Colonization overseas by long-range aerial drift in a Formicoxenine ant (Hymenoptera, Formicidae)

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Temnothorax crassispinus (Karavajev, 1926) has been found new for Sweden on the island "Hästnacken" in the Stockholm archipelago. It is morphologically extremely similar to its Swedish sibling *T. nylanderi* (Förster, 1850). Three different exploratory data analysis methods achieved a full species separation with perfectly congruent classifications in a total of 135 nest samples from the entire European range. All Swedish samples of both species were clearly classified with posterior probabilities of p>0.998 if run as wild-card in a confirmative linear discriminant analysis. The close association of both species to temperate *Quercus* forest allows to reconstruct time and routes of postglacial immigration of both species from an Italo-Iberian (*T. nylanderi*) and Balkan (*T. crassipinus*) refuge. According to this, *T. nylanderi* entered the Swedish mainland in about 8300 BP (Skåne) and spread north to the Stockholm area until 5000 BP. Simultaneously, the advance of *T. crassipinus* from SE Europe was stopped by *T. nylanderi* along a 900-km long front line running from NW Poland through East Germany south to Bavaria. Based on arguments from zoogeography, dispersal behavior, reproduction biology, meteorology and physiology, long-range aerial drift across the Baltic Sea is by far the most probable way for colonizing Hästnacken by *T. crassipinus*. The counter-hypothesis that nests were introduced with firewood needed for a brickyard run on the island between 1720 and 1830 was rejected by historical reports on wood import to the Stockholm area and the low likelihood of nest microhabitats of getting fixed to imported wood materials.

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The small Formicoxenine ants *Temnothorax nylanderi* (Förster, 1850) and *T. crassispinus* (Karavajev, 1926) are dominant elements of the forest floor fauna of European temperate woodland biomes. *T. nylanderi* is widely distributed throughout deciduous forests in Western Europe, whereas *T. crassispinus* inhabits similar habitats in Eastern Europe (Seifert 2007). The two species have repeatedly stood in the focus of studies after Seifert (1995) presented evidence of their heterospecificity and showed that they form parapatric sibling species having spread from an Ibero-Italian and Balkan Pleistocene refuge respectively. These refuge areas probably have been used with similar topography and migration routes during all glaciations since then. Data of mtDNA (Pusch et al. 2006a) suggest the splitting of both species in separate glacial refuges to have occurred already in Early Pleistocene ± 1.4 Myr BP and very low within-species sequence divergence (0.14% in *T. nylanderi* and 0.29% in *T. crassispinus*) indicates a rapid postglacial spreading. The species are ecologically most similar, vicariant species that have met in Germany along a 900-kilometers-long front line latest during the Atlantic some 7500 years BP (Seifert 1995). This front line currently runs from NE Germany (Anklam) south to Bavaria (München). The depth of interspecific geographic overlap along the front line is not larger than 25 km whereas the east-west extension of both species' range is 3600 km at least. Despite frequent occurrence of F1-hybrid samples *T. crassispinus x nylanderi* within this narrow contact zone (Seifert 1995, Pusch et al. 2006a), the absence of backcrosses saves the genetic integrity of both species (Seifert 2007). Recently, a third cryptic species from SE Europe – *T. crasecundus* Seifert & Csösz, 2015 – has been added to the *T. nylanderi* species complex (Seifert & Csösz 2015).

T. nylanderi is the only species of this complex reported so far from Sweden and was hitherto known to occur here from Skåne north to Östergötland and Dalsland (Douwes 2012). However, our own investigations showed its distribution north to Uppland at least (Näsudden). The population may reach extremely high nest densities of up to ten nests per square meter (e.g. Trollskogen in the north of Öland).

Colonies of *T. nylanderi* and *T. crassispinus* consist of a few dozen workers and a single queen (monogyny) and inhabit any microspace offering adequate microclimate. This is as a rule on soil surface and rarely basally at tree stems up to 30 cm above ground. Most frequent nesting substrates are dead wood, hollow acorns, nuts or galls and bark, occasionally also leaf litter, snail shells or soil under stones down to 4 cm depth (Seifert 2007). However, *T. crassipinus* has been shown recently to nest locally in tree canopies (Seifert et al. 2013).

T. crassispinus has never been reported from Sweden before and was not expected to occur here for strong zoogeographical arguments. Yet, during a visit to an island in Stockholm archipelago, Hästnacken, 19 July 2012, the junior author examined a rotten oak twig lying on the ground. The ants inhabiting the twig seemed, at first glance, to be *T. nylanderi*. However, when compared with other *T. nylanderi* collected on Öland, they differed by much stronger propodeal spines. A few specimens were sent to the senior author who confirmed that these belonged to *T. crassispinus*.

This paper aims to give firm evidence for the occurrence of *T. crassispinus* in Sweden, to improve the knowledge on the northern distribution of *T. nylanderi* and to show that long-range aerial drift across the Baltic Sea is a most probable way for extension of geographical range in these small ants.

