdot sqPDO - 0.45 \cdot TERG + 0.100 \cdot nCox + 0.064 \cdot nMet - 7.9705.$$

Individuals with $D(7) < 0$ were classified as Rubens morph and those with larger values as Normal morph. This discriminant classified 94.9% of the 431 specimens with posterior probabilities > 0.90 (the recognition threshold used in the DIMORPH test, see below). Figure 1 presents a bivariate plot of D(7) and the first factor of a PCA considering these seven characters. Table 1 shows that the morphs are strongest separated by clypeal setae conditions (ClySet). The composition of the type samples is given in Table 2. Only Rubens morph workers were observed within the type series of *F. rubens* Forel, 1874 and *F. etrusca* Emery, 1909. Eight workers of the type series of *F. nemoralis* Dlussky, 1964 belonged to Rubens but one worker to Normal whereas all three investigated type specimens of *F. dalcqi* Bondroit, 1918 belonged to Normal.

Evidence for conspecificity of the Normal and Rubens morph

Within 152 nest samples from the Palaearctic west of 59°E, 104 samples contained only the Normal morph, 28 only the Rubens morph and 20 a mixture of both the Normal and Rubens morph. This figure of 13.2% of mixed nests already indicates heterospecificity to be most unlike-

Table 2. Morph composition in type series of taxa synonymized with *Formica exsecta* Nylander, 1846. D(7) is the discriminant value considering seven phenotypic characters, p(Norm) and p(Rube) are the posterior probability for the Normal and Rubens morph. Data indicating the Normal morph are shaded in grey.

Taxon; site; specimen no.	D(7)	p(Norm)	p(Rube)
<i>F. exsecta rubens</i> Forel, 1874; Apples; no. 1	-1.692	0.0004	0.9996
<i>F. exsecta rubens</i> Forel, 1874; Apples; no. 2	-2.582	0.0000	1.0000
<i>F. exsecta rubens</i> Forel, 1874; Apples; no. 3	-0.665	0.0364	0.9636
<i>F. exsecta rubens</i> Forel, 1874; Apples; no. 4	-2.769	0.0000	1.0000
<i>F. exsecta etrusca</i> Emery, 1909; Praccia; no. 1	-2.396	0.0000	1.0000
<i>F. exsecta etrusca</i> Emery, 1909; Praccia; no. 2	-2.107	0.0001	0.9999
<i>F. exsecta etrusca</i> Emery, 1909; Praccia; no. 3	-1.862	0.0002	0.9998
<i>F. exsecta etrusca</i> Emery, 1909; Praccia; no. 4	-1.945	0.0001	0.9999
<i>F. exsecta etrusca</i> Emery, 1909; Praccia; no. 5	-0.3925	0.1114	0.8886
<i>F. dalcqi</i> Bondroit, 1918; Mount Canigou; no. 1	2.256	0.9999	0.0001
<i>F. dalcqi</i> Bondroit, 1918; Mount Canigou; no. 2	0.568	0.8954	0.1046
<i>F. dalcqi</i> Bondroit, 1918; Mount Canigou; no. 3	3.414	1.0000	0.0000
<i>F. nemoralis</i> Dlussky, 1964; Voronesh Zapovednik; no. 1	-3.134	0.0000	1.0000
<i>F. nemoralis</i> Dlussky, 1964; Voronesh Zapovednik; no. 2	-2.601	0.0000	1.0000
<i>F. nemoralis</i> Dlussky, 1964; Voronesh Zapovednik; no. 3	-2.939	0.0000	1.0000
<i>F. nemoralis</i> Dlussky, 1964; Voronesh Zapovednik; no. 4	-2.874	0.0000	1.0000
<i>F. nemoralis</i> Dlussky, 1964; Voronesh Zapovednik; no. 5	-2.554	0.0000	1.0000
<i>F. nemoralis</i> Dlussky, 1964; Voronesh Zapovednik; no. 6	-1.684	0.0004	0.9996
<i>F. nemoralis</i> Dlussky, 1964; Voronesh Zapovednik; no. 7	1.082	0.9880	0.0120
<i>F. nemoralis</i> Dlussky, 1964; Voronesh Zapovednik; no. 8	-3.087	0.0000	1.0000
<i>F. nemoralis</i> Dlussky, 1964; Voronesh Zapovednik; no. 9	-2.023	0.0001	0.9999

ly. Yet, checking the alternatives intraspecific dimorphism versus heterospecificity by the DIMORPH test is problematic considering the huge geographic area and heterogeneous sampling philosophies of different collectors. Among the conditions allowing to run the DIMORPH test are panmictic behaviour and random sampling, i.e., no preference to collect certain phenotypes (Seifert 2016). Both conditions are not really fulfilled in the whole data set. As a matter of fact, *F. exsecta* samples with reduced setae conditions (suspicious during field sampling or during laboratory sorting to possibly represent *F. bruni* Kutter, 1967, *F. fennica*, or *F. suecica* Adlerz, 1902) were more frequently collected (and analyzed) than the much more frequent hairy samples. This distorts the estimates of allele frequencies in favour of the Rubens morph.

