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Three Turano-European species of the *Temnothorax interruptus* group (Hymenoptera: Formicidae) demonstrated by quantitative morphology

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Abstract

The ant genus *Temnothorax* is very diverse in the Palaearctic region. It consists of many cryptic species which are hard to discover with conventional toolkits of alpha taxonomy. However, the modern, quantitative morphological approaches have been improved, and their increased accuracy and taxonomic specificity allow taxonomists to discover cryptic biological diversity on a much finer scale. In this paper, we provide quantitative morphology-based evidence in support of our contention that the Turano-European *Temnothorax interruptus* (Schenck, 1852) is, in fact, a complex of three clearly separable lineages. Species hypotheses are developed through NC-PART clustering, a highly automated protocol using two algorithms, NC-clustering and Partitioning Based on Recursive Thresholding (PART). Our results are based on a large dataset generated from 19 continuous morphometric traits measured on a total of 165 workers from 66 nest samples. Classifications returned by the exploratory analyses are confirmed by cross-validated Linear Discriminant Analysis (LOOCV-LDA) with a 0.6% error rate in 166 workers. Two known type series, *Temnothorax interruptus* (Schenck, 1852) and *Leptothorax tuberum* ssp. *knipovitshi* Karavaiev, 1916, which meet the criteria for this species complex, are nested in the same cluster, and each classification is supported with posterior p = 1.0. Therefore, *Leptothorax tuberum* ssp. *knipovitshi* is considered a junior synonym of *T. interruptus*. The two other morphological clusters are described as *T. morea* sp.n. and *T. strymonensis* sp.n. Syntopic occurrence has been found in only one case, between *Temnothorax interruptus* and *T. strymonensis*, and mixed colonies were not observed. *Temnothorax interruptus* has been identified as a Turano-European species, with distribution from Spain to the Caucasus but completely unknown in the Mediterranean region. The two broadly sympatric East Mediterranean species, *T. morea* and *T. strymonensis*, occur widely in the region from Croatia to Turkey.

Key words: Morphometrics, species delimitation, exploratory analyses, gap statistic, biogeography, new species.

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Introduction

The genus *Temnothorax* is one of the most species-rich ant genera on the European continent. More than half of the 388 species and 42 subspecies currently known worldwide (Bolton 2016) are reported from the traditionally well-explored Mediterranean territories of Europe (Borowiec 2014). Thanks to intensive taxonomic research done in recent decades (Tinaut 1995, Radchenko 2004, Seifert 2006, Schulz & al. 2007, Csősz & al. 2014, 2015, Salata & Borowiec 2015), our knowledge of the European *Temnothorax* fauna has increased dramatically. The new data consistently support our earlier assumption concerning the exceptional diversity of this genus (Csősz & al. 2015), which contains a high number of cryptic species (sensu Seifert 2009).

In the recent past, many species groups of the West Palaearctic *Temnothorax* fauna have been revised. However, the Turano-European (Vigna Taglianti & al. 1999) *Temnothorax interruptus* has never been revised in a modern taxonomic study. Its workers can easily be separated from other *Temnothorax* taxa according to a combination of the following morphological features (explanations of the abbreviations are given in the Materials and methods section): small, tiny ants (CS < 600 µm); body colour yellow to light brown, 1st gastral tergite has a blackish band, gena darker; mesopropodeal declivity absent or inconspicuous; frontal lobes conspicuously wider than frons (FL / FR: 1.12 [1.04, 1.24]); propodeal spines long (SPST / CS: 0.38 [0.31, 0.48]) and curving downwards. Traditionally, this taxon has been considered a single species. However, the unusually wide geographic distribution (from Western Europe to the Caucasus) of this taxon and, particularly, the detected morphological differences between the cf. *Temnothorax interruptus* samples recently collected in various countries suggest hidden diversity. Hence, we were particularly interested to determine how many species we really have within this lineage.

Due to the frequently overlapping characters and the lack of sufficiently reliable diagnostic traits, *Temnothorax* species are generally considered quite challenging for taxonomists. Indeed, it is frequently not possible to determine boundaries between *Temnothorax* species by relying exclusively on conventional approaches. Subjective guesswork can hardly be counted on to reveal real biodiversity when the system under consideration contains highly similar or cryptic species.

Therefore, in this paper we assess the diversity-patterns of the Turano-European populations of "cf. *Temnothorax interruptus*" according to multivariate analyses of quantitative morphological data using NC-PART clustering described by Csősz & Fisher (2016). This complex work-flow incorporates many multivariate approaches. The exploratory analysis combines the NC-clustering (Seifert & al. 2014) that is designed to find structure in large sets of continuous morphometric data and the partitioning algorithm known as "part" (Nilsen & al. 2013), which assigns cases into subsets and determines the ideal number of clusters on the basis of a gap statistic algorithm (Tibshirani & al. 2001). This approach allows one to infer the boundaries of morphological clusters without preliminary hypotheses concerning either the number of clusters or the classification of a particular sample. Species boundaries and reliability of morphological clusters recognized by these exploratory analyses were tested by confirmatory Linear Discriminant Analysis (LDA) and cross validation (LOOCV). The high number of available large-nest series (i.e., a large number of individuals collected from the same nest) allowed robust morphometric hypothesis formation and testing, facilitated a classical assessment of the intra-species variability, and helped further our understanding of the microhabitat preferences of all species within the *T. interruptus* group.

Our findings on diversity in the *Temnothorax interruptus* complex may foster a better understanding of the biogeographic patterns in the West-Palaearctic region.

Materials and methods

Nineteen continuous morphometric traits were measured on 165 workers and 12 gynes belonging to 66 nest samples. The material is deposited in the following institutions, abbreviations after Evenhuis (2013): HNHM (Hungarian Natural History Museum, Budapest, Hungary), SIZK (Ukraine, Kiev, Schmalhausen Institute of Zoology), UWPC (Poland, Wroclaw, University of Wroclaw), ZMHB (Museum für Naturkunde der Humboldt-Universität, Berlin, Germany). A distribution map for all of the species discussed in this revisionary work is linked to the dendrogram and is generated in R (R Development Core Team 2012) with the "phylo.to.map" function using package phytools (Revell 2012). Type material is given for each species separately, the list of other material examined is provided in Table 1.

Protocol for morphometric character recording

Morphometric characters are defined in Csősz & al. (2015). All measurements were made in µm using a pin-holding stage, permitting rotations around X, Y, and Z axes. An Olympus SZX9 stereomicroscope was used at a magnification of x100 for each character. Morphometric data are provided in µm throughout the paper. All workers were measured by S. Csősz, and the gynes were measured by SS. Only one morphometric trait (MW) is explained differently for worker and gyne castes. Definitions of morphometric characters are as follows.

CL maximum length of head capsule in median line; the head must be carefully tilted to the position with the true maximum; excavations of hind vertex and / or clypeus, if any, reduce CL

CS cephalic size; the arithmetic mean of CL and CWb

CWb maximum width of head capsule, measured posterior to the eyes

EL maximum diameter of the compound eye

FL maximum distance between the frontal lobes

FR minimum distance between the frontal carinae

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

MW maximum mesosoma width; pronotal width in workers and scutum width in gynes

NOH maximum height of the petiolar node, measured in lateral view from the uppermost point of the petiolar node perpendicular to a reference line set from the petiolar spiracle to the imaginary midpoint of the transition between dorso-caudal slope and dorsal profile of caudal cylinder of the petiole (see Fig. 1 in Csősz & al. 2015)

NOL length of the petiolar node, measured in lateral view from petiolar spiracle to dorso-caudal corner of caudal cylinder; do not erroneously take as reference point the dorso-caudal corner of the helcium, which is sometimes visible

PEH maximum petiole height the chord of ventral petiolar profile at node level is the reference line perpendicular to which the maximum height of petiole is measured

PEL diagonal petiolar length in lateral view; measured from anterior corner of subpetiolar process to dorso-caudal corner of caudal cylinder

PEW maximum width of petiole

PoOC postocular distance; use a cross-scaled ocular micrometer and adjust the head to the measuring position of CL; caudal measuring point: median occipital margin; frontal measuring point: median head at the level of the posterior eye margin

PPH maximum height of the postpetiole in lateral view measured perpendicularly to a line defined by the linear section of the segment border between dorsal and ventral petiolar sclerite

PPW maximum width of postpetiole

SL maximum straight line scape length excluding the articular condyle

SPBA the smallest distance between the lateral margins of the spines at their base; 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 center 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 the real stigma opening that may be positioned eccentrically

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

For describing the degree of inclination of pilosity we use the terminology applied in HÖLLDOBLER & WILSON (1990). The adpressed (0 - 5°) hairs run parallel, or nearly parallel to the body surface. Decumbent hairs stand 10 - 15°, subdecumbent hair stands 30°, suberect hairs stand 35 - 45°, the erect hairs stand more than 45° from the body surface.