Material and Methods

Material investigated

A total of 77 nest samples of *T. crassispinus* with 222 worker individuals has been investigated morphometrically. They originated from Austria (12 samples), Bosnia (2), Bulgaria (2) Czechia (3), Germany (37), Greece (8), Italy (2), Poland (5), Slovenia (2), Sweden (2) and the Ukraine (3). In *T. nylanderi*, 58 nest samples with 151 worker individuals were investigated. These originated from Austria (1 sample), France (3), Germany (39), Italy (10), Poland (1), Sweden (3) and Switzerland (1). Hybrid samples from the contact zone in Germany were excluded from analysis.

Equipment and measuring procedures

Spatial positioning of specimens was performed by a pin-holding stage, permitting full rotations around X, Y, and Z axes and a Leica M165C high-performance stereomicroscope equipped with a 2.0 planapochromatic objective (resolution 1050 lines/mm) was used at magnifications of 120-384x. The mean relative measuring error over all magnifications was 0.3%. 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.

Method of species delimitation

Species delimitation was performed on the basis of 18 primary morphometric characters. 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. Unambiguous character definitions with figures are given in Seifert & Csösz (2015). Here we only mention the characters and describe them with a few words (the four characters needed in the simplified discriminant function are defined thoroughly):

CL – maximum cephalic length in median line.

CS – cephalic size; the arithmetic mean of CL and CW.

CW – maximum cephalic width across (including) eyes.

EYE – the arithmetic mean of the large (EL) and small diameter (EW) of the elliptic compound eye.

FRS – distance of the frontal carinae immediately caudal of the posterior intersection points between frontal carinae and the lamellae dorsal of the torulus.

MGr – depth of metanotal groove.

MH – maximum mesosoma height perpendicular to its longitudinal axis.

ML – mesosoma length.

MW – maximum mesosoma width.

PEH – maximum petiole height perpendicular to its ventral profile.

PEL – diagonal petiolar length in lateral view; measured from anterior corner of subpetiolar process to dorsocaudal corner of caudal cylinder.

PEW – maximum width of petiole.

PoOc – postocular distance.

PPW – maximum width of postpetiole.

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

SP – maximum length of propodeal spines.

SPBA – the smallest distance of the lateral margins of the spines at their base. This should be measured in dorsofrontal view since the wider parts of the ventral propodeum do not interfere with the measurement in this position. If the lateral margins of spines diverge continuously from the tip to the base, a smallest distance at base is not defined. In this case, SPBA is measured at the level of the bottom of the interspinal meniscus.

SPST – distance between the centre of propodeal stigma and spine tip. The stigma centre refers to the midpoint defined by the outer cuticular ring but not to the centre of real stigma opening that may be positioned eccentrically.

SPTI – the distance of spine tips in dorsal view; if spine tips are rounded or truncated, the centers of spine tips are taken as reference points.

Explorative and supervised data analyses and classification methods

Before the data were introduced into the explorative and hypothesis-driven data analyses, removal of allometric variance (RAV) was performed with the procedure described by Seifert (2008). The delimitation of the cryptic species was done by an interaction of Nest-Centroid Clustering (NC clustering) and a confirmative 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/. Additionally, as a third explorative data analysis, a principal component analysis (PCA) was run. PCA and LDA were performed with the software package SPSS 15.0.

Results and Discussion

Identification of the Swedish samples

All three explorative data analyses NC-Ward (Fig. 1), NC-K-Means (not shown) and PCA (Fig. 2) showed 100% congruent classifications. The former two analyses were run with all 18 characters, those of the PCA with the 13 most informative characters. If run as wild-card in a confirmative LDA, all Swedish samples are clearly classified: the samples Hästnacken-2012.07.19 and Hästnacken-2014.07.26-3 are allocated to *T. crassispinus* with posterior probabilities of p=0.9984 and 0.9999 respectively whereas the samples Näsudden-2014.08.10-4, Byrums Sandvik -1992.06.14-73 and Röstanga-