The only coherent geographic area with random, unbiased sampling and evaluation of *F. exsecta* samples in-

cluded Finland, Sweden, and northern Denmark, largely based on the collecting activity of the Senckenberg Museum of Natural History Görlitz. Selecting this area makes also sense because the geographic reference is then well comparable with that in the study of Hakala et al. (2018).
The DIMORPH test was run for this area with the following basic data and parameters. Among 58 nest samples, 42 samples contained only the Normal morph, seven samples only the Rubens morph, and nine samples a mixture of both morphs. These data are based on a recognition threshold of $p>0.90$ in the LDA considering seven characters. Of

the 157 individuals in the data set, 74.5% belonged to the Normal morph and 25.5% to the Rubens morph. Supposing a dominant-recessive inheritance and the Hardy-Weinberg model of population genetics, this would result in a frequency of the recessive ‘allele’ of 0.505 if Rubens is recessive and of 0.863 if Normal is recessive. Using these parameters, the DIMORPH test was run for both assumptions with 500 repeats each and the data were averaged. The clear results are presented in Table 3. Applying Fisher’s exact test, observed and predicted morph distributions differed with $p=0.017$ for the scenario of parabiosis

Table 3. DIMORPH test comparing 58 observed within-nest phenotype compositions with four prediction models. Agreement of observation and predictions was tested by Fisher’s exact test (p) and the Chi-squared test (χ^2 , p).

within-nest phenotype composition	observed	prediction heterospecificity			prediction intraspecific dimorphism
		parabiosis	temporary social parasitism	permanent social parasitism	
only Rubens	7	8.20	2.08	0.00	8.41
Rubens + Normal	9	0.58	0.09	1.16	12.20
only Normal	42	49.22	55.84	56.84	37.39
Fisher’s p		0.017	0.0004	0.0001	0.659
χ^2 , p		8.07, 0.018	13.4, 0.001	15.28, 0.0001	0.88, 0.547