Tab. 1: The list of non-type material examined by means of morphometrics. Unique sample identifiers are provided in the following format: final species hypothesis followed by abbreviated country code, locality name, date of collection, and a special collection code separated by underscore. w = worker. For depository abbreviations, see Materials and methods.

Locality code	**Country**	**Locality information**	**Depository**
interruptus-ARM:Amberd-03061985	Armenia	Bjura.Kak usch [shore], r ["reka"=river], Amberd, 03.06.1985, leg. Radchenko, N 40.3886, E 44.2264, 2046 m a.s.l.	2 w, SIZK
interruptus-ARM:Yerevan-136_88	Armenia	Yerevan, #136.88, 09.06.1988, leg. Radchenko, N 40.18, E 44.5, 1000 m a.s.l.	2 w, SIZK
interruptus-FRA:laporge-10072010	France	Le Porge, 10 km, 10.07.2010, leg. Galkowski, N 44.5443, E 1.1251, 30 m a.s.l.	3 w, HNHM
interruptus-FRA:LePorge-19072010-54	France	Le Porge, 19.06.2009, leg. Galkowski, N 44.53, E 1.12, 30 m a.s.l.	3 w, HNHM
interruptus-HUN:Budapest-19191109	Hungary	Budapest, Hármashatár-hegy, 19.10.1919, leg. Biró, N 47.555, E 18.997, 480 m a.s.l.	2 w, HNHM
interruptus-HUN:Budapest-19191119	Hungary	Budapest, Hármashatár-hegy, 19.10.1919, leg. Biró, N 47.555, E 18.997, 480 m a.s.l.	4 w, HNHM
interruptus-POL:Pińczów-00370	Poland	Wyż. Małopolska Pińczów, 01.05.2008, leg. Borowiec, N 50.533, E 20.05, 280 m a.s.l.	2 w, HNHM
interruptus-POL:Przemków-00435	Poland	Lower Silesia 9 km SW of Przemków, 19.06.-11.07.2015, leg. Wiśniewski, N 51.46705, E 15.69892, 151 m a.s.l.	2 w, HNHM
interruptus-POL:Przemków-00439	Poland	Lower Silesia 9 km SW of Przemków, 08-29.05.2015, leg. Wiśniewski, N 51.46705, E 15.69892, 151 m a.s.l.	2 w, HNHM
interruptus-RUS:Achikulak-10062006-062	Russia	Pervaja lesnaja dacha Neftekumsk Achikulak, Stavropolskij kraj, 10.06.2006, leg. Csősz, N 44.55, E 44.833, 70 m a.s.l.	3 w, HNHM
interruptus-RUS:Achikulak-10062006-069	Russia	Pervaja lesnaja dacha Neftekumsk Achikulak, Stavropolskij kraj, 10.06.2006, leg. Csősz, N 44.55, E 44.833, 70 m a.s.l.	3 w, HNHM
interruptus-RUS:Gelendzhik-05062006-121	Russia	Gelendzhik, 2 km SSE Krasnodarskij kraj, 05.06.2006, leg. Csősz, N 44.535, E 38.17, 165 m a.s.l.	3 w, HNHM
interruptus-RUSGelendzhik-04062006-239	Russia	Gelendzhik, oak forest 5 km South-SE, 04.06.2006, leg. Csősz, N 44.535, E 38.17, 165 m a.s.l.	3 w, HNHM
interruptus-SWI:Pfynwald-08101998	Switzerland	Pfynwald Wallis Kiefernwald unter Steinen, 08.10.1988, leg. Anonymus, N 46.3, E 7.62, 650 m a.s.l.	3 w, HNHM
interruptus-TUR:Antakya-032	Turkey	Prov. Antakya, Nur Daglari, 14 road km W. Hassa, 11.05.1997, leg. Schulz, Vock, Sanetra, N 36.8414, E 36.4309, 1600 m a.s.l.	3 w, HNHM
interruptus-TUR:Cumacay-18061986	Turkey	Kars, rte Pour Cumacay, 18.06.1986, leg. Besuchet, Löbl & Burckhardt, N 39.92, E 43.195, 1600 m a.s.l.	3 w, HNHM
interruptus-TUR:Kayseri-09051997-250	Turkey	Prov. Kayseri, Ziyarettepesi Gecidi, (ca. 130 km E. Kayseri), 09.05.1997, leg. Schulz, Vock & Sanetra, N 38.8855, E 36.8217, 1900 m a.s.l.	3 w, HNHM
interruptus-TUR:Kayseri-09051997-259	Turkey	Prov. Kayseri, Ziyarettepesi Gecidi, (ca. 130 km E. Kayseri), 09.05.1997, leg. Schulz, Vock & Sanetra, N 38.8855, E 36.8217, 1900 m a.s.l.	3 w, HNHM
interruptus-TUR:Kayseri-09051997-477	Turkey	Prov. Kayseri, Ziyarettepesi Gecidi, (ca. 130 km E. Kayseri), 09.05.1997, leg. Schulz, Vock, Sanetra, N 38.8855, E 36.8217, 1900 m a.s.l.	3 w, HNHM
interruptus-TUR:Kazigman-18061986-30c	Turkey	Kars, Kağizman Sous la ville, bord fleuve Aras fauche (#30c), 18.06.1986, leg. Besuchet, Löbl, Burckhardt, N 40.1405, E 43.1198, 1400 m a.s.l.	3 w, HNHM
interruptus-Crimea:Chatyr-dag-249_85	Ukraine	Krym, Chatyr-dag (#249.85), 09.06.1985, leg. Radchenko, N 44.7367, E 34.2821, 1200 m a.s.l.	2 w, SIZK
interruptus-Crimea:Chatyr-dag-39_95	Ukraine	Krym, Chatyr-dag (#39.95), 14.08.1985, leg. Radchenko, N 44.7367, E 34.2821, 1200 m a.s.l.	2 w, SIZK