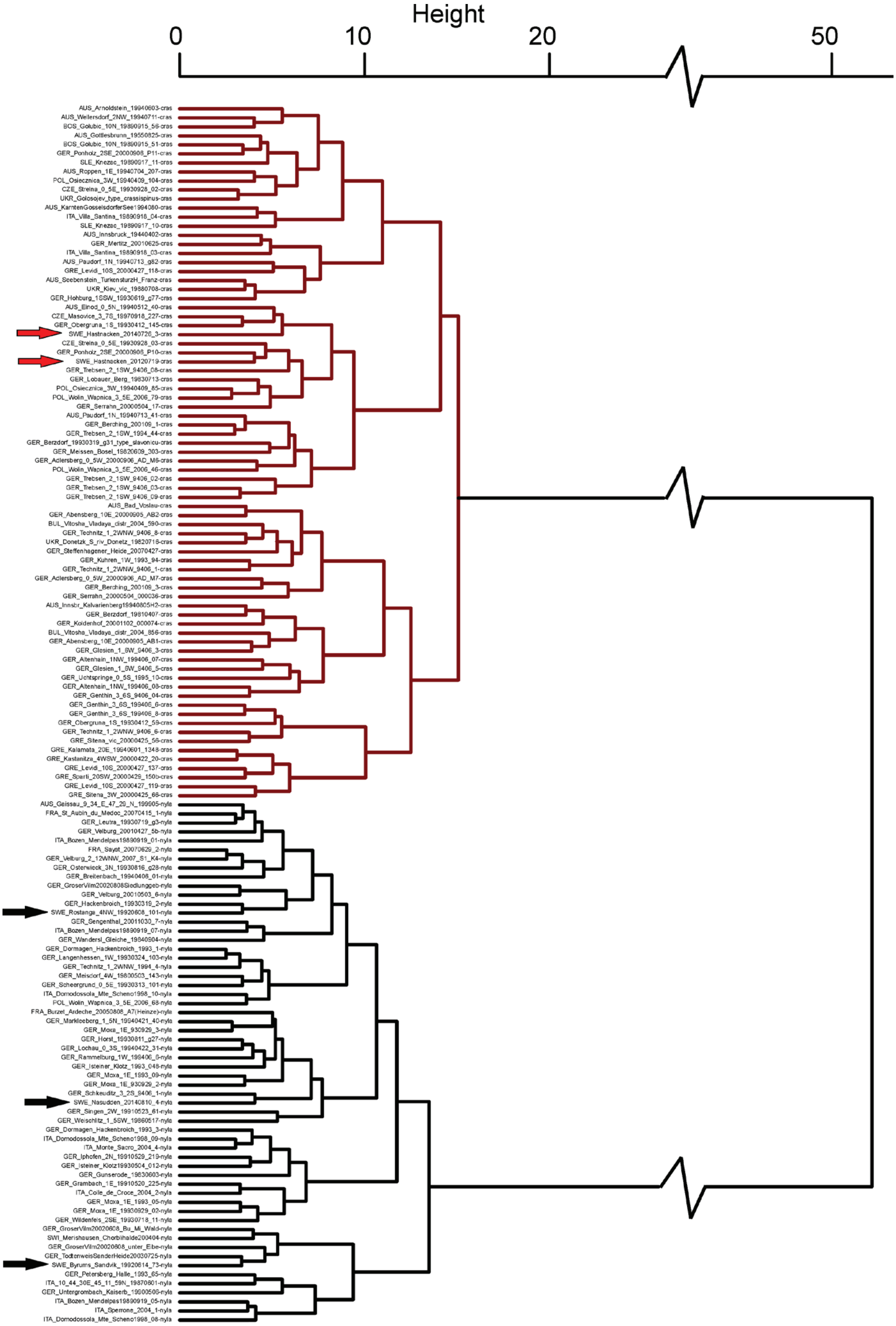

Figure 1. NC-Ward dendrogram showing 58 nest samples *Temnothorax nylanderi* (black) and 77 nest samples of *T. crassispinus* (red) computing the full set of 18 morphometric characters. The arrows show the positions of the investigated samples from Sweden.

NC-Ward dendrogram som visar likheten mellan 58 boprover av *Temnothorax nylanderi* (svart) och 77 boprover av *T. crassispinus* (röd) beräknat på 18 morfometriska egenskaper. Pilarna visar positionerna för proverna från Sverige.

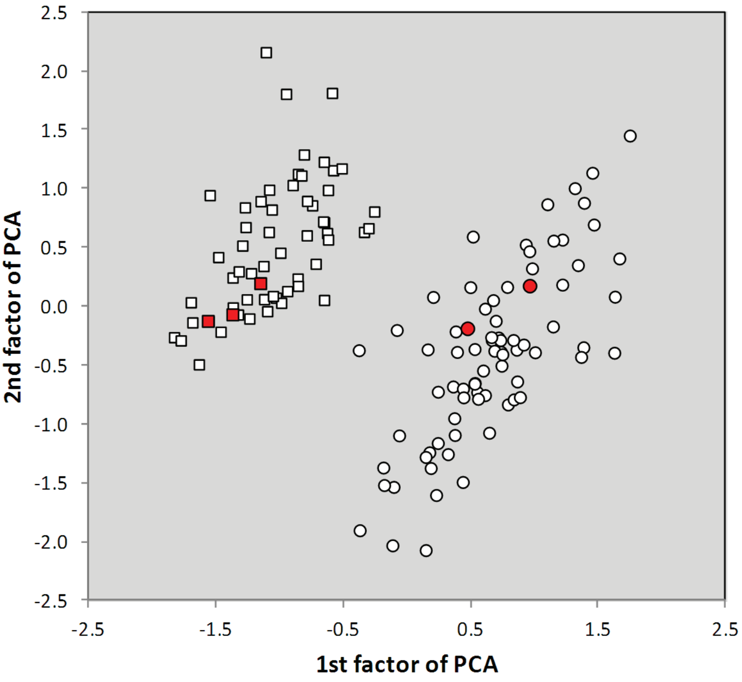

Figure 2. Arithmetic nest sample means of the first two factors of principal component analysis of *Temnothorax nylanderi* (squares, n=58) and of *T. crassispinus* (circles, n=77) considering the 13 most informative morphometric characters. Symbols filled in red show the investigated samples from Sweden.