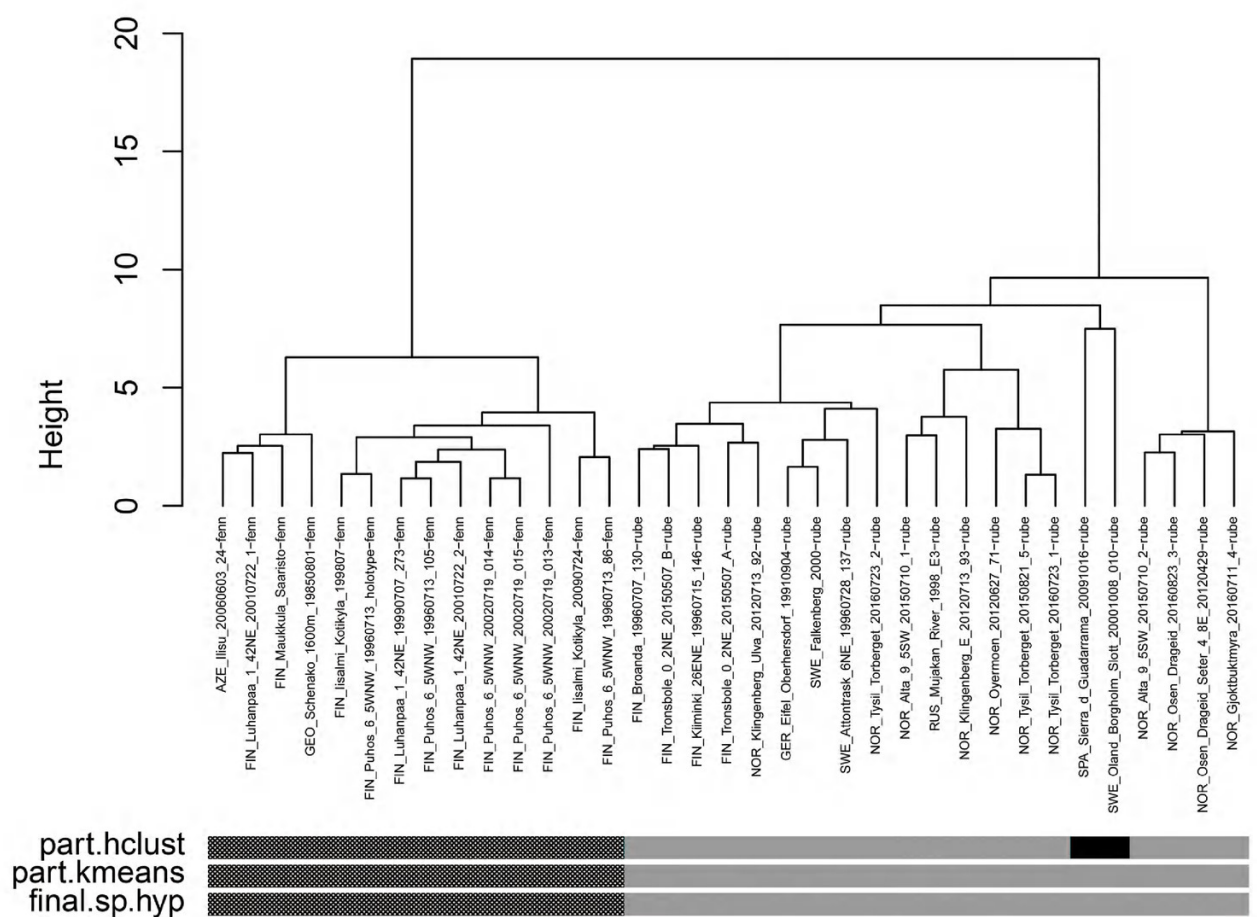


Figure 2. Three exploratory and a hypothesis-driven data analysis using nest centroids (NC) as input data. Evaluated were 21 nest samples of *Formica exsecta* containing only Rubens morph workers (grey bars right) and 14 nest samples of *F. fennica* (textured grey bars left). The classifications of NC-Ward and NC-part.kmeans coincide completely whereas NC-part.hclust is also in general agreement but exposes two outlier samples (black bar).

of independent species, with $p=0.0004$ for the scenario of temporary social parasitism and with $p=0.0001$ for the scenario of permanent social parasitism. In contrast, no significant difference was found between the observed distribution and the prediction for intraspecific dimorphism (Fisher's test $p=0.659$, χ^2 test $p=0.547$).

The separation of the Rubens morph from *Formica fennica*

Nest samples of *Formica exsecta* containing only worker individuals of the Rubens morph are at increased risk of being confused with *F. fennica*. Only these critical samples, but this time originating from the whole of the Western Palaearctic and having T3f data available, were included in the following analyses. These were 21 nest samples of the Rubens morph with 82 workers and 14 samples of *F. fennica* with 54 workers.

In first analytic step all 18 NUMOBAT characters were used unselectively as input and for the exploratory data analyses NC-Ward, NC-part.hclust, and NC-NMDS-k-means. After running samples with classifications disagreeing between the different methods as wild cards, NC-Ward clustering and NC-part.hclust both showed a classification error of 0% with the latter exposing two samples as outliers (=5.7%), whereas NC-NMDS-k-means showed an error of 5.7%. NC-part.kmeans was not able to confirm the existence of two clusters for the complete unselected character set.

Accepting the former hypotheses, the character set was reduced by a stepwise LDA to the eight characters CS, CL/CW, ClySet, nOce, sqPDG, nCox, T3f, and F2L/F3L. Under this setting, all four NC-clustering algorithms achieved a classification error of 0% with NC-part.hclust exposing two samples (5.7%) as outliers (Fig. 2). On the individual level, the classification error of the LDA was 2.9% in 136 workers. The sample from Norway, Osen: Drageid: Seter-4.8 km E, 2012.04.29 [64.392N, 10.589E, 45 m] is determined under this setting with a sample mean of $p = 0.9032$ as Rubens morph if the three available specimens are run as wild-cards. A wild-card run considering all 18 characters results in a determination with $p=0.9916$. This should be emphasized as, based on a much weaker data basis available in the year 2012, I had erroneously determined this sample as *F. fennica* (published by Suvák 2013).

Data on zoogeography and climate niche do also not support the presence of *F. fennica* in Norway. Since *F. fennica* apparently does not spread north to the boreal zone and does not elevate to the subalpine zone (Seifert 2018), the high Skandinavian Fjäll should represent a strong distributional barrier for postglacial immigration from the east. The much narrower climate niche of *F. fennica* is explicitly indicated by the mean air temperature TAS of the sites from 1 May to 31 August. TAS is 11.98 ± 3.28 [4.75, 18.44] °C for 111 sites of *F. exsecta* and 13.78 ± 0.90 [12.72, 15.09] °C for the six known sites of *F. fennica*. Immigration to Norway, if at all, appears only possible via Skåne (Sweden) and along the Oslo Fjord.

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