Locality code	Country	Locality information	Depository
interruptus-UKR:Lugansk-29062011	Ukraine	Lugansk Prov., Stanichno-Lugansky Nat. Res., 29.06.2011, leg. Radchenko, N 48.5, E 38.3, 70 m a.s.l.	2 w, SIZK
morea.sp.n-CRO-Bol-15072010-110	Croatia	(south), 3 km E. Bol, 15.07.2010, leg. Schulz, N 43.2722, E 16.7061, 100 m a.s.l.	3 w, HNHM
morea.sp.n-CRO-Makarska-15072010-105	Croatia	Biokovo Mt. 4 km E. Makarska, 15.07.2010, leg. Schulz, N 43.2608, E 17.0856, 400 - 500 m a.s.l.	2 w, HNHM
morea.sp.n-CRO-Makarska-15072010-106	Croatia	Biokovo Mt. 4 km E. Makarska, 15.07.2010, leg. Schulz, N 43.2608, E 17.0856, 400 - 500 m a.s.l.	3 w, HNHM
morea.sp.n-CRO-Podgora-15072010-108	Croatia	between Podgora and Makarska, 15.07.2010, leg. Schulz, N 43.2687, E 17.058, 50 - 100 m a.s.l.	3 w, HNHM
morea.sp.n-GRE:Gythio-28042011-192	Greece	6 km SW Gythio, 28.04.2011, leg. Schulz, N 36.737, E 22.513, 100 m a.s.l.	3 w, HNHM
morea.sp.n-GRE:Kamarina-20051996-277	Greece	Prov.: Préveza, 3 road km NE. Kamarina, 20.05.1996, leg. Schulz & Vock, N 39.1478, E 20.84, 400 - 600 m a.s.l.	2 w, HNHM
morea.sp.n-GRE:Korfu-07062013-1173	Greece	Ionian is., Korfu Pandokrator, 07.06.2013, leg. Borowiec, N 39.4485, E 19.51824, 736 m a.s.l.	1 w, HNHM
morea.sp.n-GRE:Korfu-08062013-1142	Greece	Ionian is., Korfu n. Ag. Anna, 08.06.2013, leg. Borowiec, N 39.4226, E 19.4426, 414 m a.s.l.	2 w, HNHM
morea.sp.n-GRE:Preveza-21051996-025	Greece	Prov.: Préveza, vic. Papadátes, 21.05.1996, leg. Schulz & Vock , N 39.44, E 20.84, 600 - 800 m a.s.l.	3 w, HNHM
morea.sp.n-GRE:Taygethos-29042000-158	Greece	Peloponnes, Prov. Lakonia, Oros Taigetos, 20 km SW. Sparti, 29.04.2000, leg. Schulz, N 36.58, E 22.21, 1800 - 2100 m a.s.l.	3 w, HNHM
morea.sp.n-GRE:Taygethos-30042011-276	Greece	Taygethos Oros, Trail to Profiti Ilias, 30.04.2011, leg. Schulz, N 36.96, E 22.396, 1000 - 1200 m a.s.l.	3 w, HNHM
morea.sp.n-GRE:Taygethos-30042011-286	Greece	Taygethos Oros, Trail to Profiti Ilias, 30.04.2011, leg. Schulz, N 36.948, E 22.377, 1400-1600 m a.s.l.	3 w, HNHM
morea.sp.n-GRE:Taygethos-30042011-295	Greece	Taygethos Oros, Trail to Profiti Ilias, 30.04.2011, leg. Schulz, N 36.948, E 22.377, 1400 - 1600 m a.s.l.	3 w, HNHM
morea.sp.n-GRE:Taygethos_02061994-26	Greece	Taigetos Oros, Unterhalb des Profitis Ilias, 02.06.1994, leg. Schulz & Vock, N 36.955, E 22.358, 1800 - 2000 m a.s.l.	2 w, HNHM
morea.sp.n-GRE:Tripolis-061994-1389	Greece	Peloponnisos 28 km NW, Tripolis, Pass zw. Vitina u. Karakaloú, 06.1994, leg. Schulz, N 37.6565, E 22.1491, 1140 m a.s.l.	2 w, HNHM
morea.sp.n-TUR:Küthaya-10062004-02	Turkey	32 km SSE Kütahya, 10.06.2004, leg. Schulz, N 39.114, E 30.08, 1130 m a.s.l.	3 w, HNHM
morea.sp.n-TUR:Pinarhisar-10052003-06	Turkey	Vic. Islambelir, Pinarhisar to Poyrali, 10.05.2003, leg. Schulz, N 41.39, E 27.367, 300 m a.s.l.	3 w, HNHM
strymonensis.sp.n-BG:Blagoevgrad-08062009-375	Bulgaria	Relsni Mnastery, 40 km NEE. Blagoevgrad, 08.06.2009, leg. Csősz, N 42.1565, E 23.4121, 1550 m a.s.l.	3 w, HNHM
strymonensis.sp.n-BG:Kresna-08062009-188	Bulgaria	Maleshevska Planina Mts vic. Gorna Breznitsa, 5 km W Kresna, 08.06.2009, leg. Csősz, N 41.7523, E 23.1106, 350 m a.s.l.	3 w, HNHM
strymonensis.sp.n-BG:Marikostinovo-09062009-223	Bulgaria	Slavyanka Mts 2 km E: Mikrevo, 10 km E Marikostinovo, 09.06.2009, leg. Csősz, N 41.4426, E 23.4495, 200 m a.s.l.	3 w, HNHM
strymonensis.sp.n-BG:Mikrevo-09062009-238	Bulgaria	Maleshevska Planina Mts 2 km SW Mikrevo, 09.06.2009, leg. Csősz, N 41.6093, E 23.1806, 350 m a.s.l.	3 w, HNHM
strymonensis.sp.n-BG:Mikrevo-09062009-239	Bulgaria	Maleshevska Planina Mts 2 km SW Mikrevo, 09.06.2009, leg. Csősz, N 41.6093, E 23.1806, 350 m a.s.l.	3 w, HNHM
strymonensis.sp.n-CRO-Ljubotic-15072010-104	Croatia	Southern Velebit Mt. vic. Ljubotic, 15 km NW. Satrigrad, 15.07.2010, leg. Schulz, N 44.36, E 15.3794, 500 m a.s.l.	2 w, HNHM
strymonensis.sp.n-CRO:Zelenika-08041913	Croatia	Zelenika, 08.04.1913, leg. Szabó, N 42.45, E 18.58, 70 m a.s.l.	2 w, HNHM
strymonensis.sp.n-GRE:Arta-29031978-12	Greece	Epire, Menidion S Arta, maquis, tamis, ravin, humide (#12), 29.03.1978, leg. Vit, N 39.13, E 20.98, 10 m a.s.l.	2 w, UWPC
strymonensis.sp.n-GRE:Chalandritsa-21041979	Greece	Péloponnése Achaïe, Chalandritsa maquis feuilles mortes, 21.04.1979, leg. Vit, N 38.12, E 21.38, 350 m a.s.l.	2 w, UWPC
strymonensis.sp.n-GRE:Dramas-10081999	Greece	Makedonia, Dramas Paranesti-Thermia, 10.08.1999, leg. Nikolakakis, N 41.3787, E 24.4513, 350 m a.s.l.	2 w, UWPC

Locality code	Country	Locality information	Depository
strymonensis.sp.n-GRE:Evros-01092015-1933	Greece	Thrace, Evros, rd. Dikela-Avra loc. 1, 28.08.2015, leg. Borowiec, N 40.90827, E 25.68754, 233 m a.s.l.	2 w, HNHM
strymonensis.sp.n-GRE:Evros-28082015-1932	Greece	Thrace, Evros, 4.9 km W of Dadia, 01.09.2015, leg. Borowiec, N 41.1206, E 26.16635, 183 m a.s.l.	2 w, HNHM
strymonensis.sp.n-GRE:Gythion-17041979	Greece	Péloponnése Laconie, Taygéte Aejiae, N Gythion ravin, humus, 17.04.1979, leg. Vit, N 36.76, E 22.55, 60 m a.s.l.	2 w, UWPC
strymonensis.sp.n-GRE:Ioannia-22051996-028	Greece	Prov.: Ioánnina, 3 km SW. Nikánor, 5 km N. Kónitsa, 22.05.1996, leg. Schulz, Vock, N 40.1301, E 20.9774, 500 m a.s.l.	3 w, HNHM
strymonensis.sp.n-GRE:Kassandra-29082009	Greece	Halkidiki, Kassandra, Siviri-Elani rd., 29.08.2009, leg. Borowiec, N 40.01, E 23.25, 41 m a.s.l.	2 w, HNHM
strymonensis.sp.n-GRE:Kefalonia-27062014-01487	Greece	Ionian is., Kefalonia rd. Sami-Razata, 28.06.2014, leg. Borowiec, N 38.19937, E 20.596885, 553 m a.s.l.	2 w, HNHM
strymonensis.sp.n-GRE:Kefalonia-28062014-01488	Greece	Ionian is., Kefalonia rd. Poros-Skala, 27.06.2014, leg. Borowiec, N 38.12813, E 20.79509, 13 m a.s.l.	2 w, HNHM
strymonensis.sp.n-GRE:Larissa-08092012-829	Greece	Thessalia, Larissa distr., Ossa Mts. Ag. Dimitrios Mon. N. Stomilo, 08.09.2012, leg. Borowiec, N 39.51544, E 22.44418, 162 m a.s.l.	1 w, HNHM
strymonensis.sp.n-GRE:Neraida-25031978-03	Greece	Epire, E Neraida entre Igoumenitsa et loannina souche pourrie de laurier (#3), 25.03.1978, leg. Vit, N 39.57, E 20.76, 600 m a.s.l.	1 w, UWPC
strymonensis.sp.n-TUR:Sinop-03071993-1702	Turkey	Sinop-5 km S Kabali 30 km S Sinop Kiefernwald 50%Südhang, 03.07.1993, leg. Schulz, N 41.8555, E 34.9693, 500 m a.s.l.	3 w, HNHM
strymonensis.sp.n-TUR:Van-18061993-1093	Turkey	Van-13-20 km-NW Catak Steppenvegetation, 18.06.1993, leg. Schulz, N 38.08, E 43.08, 2600 m a.s.l.	2 w, HNHM
strymonensis.sp.n-TUR:Van-18061993-1096	Turkey	Van-13-20 km-NW Catak Steppenvegetation, 18.06.1993, leg. Schulz, N 38.08, E 43.08, 2600 m a.s.l.	3 w, HNHM
strymonensis.sp.n-TUR:Kayseri-09051997-248	Turkey	Prov. Kayseri, Ziyarettepesi Gecidi, (ca. 130 km E. Kayseri), 09.05.1997, leg. Schulz, Vock & Sanetra, N 38.8855, E 36.8217, 1900 m a.s.l.	2 w, HNHM
strymonensis.sp.n-TUR:Kayseri-09051997-249	Turkey	Prov. Kayseri, Ziyarettepesi Gecidi, (ca. 130 km E. Kayseri), 09.05.1997, leg. Schulz, Vock & Sanetra, N 38.8855, E 36.8217, 1900 m a.s.l.	2 w, HNHM