Principalkomponentanalys av de 13 mest informativa karaktärerna för *Temnothorax nylanderi* (fyrkanter, n = 58) och *T. crassispinus* (cirklar, n = 77). Digrammet visar de två första axlarna från analysen. Varje punkt illustrerar ett boprov och de som ligger nära varandra är lika i morfometriska karaktärer och tvärtom. Symboler fyllda med rött visar de undersökta proverna från Sverige.

4NW-1992.06.08-101 are allocated to *nylanderi* with p=1.0000, 1.0000 and 0.9999 respectively. Over the whole range of both species, the rate of misclassification was 0.5% in 371 worker individuals.

The separation of *T. nylanderi* and *T. crassispinus* is most difficult and identification by simple eye inspection of experienced experts is problematic in a number of cases. There is no shape character without strong interspecific overlap and removal of allometric variance reduced the interspecific overlap only very little in these weakly allometric and equal-sized ants (Table 1).

As it is most difficult for practitioners of ecosystem research to reproduce the very complex species delimitation procedures used above, it may be asked if there is a more simple way of identification showing an acceptable error rate. In a first step, the key presented in Douwes (2012: p. 110-112) and finally leading to "*T. nylanderi*" can be used with good success to separate the *T. nylanderi* complex species from other Swedish congenerics. Then, in distinguishing *T. nylanderi* and *T. crassispinus*, the most diagnostic characters which can be assessed by simple eye inspection are the basal and apical distance and length of propodeal spines which are lower in *T. nylanderi*. The latter also differs from average *T. crassispinus* in having a shallower metanotal depression and no suggestion of a downward curvature of propodeal spines (Fig. 3).

Yet, these characters are variable and it is clearly more reliable to apply a simple morphometric method: the species can be distinguished by a discriminant function of four characters. With all measurements given in mm the discriminant

$$D(4) = -45.749\ CW + 18.938\ SPBA + 44.552\ SPTI + 59.744\ SPST + 4.448$$

resulted in 3.2% misclassifications in 371 individuals and no errors in 135 nest sample means of three workers. Specimens/samples with D(4) < 0 belong to *T. nylanderi* and those with larger values to *T. crassispinus*. Along the interspecific front line in Central Europe, hybrids have to be expected and the performance of the function will be reduced. In 11 nest samples of F1

Table 1. Data of absolute head size (CS) and 17 shape variables of the workers of the cryptic species *Temnothorax nylanderi* (Förster, 1850) and *T. crassispinus* (Karavajev, 1926). Abbreviations of measured structures are explained in Material & Methods. Removal of allometric variance was performed for the assumption of each individual having CS=650 µm. Arrangement of data: arithmetic mean ± standard deviation [minimum, maximum]. F values and significance levels p are from an univariate ANOVA; the F values of the most separating characters are given in bold type.

Mått på huvudstorlek (CS) och 17 olika kvoter mellan mått på kroppen och huvudets storlek för de svårskilda arterna *Temnothorax nylanderi* (Förster, 1850) och *T. crassispinus* (Karavajev, 1926). Förkortingarna till kroppsmåtten finns förklarade i Material och Metoder. "Primary data" är de råa måtten, medan värdena till höger i tabellen tar hänsyn till att olika karaktärer påverkas olika vid varierande kroppsstolek. Måtten anges som medelvärde ± standardavvikelse [max, min]. F värden och signifkansvärden p anges för en univariat ANOVA, med F-värdena för de mest separerande karaktärerna angivna i fet stil.