Multivariate statistics – arriving at a final morphospecies hypothesis

Exploratory analyses through NC-PART clustering: The prior species hypothesis was generated based on workers through combined application of NC clustering (Seifert & al. 2014) and Partitioning Based on Recursive Thresholding (PART) (Nilsen & Lingjaerde 2013). The script for NC-clustering combined with PART was written in R and can be found in Appendix S1 in Csősz & Fisher (2016). The low number of gynes hinders their use in statistical analyses. Our exploratory data analysis approach follows the protocol described by Csősz & Fisher (2016) with the following specific settings: bootstrap iterations in PART were set to "b = 1000", and the minimum size of clusters was set to "minSize = 3" for both "hclust" and "kmeans". The optimal number of clusters and the partitioning of samples are accepted as the preliminary species hypothesis in every case in which the two clustering methods, "hclust" and "kmeans" through PART, have yielded the same conclusion.

Hypothesis testing by confirmatory analyses: The validity of the prior species hypothesis was tested by Cross validated LDA (LOOCV-LDA). Classification hypotheses were imposed for all samples that were congruently classified by partitioning methods, while wild-card settings (i.e., no prior hypothesis imposed on its classification) were given to samples that were incongruently classified by the two methods. In order to find the most discriminative ratios between species, we applied multivariate ratio analysis (MRA) (Baur & Leuenberger 2011).

Tab. 2: Frontal lobe / Scape length (FL / SL) ratio calculated for each species based on individuals. Mean ± SD, minimum and maximum values (in parentheses) are given.

Species	FL / SL body ratio
T. interruptus (n = 67)	0.574 ± 0.02 [0.529, 0.611]
T. morea sp.n. (n = 44)	0.429 ± 0.01 [0.402, 0.455]
T. strymonensis sp.n. (n = 54)	0.467 ± 0.01 [0.446, 0.495]

Results and discussion

The two clustering methods "hclust" and "kmeans" of PART, in combination with NC-clustering, yielded different numbers of clusters (Fig. 1): the clustering method "kmeans" yielded three clusters, but "hclust" identified a satellite cluster encompassing four samples. We resolved the conflict in

Tab. 3: Mean of morphometric ratios calculated for *Temnothorax interruptus*, *T. morea* and *T. strymonensis* based on individuals. Morphometric traits are divided by either cephalic length (CL), cephalic width (CWb) or cephalic size (CS), ± SD are provided in the upper row, minimum and maximum values are given in parentheses in the lower row.

morphometric ratios	*T. interruptus* (n = 67)	*T. morea* (n = 44)	*T. strymonensis* (n = 54)
CS	533 ± 30 [450, 605]	546 ± 22 [482, 593]	515 ± 29 [461, 592]
CL / CWb	1.228 ± 0.02 [1.161, 1.276]	1.239 ± 0.02 [1.201, 1.283]	1.237 ± 0.02 [1.199, 1.267]
PoOC / CL	0.391 ± 0.01 [0.356, 0.417]	0.398 ± 0.01 [0.383, 0.411]	0.405 ± 0.01 [0.378, 0.435]
FR / CS	0.393 ± 0.01 [0.364, 0.423]	0.353 ± 0.01 [0.330, 0.372]	0.367 ± 0.01 [0.342, 0.389]
FL / CS	0.459 ± 0.01 [0.428, 0.487]	0.383 ± 0.01 [0.358, 0.404]	0.400 ± 0.01 [0.384, 0.416]
SL / CS	0.800 ± 0.02 [0.748, 0.843]	0.894 ± 0.02 [0.845, 0.931]	0.856 ± 0.02 [0.813, 0.890]
EL / CS	0.259 ± 0.01 [0.231, 0.278]	0.252 ± 0.01 [0.234, 0.271]	0.251 ± 0.01 [0.234, 0.269]
ML / CS	1.223 ± 0.03 [1.167, 1.303]	1.251 ± 0.02 [1.214, 1.301]	1.222 ± 0.04 [1.164, 1.382]
PEH / CS	0.398 ± 0.02 [0.362, 0.432]	0.388 ± 0.01 [0.363, 0.415]	0.384 ± 0.01 [0.355, 0.404]
NOH / CS	0.181 ± 0.01 [0.153, 0.206]	0.180 ± 0.01 [0.162, 0.202]	0.177 ± 0.01 [0.156, 0.200]
NOL / CS	0.277 ± 0.01 [0.244, 0.315]	0.283 ± 0.01 [0.263, 0.309]	0.274 ± 0.01 [0.249, 0.304]
PPH / CS	0.376 ± 0.02 [0.341, 0.412]	0.360 ± 0.01 [0.336, 0.386]	0.365 ± 0.01 [0.335, 0.392]
SPST / CS	0.356 ± 0.02 [0.314, 0.392]	0.403 ± 0.03 [0.358, 0.478]	0.384 ± 0.03 [0.322, 0.429]
MW / CS	0.660 ± 0.02 [0.629, 0.716]	0.633 ± 0.02 [0.608, 0.678]	0.628 ± 0.02 [0.594, 0.676]
PEW / CS	0.302 ± 0.01 [0.277, 0.347]	0.275 ± 0.01 [0.253, 0.293]	0.288 ± 0.01 [0.266, 0.317]
PPW / CS	0.408 ± 0.02 [0.370, 0.460]	0.380 ± 0.01 [0.353, 0.404]	0.393 ± 0.02 [0.360, 0.447]
SPBA / CS	0.321 ± 0.02 [0.289, 0.378]	0.281 ± 0.01 [0.256, 0.319]	0.294 ± 0.01 [0.270, 0.321]
SPTI / CS	0.406 ± 0.03 [0.340, 0.481]	0.387 ± 0.03 [0.338, 0.456]	0.418 ± 0.03 [0.361, 0.491]
PEL / CS	0.497 ± 0.02 [0.465, 0.564]	0.501 ± 0.02 [0.450, 0.533]	0.502 ± 0.02 [0.456, 0.536]

partitioning created by the two clustering methods "hclust" and "kmeans" by accepting the three-cluster hypothesis, returned by "kmeans", as the most parsimonious solution. Accordingly, the elements of this satellite cluster were set to wild-cards in the confirmatory analysis (i.e., no species label swere added). The cross validated LDA-confirmed separation of three clusters with overall classification success of 99.4%. Species-wise classification via LOOCV-LDA yields: *interruptus* 100%, *morea* sp.n. 100%, *strymonensis* sp.n. 98.1% (1 out of the total 54 workers was classified differently by the NC-PART clustering and LOOCV-LDA). The wild-card cases were classified as cluster 3.

One of the clusters (cluster 1, see Fig. 1) is identical with the type material of *Temnothorax interruptus* (Schenck, 1852). Classification of the three syntype workers of *Temnothorax interruptus* (Schenck, 1852) was confirmed via wild-card settings in LDA with posterior probabilities of 1.0 for each type specimen. Type material of *Leptothorax tuberum* subsp. *knipovitshi* Karavaiev, 1916 was also classified as *Temnothorax interruptus* by LDA with posterior probabilities of 1.0. Therefore, we propose a new junior synonymy for this latter taxon. The two other clusters (clusters 2 and 3, see Fig. 1) are described as new species, named *Temnothorax morea* sp.n. and *T. strymonensis* sp.n. The most discriminative ratio among these three species identified by MRA is the FL / SL ratio (see Fig 2), which yields a non-overlapping range between *T. interruptus* and the other two species, *T. morea* and *T. strymonensis* (Tab. 2). The same ratio also provides an acceptable tool with which to tell the latter two species apart with 94.9% classification success based on worker caste. The species treated in this revisionary work also differ from one another in many qualitative traits and body ratios (Tab. 3).

The morphological differences among workers are more conspicuously expressed in gynes. While workers of the two new species, *Temnothorax morea* and *T. strymonensis*, are very similar (excluding a few diagnostic traits), their gynes differ remarkably from each other, leaving no doubt about the validity of their species status.