	Primary data				Data after removal of allometric variance, shapes corrected for CS=650 µm			
	nylanderi	*crassispinus*	ANOVA		*nylanderi*	*crassispinus*	ANOVA	
	(n=151)	(n=222)	F	p	(n=151)	(n=222)	F	p
CS [µm]	652 ± 34 [514,724]	648 ± 37 [526,769]	0.85	n.s.	652 ± 34 [514,724]	648 ± 37 [526,769]	0.85	n.s.
CL/CW	1.053 ± 0.020 [1.001,1.111]	1.051 ± 0.018 [1.003,1.096]	1.39	n.s.	1.053 ± 0.019 [1.002,1.112]	1.051 ± 0.017 [0.999,1.096]	1.88	n.s.
SL/CS	0.750 ± 0.013 [0.720,0.786]	0.762 ± 0.016 [0.707,0.801]	46.64	0.000	0.751 ± 0.012 [0.721,0.785]	0.761 ± 0.016 [0.709,0.799]	47.51	0.000
PoOc/CL	0.396 ± 0.009 [0.374,0.421]	0.390 ± 0.010 [0.357,0.416]	26.98	0.000	0.396 ± 0.009 [0.374,0.421]	0.390 ± 0.010 [0.357,0.416]	26.90	0.000
EYE/CS	0.215 ± 0.007 [0.192,0.229]	0.217 ± 0.007 [0.198,0.238]	12.30	0.001	0.214 ± 0.007 [0.192,0.228]	0.217 ± 0.007 [0.201,0.237]	14.28	0.000
FRS/CS	0.361 ± 0.008 [0.341,0.387]	0.364 ± 0.011 [0.341,0.406]	6.58	0.011	0.361 ± 0.008 [0.341,0.386]	0.364 ± 0.011 [0.341,0.405]	6.27	0.013
SPBA/CS	0.270 ± 0.011 [0.243,0.301]	0.297 ± 0.017 [0.259,0.337]	**310.35**	0.000	0.270 ± 0.011 [0.244,0.296]	0.298 ± 0.015 [0.257,0.332]	**357.52**	0.000
SPTI/CS	0.312 ± 0.016 [0.272,0.365]	0.355 ± 0.018 [0.314,0.402]	**567.99**	0.000	0.312 ± 0.015 [0.274,0.358]	0.355 ± 0.017 [0.318,0.401]	**600.60**	0.000
SPST/CS	0.276 ± 0.016 [0.238,0.310]	0.325 ± 0.017 [0.258,0.372]	**762.87**	0.000	0.276 ± 0.016 [0.238,0.310]	0.325 ± 0.017 [0.256,0.371]	**791.99**	0.000
SP/CS	0.208 ± 0.017 [0.170,0.242]	0.264 ± 0.017 [0.216,0.330]	**994.07**	0.000	0.208 ± 0.016 [0.170,0.250]	0.264 ± 0.016 [0.222,0.304]	**1131.7**	0.000
PEW/CS	0.257 ± 0.010 [0.236,0.293]	0.261 ± 0.011 [0.236,0.294]	13.74	0.000	0.257 ± 0.010 [0.234,0.294]	0.262 ± 0.011 [0.236,0.292]	16.43	0.000
PPW/CS	0.377 ± 0.013 [0.339,0.415]	0.370 ± 0.017 [0.326,0.433]	20.44	0.000	0.377 ± 0.013 [0.339,0.415]	0.370 ± 0.016 [0.331,0.428]	19.45	0.000
PEH/CS	0.369 ± 0.011 [0.346,0.398]	0.366 ± 0.012 [0.336,0.420]	6.65	0.010	0.369 ± 0.010 [0.345,0.397]	0.366 ± 0.012 [0.336,0.420]	6.11	0.014
PEL/CS	0.481 ± 0.016 [0.443,0.524]	0.485 ± 0.017 [0.439,0.530]	3.26	n.s.	0.481 ± 0.014 [0.446,0.515]	0.485 ± 0.016 [0.440,0.521]	7.48	0.007
ML/CS	1.182 ± 0.021 [1.134,1.251]	1.192 ± 0.020 [1.137,1.264]	20.33	0.000	1.182 ± 0.020 [1.134,1.242]	1.192 ± 0.020 [1.149,1.262]	22.98	0.000
MW/CS	0.604 ± 0.012 [0.574,0.632].	0.604 ± 0.015 [0.571,0.642]	0.00	n.s	0.604 ± 0.010 [0.570,0.625]	0.604 ± 0.013 [0.569,0.642]	0.30	n.s.
MH/CS	0.533 ± 0.015 [0.482,0.583]	0.533 ± 0.016 [0.495,0.582]	0.00	n.s.	0.533 ± 0.015 [0.482,0.583]	0.533 ± 0.016 [0.495,0.582]	0.04	n.s.
MPGR[%]/CS	1.51 ± 0.55 [0.00,3.45]	2.14 ± 0.71 [0.53,4.46]	83.40	0.000	1.51 ± 0.54 [0.00,3.36]	2.15 ± 0.68 [0.54,4.44]	92.87	0.000

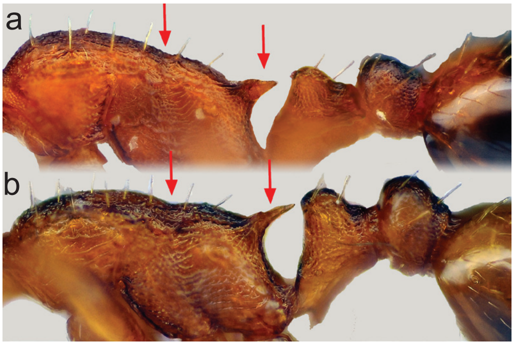

Figure 3. Comparison of mesosomal profile of – a) *Temnothorax nylanderi* and – b) *T. crassispinus* (below). Arrows point to the differences in propodeal spine length and depth of metanotal depression. Photo: A. Hagman.