The geographic distribution of these newly outlined taxa may slightly overlap (Fig. 3). *Temnothorax interruptus* and *T. strymonensis* populations are known to occur syntopically in Anatolia, and *T. morea* may co-occur with *T. strymonensis* on the Peloponnese peninsula. Despite relatively frequent syntopical occurrence, no hints or traces of classical hybridization syndromes were detected in these contact zones.

Synopsis of the Turano-European elements of the *Temnothorax interruptus* species group

T. interruptus (Schenck, 1852)
= *T. tuberum* subsp. *knipovitshi* Karavaiev, 1916 **syn.n.**
T. morea **sp.n.** Csősz, Salata & Borowiec
T. strymonensis **sp.n.** Csősz, Salata & Borowiec

Key to workers

1 Frontal lobe wide, scape relatively short, FL / SL ratio > 0.51 (Fig. 2, Tab. 2). Antennal scape short, not reaching occipital margin of head .... ***T. interruptus***
– Frontal lobe narrower, scape relatively longer, FL / SL ratio < 0.51 (Fig. 2, Tab. 2). Antennal scape long, reaching occipital margin of head 2

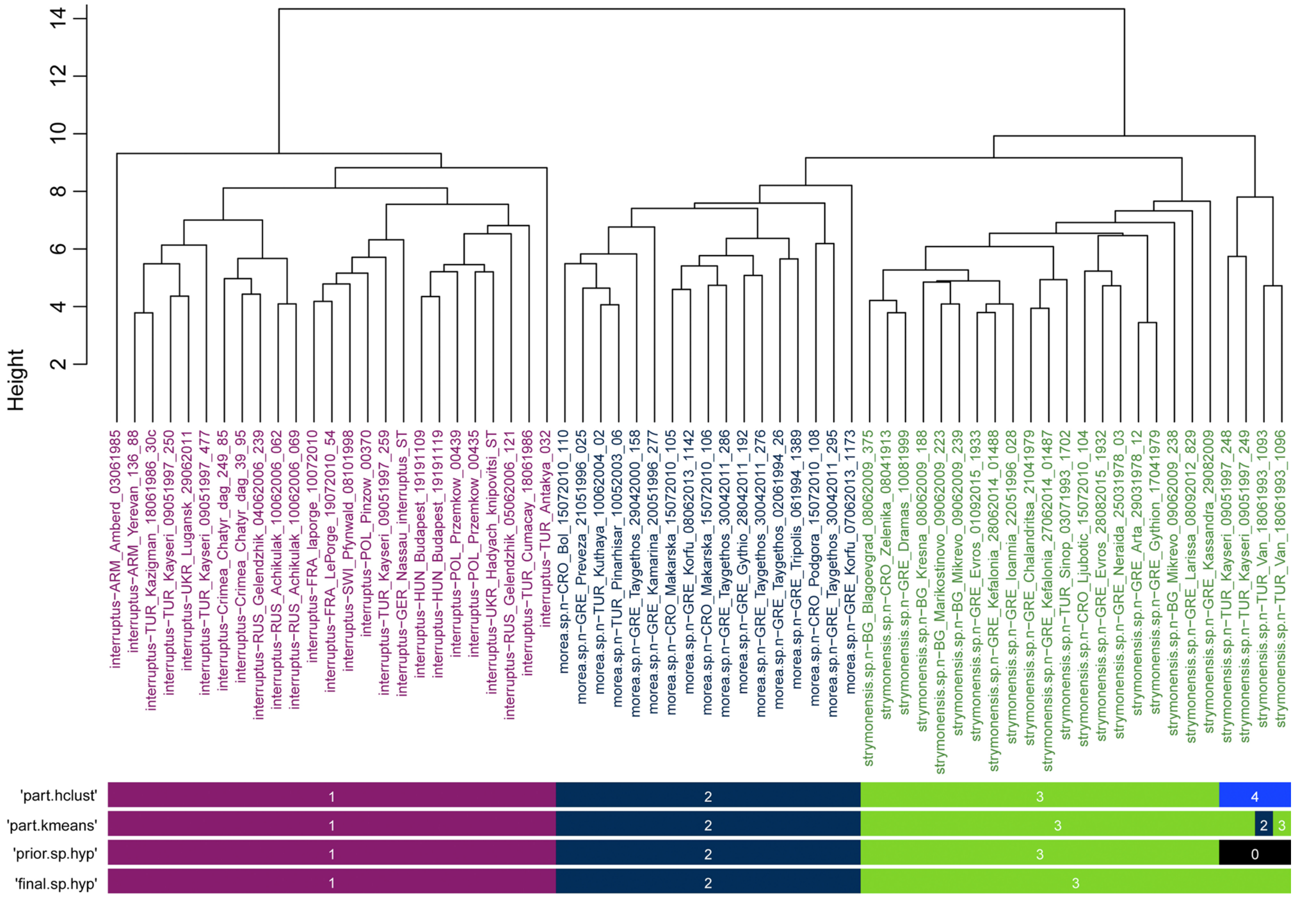


Fig. 1: Dendrogram solution for the Ponto-Mediterranean *Temnothorax interruptus* species-group. Sample information in the dendrogram follows this format: final species hypothesis followed by abbreviated country code, locality name, date of collection and a special collection code separated by underscore. Four columns of rectangles represent results of partitioning resulted by method PART using two cluster methods 'hclust' and 'kmeans', the prior species hypothesis generated by the former two algorithms and final species hypothesis. Different colours distinguish species. *Temnothorax interruptus* (Schenck): lillac (cluster 1), *T. morea* sp.n.: dark bluish-green (cluster 2), *T. strymonensis* sp.n.: light green (cluster 3). The satellite cluster recognized by cluster method 'hclust' is marked by blue (cluster 4), wild-card samples in prior species hypothesis are marked by black (cluster 0).

2 FL / SL ratio < 0.45 (Fig. 2, Tab. 2). Transverse band, in the apical part of the first gaster tergite, always reaches one half-length of tergite on its sides and usually has broad interruption in the central part (Figs. 18 - 19). The interruption edges never parallel thus yellow interruption appears more or less V-shaped. The non-overlapping range of discriminants calculated on a reduced character set (D4 = + 0.0718*SL - 0.1213*FL + 0.0558*SPSP - 0.0445 SPTI - 10.1086) helps to separate the most difficult cases, *morea* (n = 44) = 2.429 ± 1.14 [- 0.357, + 4.637] .... ***T. morea*** **sp.n.**

– FL / SL ratio > 0.45. (Fig. 2, Tab. 2). Transverse band, in the apical part of the first gaster tergite, occupies apical 1 / 3 to 1 / 2 length, its anterior margin straight or on sides only slightly protruding anterad (Figs. 20 - 21). Rarely, transverse band on the first tergite narrower than 1 / 3 length of the tergite, narrowly interrupted along the middle and laterally distinctly protruding anterad. The non-overlapping range of discriminants calculated on a reduced character set (D4 = + 0.0718*SL - 0.1213*FL + 0.0558*SPSP - 0.0445 SPTI - 10.1086) helps to separate the most difficult cases, *strymonensis* (n = 54) = -1.979 ± 0.88 [-4.285, -0.460] .... ***T. strymonensis*** **sp.n.**

Key to gynes

1 Body brown to dark brown. Antennal scape short, not reaching occipital margin of head, scutum with thick, dense longitudinal costae .... ***T. interruptus***

– Body orange to bright orange. Antennal scape long, reaching occipal margin of head, scutum with sparse longitudinal costae, sometimes main sculpture absent 2

2 Propodeal spines shorter (SPST / CS < 0.3), scutellum entirely smooth and shiny, sometimes sides with sparse wrinkles. Area above propodeal spines with very sparse, transverse and gentle costulae or sparse irregular rugosity, interstices microreticulate .... ***T. strymonensis*** **sp.n.**

– Propodeal spines longer (SPST / CS > 0.3), scutellum with sparse, and very gentle longitudinal costulae, sometimes main sculpture disappears on side edges. Area above propodeal spines with very sparse, thick and irregular rugosity, interstices smooth and shiny .... ***T. morea*** **sp.n.**

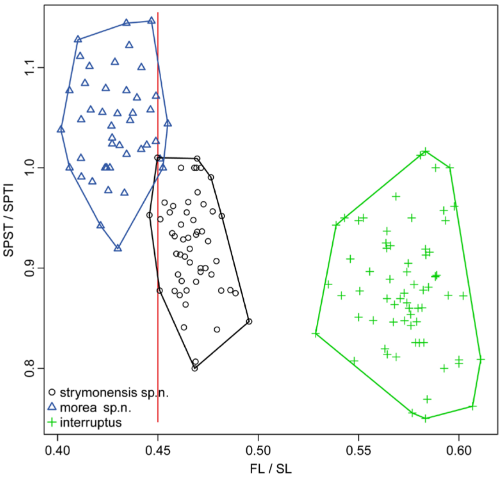


Fig. 2: First and second best morphometric ratios. Scatterplots of the two most discriminating ratios between workers of Ponto-Mediterranean *Temnothorax interruptus* species-group; *T. strymonensis* sp.n.: black circle, *T. morea* sp.n.: blue triangle and *T. interruptus*: green cross. The thin red line illustrates the position of FL/SL =0.45, which is the level to separate workers of *T. morea* and *T. strymonensis*.