Jämförelse av mellankroppsprofilen mellan – a) *Temnothorax nylanderi* och – b) *T. crassispinus*. Pilarna visar på skillnaden i ryggtaggarnas längd och fördjupningen mellan mellanrygg och efterrygg. Foto: A. Hagman.

hybrids which were identified by enzyme polymorphism (Pusch et al. 2006a), mean D(4) varied between –0.98 and 2.30 whereas the data of all 146 samples of both species ranged between –3.24 and 3.96.

Description of the collecting sites

The island Hästnacken is located in the middle of Stockholm archipelago, Sweden, Värmdö: WGS84 dec latitude 59.42647°N, longitude 18.66707°E; RT90 6593037/1662419. The collecting site is a sheep pasture on granite bedrock with the main tree species *Pinus sylvestris*, *Quercus* sp. and *Juniperus*. The soil surface is characterized by the presence of numerous acorns and rotten pine or oak twigs which are suitable nest sites (Fig. 4). This habitat is typical for the northern range of the species (Seifert 2007). The first colony was found in a rotten oak twig in 2012 (Fig. 5b). A further colony was found in a hollow acorn (Fig. 5a) during a re-visit of Hästnacken in 2014. Despite repeated search, no additional colonies were found on Hästnacken or on nearby islands (Lådna, Hjälmö and Svartsö).

The northernmost site of *T. nylanderi* known for its entire range was discovered by the junior author on Näsudden, Åkersberga, 10 August 2014, WGS84 dec latitude 59.458655°N, longitude 18.292666°E; RT90 6595767/1641044. This finding shifts the known distributional border in E Sweden by 100 km to the north. The ants were found in an oak twig consisting of a queenless society with 8 workers and as many males. The habitat was similar to that on Hästnacken: a pasture with oaks, pines and junipers.

Routes and timing of postglacial immigration to Sweden

The geographic distribution of *T. nylanderi* is congruent with the natural geographical range of broad-leafed deciduous forest, typically *Quercus-Tilia-Carpinus* forest, but not with the range of woodland biomes dominated by *Picea abies*, *Abies alba* and *Pinus sylvestris*. *T. crassipinus* shows similar affinities to oak but is additionally associated to south-temperate continental *Pinus sylvestris* forest (Seifert 2007). Accordingly, glacial refuge area and postglacial spreading of *T. nylanderi* and *crassispinus* in time and space can be approximated by the data known from *Quercus*. The situation in *Quercus*, as major component of temperate woodland, is well documented by pollen diagrams (Hewitt 1999) indicating major Pleistocene refuges in Iberia, Italy and the Balkans. There is evidence from macrofossils that small refuges of broad-leafed trees have existed in West and Central Europe north of 47°N in climatically buffered local microclimates during the climax of the last glaciation – one of *Quercus* in NE France (Stewart & Lister 2001) and one of *Carpinus betulus* in NE Hungary (Willis et al. 2000). If *Temnothorax nylanderi* complex species should really have survived in these local spots, for which is no proof, this does not contradict the supposed postglacial re-colonization routes of the two species and the following conclusions on the timing of immigration in Sweden and the Stockholm area in particular .

Quercus was present in south Sweden latest 8300 BP (Kullman 1998) and reached the Stockholm area in about 5000 BP (Mattson & Östlund 1992). Basically the same timing of immigration may be assumed for *T. nylanderi* that also invaded via the Denmark-Skåne route. *T. crassispinus* immigrated Central Europe through the Pannonian Basin and along a route

Figure 4. Habitat of *Temnothorax crassispinus* on the island Hästnacken. Sheep pasture with *Juniperus*, *Pinus sylvestris* and *Quercus*. Topsoil with numerous acorns, decaying pine and oak twigs offering suitable nest sites. Photo A. Hagman.

Lokalen där *Temnothorax crassispinus* hittades på ön Hästnacken. En hage betad av får med inslag av gamla träd som tex enar, tallar och ekar. Markskiktet innehåller stort antal ekollon, murkna tall och ekkvistar som är lämpliga boplatser. Foto: A. Hagman.

north of the Carpathians and met *T. nylanderi* in East Germany and Northwest Poland latest 7600 BP (Seifert 1995). The following combination of factors fully excludes that *T. crassispinus* has ever reached Denmark and Sweden in this time, allowing *T. nylanderi* to re-colonize Sweden north to Uppland fully undisturbed by its competing sister species.