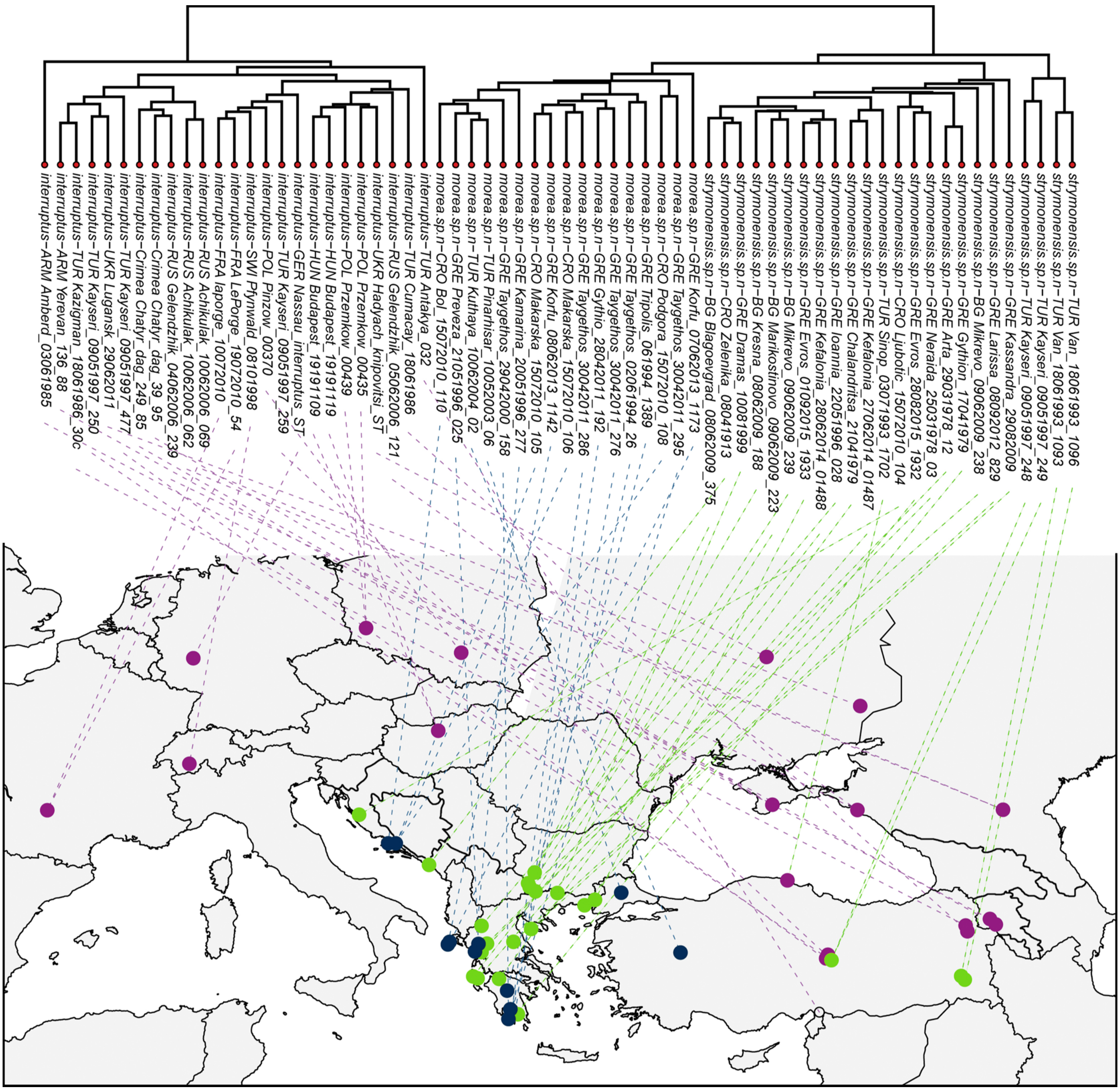


Fig. 3: Dendrogram to geographic map. Dendrogram solution is linked on the map of Europe and Turkey. Colour codes for species are as follows: *Temnothorax interruptus*: lillac, *T. morea* sp.n.: dark bluish-green, *T. strymonensis* sp.n.: light green.

Figs. 4 - 6: Worker, dorsal. (4) *Temnothorax interruptus*; (5) *T. morea* sp.n.; (6) *T. strymonensis* sp.n.

General characteristics of the *Temnothorax interruptus* group

Worker: Head longer than wide [CL / CW: 1.161 - 1.283], lateral surface below eyes straight, posterior profile gently rounded (Figs. 13 - 15). Anterior margin of the clypeus rounded. Eyes small, oval [EL / CS: 0.231 - 0.278]. Funiculus short, with three-segmented thin club, first segment elongate, triangular, approximately 1.2 times as long as wide on apex, segments 2 - 8 approximately 0.5 times as long as wide, club very long, 0.75 times as long as segments 1 - 9 combined. (Figs. 10 - 12). Surface of the scape with very fine microsculpture, shiny, covered with short, moderately dense, decumbent or adpressed setae. Club always darker than the funiculus, infuscate to black. Mandibles rounded, longitudinally striate, shiny; inner margin with 5 - 6 teeth, the apical tooth massive and long. Frontal lobes wide [FL / CS > 0.35]. Clypeus shiny with diffuse, longitudinal carinulae, medially smooth. Mesosoma elongate, approximately 1.2 times as long as CS, flat or slightly rounded in profile view, metanotal groove absent or inconspicuous. Promesonotal suture absent or inconspicuous, visible only on the lateral surface. Pronotum rounded on sides. Propodeal spines long [SPST / CS > 0.3]. Petiole with short peduncle, in lateral view its anterior face straight, node flat or slightly rounded on dorsal surface, posterior face slightly convex or straight. Postpetiole in lateral view low, regularly rounded, in dorsal view, regularly rounded, apical half with gently rounded sides (Figs. 4, 7). Legs short. Gaster smooth and shiny, bearing sparse, long, suberect to erect setae. Dorsal surface of tibia and femora sometimes with short, sparse, adpressed or suberect to the surface setae, inner margins sometimes with a row of sparse, short, suberect setae (Figs. 7 - 9).