Firstly, there is an extreme habitat saturation by *T. nylanderi* in the large territories west of the Polish-German front line which blocked any movement of *T. crassispinus* northwest to Denmark. A mated gyne of *T. crassispinus* drifting more than 10 kilometers across the front line into the *T. nylanderi* territory will experience aggression and strong competition by the resident ants. If successfully founding a colony, this gyne has only minute chances to have her offspring mated with conspecific partners. This is explained by the synchronous nuptial flights of both species and by the *T. nylanderi* alates outnumbering the *T. crassispinus* in the swarm by several orders of magnitude. Crossmated gynes can found a strong colony with many hybrid workers but will produce few and smaller gynes with reduced fertility. These F1-gynes reproduce rarely (Pusch et al. 2006b). This dead-end hybridization trap is responsible for the extremely clear-cut parapatric distribution of both species .

The facts outlined above explain why an establishment of a *T. crassispinus* population in Sweden can only be initiated from the east or southeast by crossing the Baltic Sea. However, an arriving gyne can only found a population when landing in a suitable habitat without a *T. nylanderi* population. This is unlikely on the Swedish mainland but there is a chance to be successful on an offshore island.

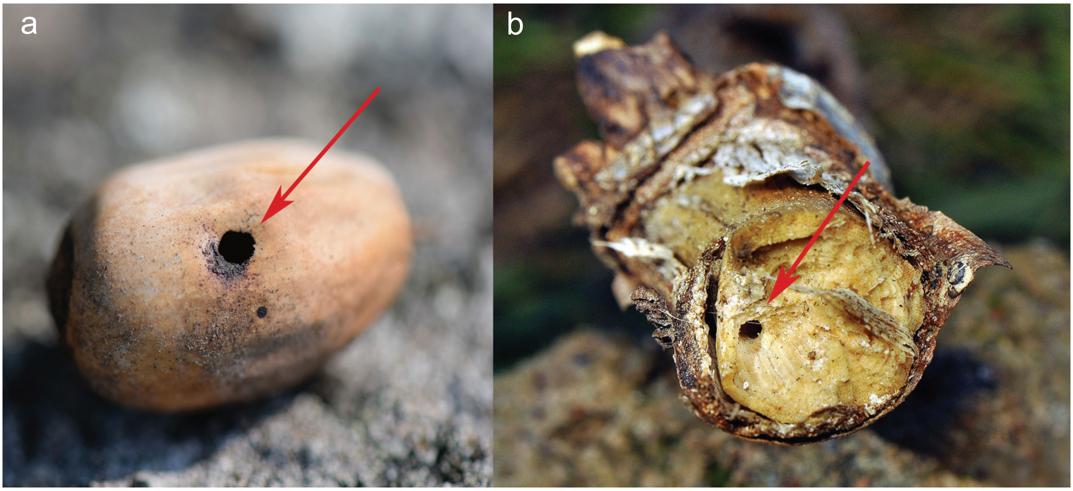

Figure 5. Nest microhabitats of *Temnothorax crassispinus* on the island Hästnacken: – a) in a hollow acorn and – b) in a decaying oak twig. The arrows indicate the narrow entrance hole. Photo A. Hagman.

Boplatsmiljö för *Temnothorax crassispinus* på ön Hästnacken; – a) Ena boet påträffades i ett ekollon och – b) den andra i en murken ekkvist. Pilarna visar de små ingångshålen till bona. Foto: A. Hagman.

T. crassispinus colonized Hästnacken by long-range aerial drift over the Baltic Sea

We first present an explanation for the colonization of Hästnacken by *T. crassispinus* that is in our opinion clearly the most probable one. Our favored hypothesis is based on data on geological history, population biology and meteorology. The glacial isostatic uplift of the Scandinavian Plate after the melting of the thick inland ice caused a dynamic change of the Swedish coastline. Hästnacken is estimated to have appeared from the sea not earlier than 2000 BP (Sund 2010) and a *Pinus-Quercus* woodland should have established here as late as about 1000 BP because the buildup of a soil horizon on the stripped bedrock was certainly slow. The *T. nylanderi* population in the Stockholm mainland area is very weak and local. Despite repeated search by the junior author, only a small population at Näsudden was discovered in this region. This population would not emit a lot of flying mated gynes and there is quite a high probability that a lately emerging island offering suboptimal conditions was not colonized even if situated only a few kilometers off from the mainland. Furthermore, 60% of the winds during weather conditions eliciting nuptial flight come from the south and east (see below) which additionally hampers colonization from the mainland.

The next populations of *T. crassispinus* occur overseas in Latvia some 275 km SE of Hästnacken (Czechowski et al. 2013). If the range should extend north to the Estonian island Saaremaa, which is not confirmed, the distance would reduce to 220 km ESE. The gynes of the *Temnothorax nylanderi* complex are weak active flyers. However, due to their small body size and low wingload, they are best objects for passively ascending with upcurrents and for long-range horizontal air drifting. Swarms of both *T. nylanderi* and *T. crassipinus* occur in the period of 15 July to 15 September during warm high pressure weather situations. Main wind directions in the Stockholm area in this time period and under these meteorological conditions are 27% E, 33% S, 18% W and 22% N (SMHI 2014). Accordingly, there is a fair probability that a few gynes from mass swarming events in Latvia or even NE Poland could arrive in Sweden. Within the spectrum of natural modes of dispersal, passive aerial drifting is in our opinion the only reasonable explanation. This idea is supported by findings in another arthropod group with similar body size and wingload: significant long-range wind-drift overseas into Sweden is documented for aphids (Wiktelius 1984). Furthermore, passive aerial dispersal high in the air has been confirmed for other Hymenoptera with similar body-size-wingload relations (Duelli & al. 1989, Wahlberg & Solbreck 2013). The other mode of natural dispersal, drifting on sea surface, either as gynes or whole nests within woody structures, is extremely unlikely – *Temnothorax* species belong to those ants dying very soon when drenched in water.

Counter-hypothesis: T. crassispinus was introduced to Hästnacken by human commerce

An alternative explanation for the presence of *T. crassipinus* on Hästnacken has to be considered: anthropogenous introduction. A brickyard was run on the island between 1720 and 1830. It burnt approximately 180 cubic meters of firewood per year (Södergren 1982) and the idea that nests possibly attached to imported wood were introduced has to be considered. The wood was usually harvested at that time from areas near to places from which it could be transported with ships. After cutting, the wood was frequently dragged over the forest floor by horses and there is some probability that nest microhabitats of *T. crassipinus* (acorns, nuts and twigs) got fixed in big bark crevices of the stems. Yet, high-quality stems, in particular those of oaks, were highly requested for building ships and other construction purposes. Accordingly, brickyards preferentially should have used thick branches and other cost-efficient material. This selection will have reduced the probability of anthropogenous nest transfer to Hästnacken. More important than the bark-crevice issue is the low probability of wood import to the Stockholm area from the Kingdom of Prussia and Latvia documented for that time. Sweden had lost its South Baltic possessions to Russia and Prussia after the Nordic Wars in 1721 and the trade with these areas stopped for a long time. According to Högberg (1969), the timber imported to the Stockholm area during the period 1738-1808 came from different parts of Sweden (Småland, Bergslagen region, northern Sweden) and from Finland. These are areas definitely without *T. crassipinus* populations. Multiplying two low probabilities, we conclude that anthropogenous nest transfer to Hästnacken from the South Baltic Region is very unlikely.

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Sammanfattning

En ny myra för Sverige, *Temnothorax crassispinus* (Karavajev, 1926), hittades på ön ”Hästnacken” i Stockholm skärgård. *T. crassispinus* är morfologiskt extremt lik sin syskonart *T. nylanderi* (Förster, 1850), som förekommer i södra Sverige. Det finns morfologiska karaktärer som skiljer arterna åt, men eftersom många av dessa varierar starkt hittar man alltid överlapp mellan arterna då enskilda karaktärer jämförs.

Därför jämförde vi kombinationer av 18 olika karaktärer för de två syskonarterna med hjälp av tre olika analysmetoder. Ett referensmaterial av 135 samhällen av de båda arterna från hela Europa användes. Alla tre analysmetoderna kan tydligt dela upp dessa syskonarter i två diskreta grupper. De svenska proverna av arterna kunde dessutom tydligt klassificeras till respektive art (Fig. 1 och 2).

Båda arterna bygger bon i små hålrum som finns tillgängliga (Fig. 5). Båda har en tydlig koppling till tempererade ekskogar, vilket gör att man kan rekonstruera den postglaciala invandringen av båda arterna från sina ursprungsområden i Italien-Iberiska halvön (*T. nylanderi*) och Balkan (*T. crassipinus*). Enligt denna kom *T. nylanderi* till svenska fastlandet för omkring 8300 år sedan (Skåne) och hade spridit sig norrut till Stockholmsområdet för ca 5000 år sedan. *T. crassipinus* expansion från sydöstra Europa har stoppas av *T. nylanderi* längs en 900 km lång frontlinje som går från nordvästra Polen genom Östtyskland söderut till Bayern. *T. crassipinus* har troligen koloniserat Hästnacken genom att flyga med vinden över Östersjön. Eftersom *T. nylanderi* saknas på ön kunde en kolonisering bli av. Det är även känt att myror kan driva lång väg i luften.

Den alternativa förklaringen att bon kan ha införts med ved som behövdes för driva det tegelbruk som fanns på ön Hästnacken mellan 1720 och 1830 är mindre trolig. Historiska rapporter visar att träimport från de baltiska länderna var marginell efter rysskriget. Dessutom är det inte sannolikt att bon skall fastna i det importerade trämaterialet pga artens speciella mikrohabitat (ekollon, nötter och kvistar på marken).