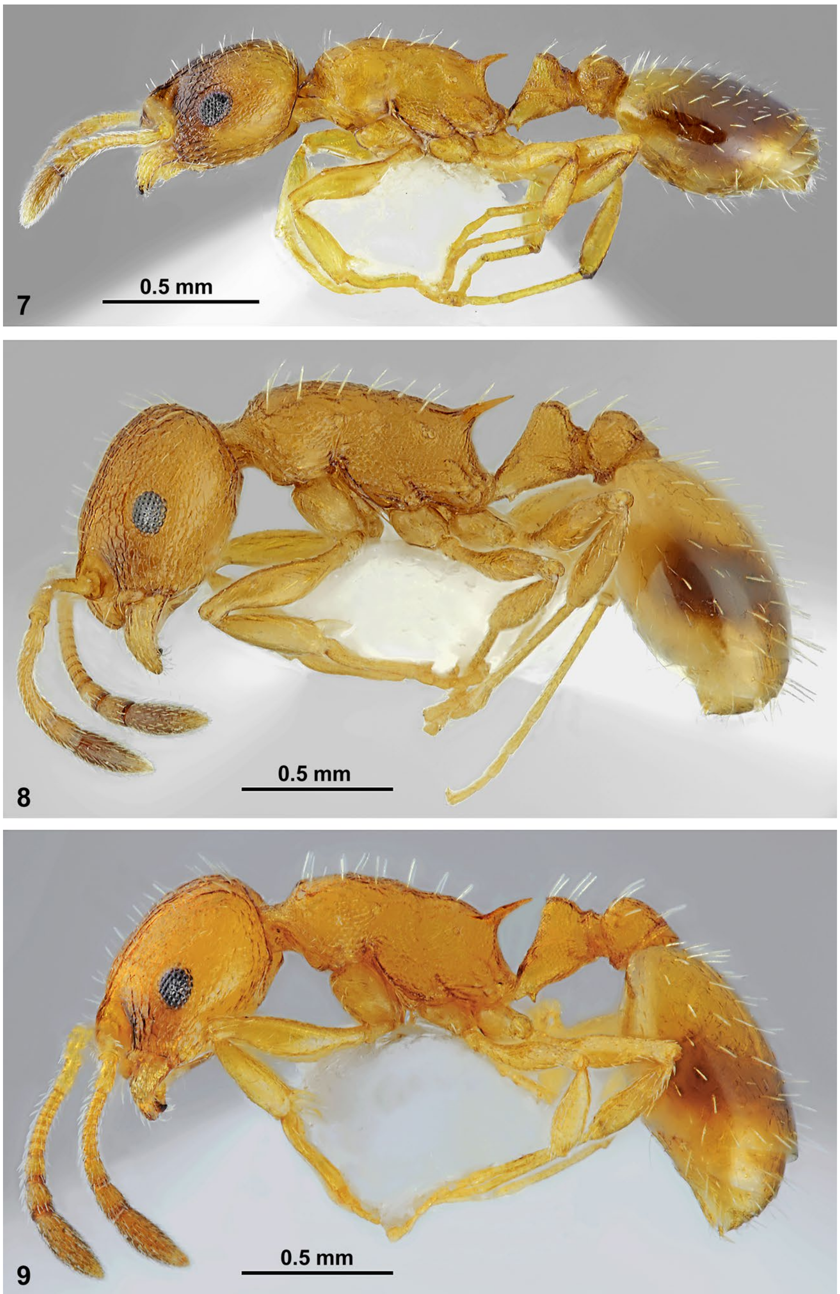
Gyne: Head trapezoidal, slightly longer than wide, lateral surfaces below eyes gently rounded on the posterior edges (Figs. 28 - 30). Anterior margin of the clypeus rounded. Funiculus short, with three-segmented thin club, first segment elongate, triangular, 2 times as long as wide on apex, segments 2 - 8 quadrate, as long as wide, club very long, as long as segments 2 - 9 combined. (Figs. 28 - 30). Surface of the scape with very fine microsculpture, shiny, covered with short, moderately dense, decumbent or adpressed setae. Mandibles rounded with fine longitudinal striae, shiny, inner margin with 5 - 6 teeth, the apical tooth massive and long. Frontal carinae short, extending to 1 / 3 length of eye. Mesosoma, elongate [ML / CS: 1.709 - 1.859], flat in profile view, metanotal groove absent. Pronotum rounded on sides. Propodeal spines never short SPST > 0.2. Petiole with short peduncle, in lateral view its anterior face straight, node flat or slightly rounded on dorsal surface, posterior face slightly convex or straight. Postpetiole in lateral view low, regularly rounded, in dorsal view, regularly rounded, apical half with gently rounded sides (Figs. 22 - 27). Legs short, dorsal surface of tibia and femora sometimes with short, sparse, decumbent or adpressed setae, inner margins sometimes with a row of sparse, short, suberect setae (Figs. 23, 25, 27).

Description and redefinition of species

***Temnothorax interruptus* (Schenck, 1852)**
(Figs. 4, 7, 10, 13, 16 - 17, 22, 23, 28, Tabs. 1 - 3)

= *Leptothorax tuberum* ssp. *knipovitshi* Karavaiev, 1916: 499; **syn.n.**

Type material examined: Syntype series of *Temnothorax interruptus* (Schenck, 1852): Germany: "Nassau",



Figs. 7 - 9: Worker, lateral. (7) *Temnothorax interruptus*; (8) *T. morea* sp.n.; (9) *T. strymonensis* sp.n.

"Leptothorax interruptus Schenck", "interruptus Schenck" Type, "GBIF-D / FoCol 2010 specimen + label data documented", ZMHB, Berlin.

Syntype series of *Leptothorax tuberum* ssp. *knipovitshi* Karavaiev, 1916: Ukraine: "Gadyach" (Karavaiev 1916) [Hadiach, specimens were collected in the woods near Psel river], SIZK, Kiev.

The other material examined is provided in Table 1.

Redescription of workers: Head orange to dark orange with brown to dark brown posterior part of gena or darker orange to brown posterior part of head. Scapes same colouration as head. Funicles same colouration as scapes or darker brown to dark brown. Mesosoma, legs, petiole and postpetiole orange to dark orange. Sometimes femora darker. Gaster orange to dark orange with complete brown to brownish-black, transverse band on the apical part of the first tergite. In most specimens the band is broad, occupies apical ⅓ to ½ length of first tergite, its anterior margin straight or on sides only slightly protruding forward (Figs. 4, 7, 10, 13, 16). In rare aberrations first tergite with transverse band narrower than ⅓ length of the tergite, narrowly interrupted along the middle and laterally distinctly protruding forward (Fig. 17).

Head quadratic (CL / CWb: 1.228 [1.161, 1.276]), (Figs. 10, 13). Eyes small, oval, (EL / CS: 0.259 [0.231, 0.278]). Antennal scape short (SL / CS: 0.80 [0.748, 0.843]), not reaching occipital margin of head (Figs. 10, 13). Surface of the scape with very fine microsculpture, shiny, covered with short, moderately dense, suberect or adpressed setae.

Mesosoma elongate (ML / CS: 1.223 [1.167, 1.303]), dorsal contour line in profile slightly rounded. Propodeal spines long (SPST / CS: 0.356 [0.314, 0.392]), wide at base, curved downwards with pointed apex.

Frontal carinae short, extending to ⅓ length of eye; antennal fossa shallow, rugulose with costae. Frontal lobes distinctly wider than frons (FL / FR: 1.168 [1.111, 1.236]), rugulose with thick longitudinal costae, interstices smooth and shiny. Frons longitudinally costate and sometimes rugose, interstices shiny. Postocular area of head rugulose, sometimes longitudinally costulate. Genae sometimes with sparser rugosity. Interstices feebly microreticulate, shiny (Figs. 7, 10, 13). Entire head bearing suberect to erect, pale and thin setae.

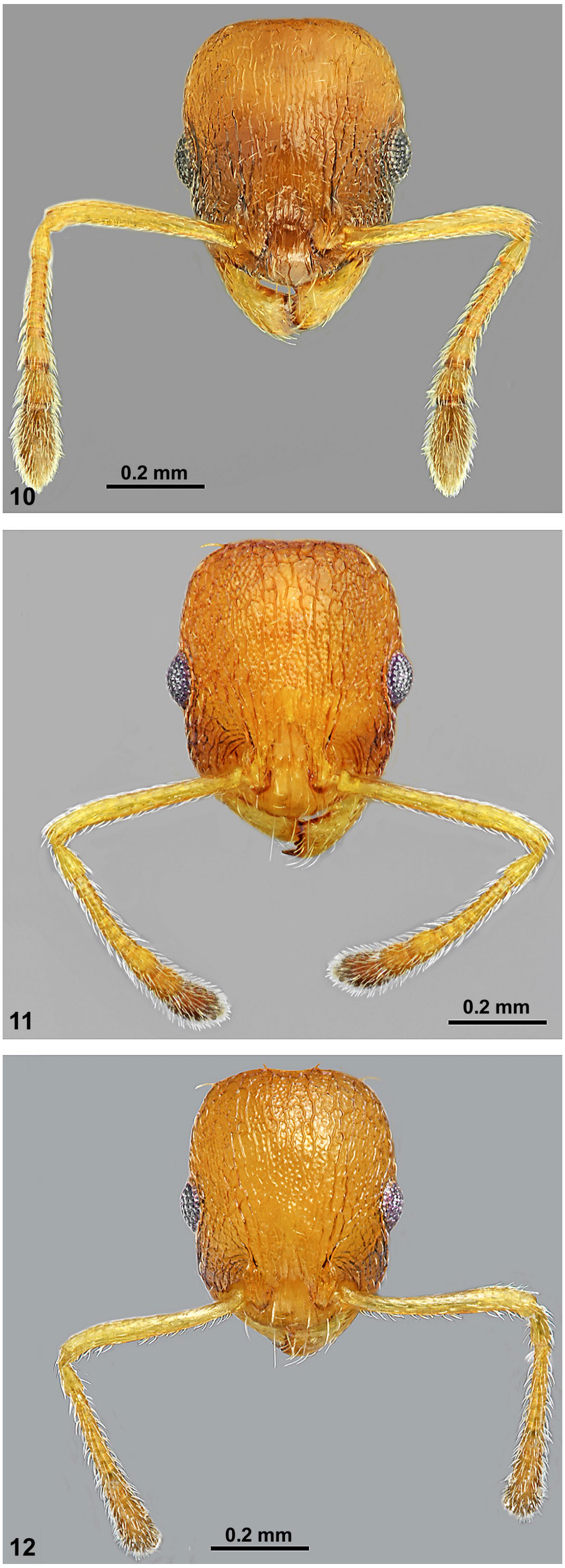
Dorsum of mesosoma densely rugose. Lateral surface of promesonotum longitudinally costulate. Lateral surface of propodeum rugulose. Interstices shiny with microreticulation or micropunctation. Area between and below propodeal spines shiny and punctate. Dorsal surface of mesosoma with sparse, erect, long, thick and pale setae (Figs. 4, 7). Petiole punctate to rugulose, interstices shiny.

Redescription of gynes: Head dark brown, sometimes temples orange. Antennal club brown to bright brown. Mesosoma, petiole and postpetiole dark brown to brown, sometimes with brighter spots on the pronotum. Legs orange. First gastral tergite mostly brown with orange spot basally but apical margin always pale, remaining tergites yellow-orange basally and brown apically but the light goes dark gradually (Figs. 22, 23, 28).

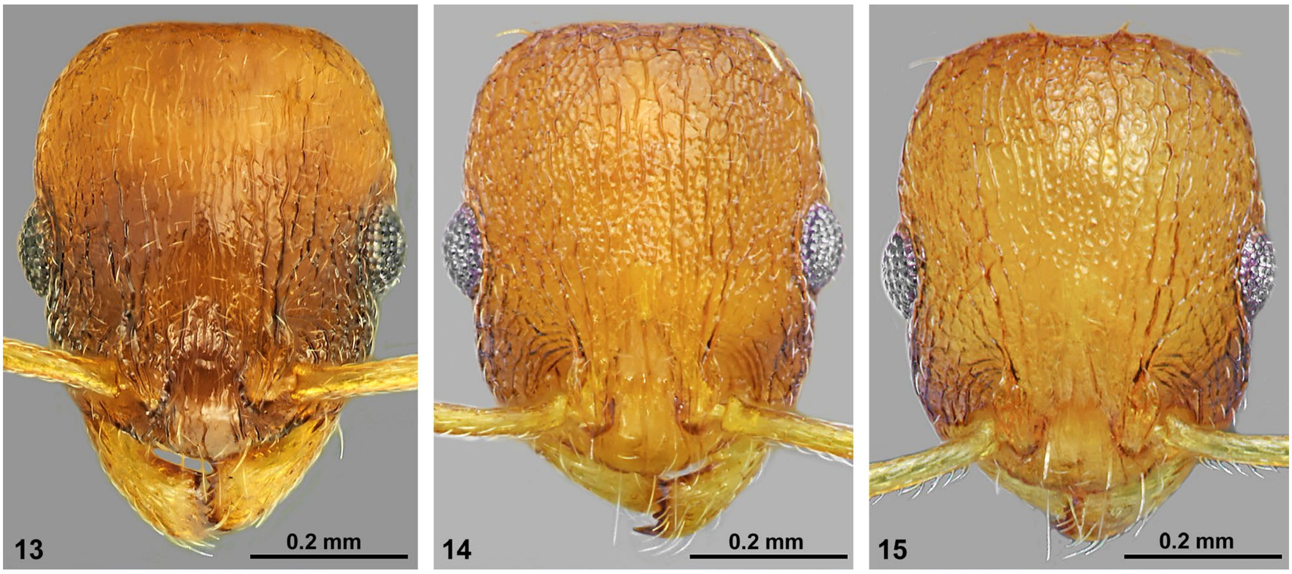
Eyes big, oval [EL / CS: 0.34 ± 0.004]. Antennal scape short [SL / CS: 0.76 ± 0.03], not reaching occipital margin of head. Propodeal spines medium length [SPST / CS: 0.38 ± 0.01], wide at base, triangular, straight, with acute apex. Clypeus shiny with diffuse, longitudinally carinulae, interstices smooth. Antennal fossa deep, rugulose with concentric carinae. Frontal lobes wide [FLS / CS: 0.46 ± 0.01], rugulose with thick longitudinal costae, interstices shiny. Frons shiny, entire surface longitudinally costate and rugose, interstices smooth and shiny. Area above eyes and sides of head rugulose and sometimes longitudinally costate, interstices shiny. (Figs. 22, 23, 28). Entire head bearing suberect to erect, pale and thin setae.

Pronotum with thick rugosity on whole dorsal surface. Sides with thick rugosity or gentle, dense longitudinal costae. Surface between rugosity smooth and shiny. Scutum with dense, thick longitudinal costae, shiny. Sometimes rugosity weaker laterally. Scutellum smooth and shiny at the centre, sides smooth or with diffuse, thick, longitudinal costae (Figs. 22, 23). Metanotum with slight sculpture, rugulose or punctate. Sometimes with a few thick wrinkles. Propodeum with variable sculpture. Area above propodeal spines with very sparse, transverse and gentle costae or sparse irregular rugosity, interstices microreticulate, shiny. Area between and below propodeal spines with dense punctation. Sides of propodeum punctate or with slight, dense rugosity. Sometimes with a few longitudinal costae, always shiny. Anepisternum and katepisternum shiny, with gentle, dense longitudinal costae. Metaepisternum and metakatepisternum, shiny, with dense, longitudinal rugosity. Surface between rugosity punctate. Dorsal surface of mesosoma with sparse, erect, long, thick and pale setae (Figs. 22, 23). Petiole and postpetiole shiny, the entire surface punctate to rugulose, dorsal surface longitudinally costulate. Gaster smooth and shiny, bearing sparse, long, suberect to erect setae (Figs. 22, 23).

Differential diagnosis: Morphological characteristics of *Temnothorax interruptus* are considered the most distinct amongst all three species treated in this revision. Its workers differ from *T. morea* and *T. strymonensis* in: 1) shorter antennal scape which never reaches occipital margin of head;



Figs. 10 - 12: Worker, head and antennae. (10) *Temnothorax interruptus*; (11) *T. morea* sp.n.; (12) *T. strymonensis* sp.n.



Figs. 13 - 15: Worker, head sculpture. (13) *T. interruptus*; (14) *T. morea* sp.n.; (15) *T. strymonensis* sp.n.

2) wide frontal lobes (FL / SL > 0.5 µm); and 3) low SL / CS ratio (0.800 ± 0.02 in *T. interruptus* vs. 0.894 ± 0.02 in *T. morea* vs. 0.856 ± 0.02 in *T. strymonensis*).

Gynes of *Temnothorax interruptus* differ from those of *T. morea* and *T. strymonensis* in: 1) darker body colour (brown to dark brown vs. orange to bright orange); 2) shorter antennal scape which never reaches occipital margin of head (in *T. morea* and *T. strymonensis* antennal scape reaches occipital margin of head); and 3) the whole surface of the scutum is conspicuously costulate (in *T. morea* and *T. strymonensis* the dorsal surface of scutum inconspicuously costulate or smooth).

Biology: This species occurs mostly in xerothermic grasslands or other open habitats, especially in northern localities, and it can often be collected in overgrown limestone or gypsum rocks. It nests in soil, under stones, in moss or in rock rubble. Sometimes specimens can be found at the edges of dry, deciduous oak forests.

Geographic distribution: This is a Turano-European species. Its known distribution stretches from Spain to the Caucasus, from Central Europe to the Mediterranean peninsula. This species, by crossing the Caucasus, also gained a foothold in Eastern Turkey, where it co-occurs with *Temnothorax strymonensis* (Fig. 3).

***Temnothorax strymonensis* sp.n.**
(Figs. 6, 9, 12, 15, 20, 21, 26, 27, 30, Tabs. 1 - 3)

Type material examined: Holotype: B u l g a r i a: Maleshevska Planina Mts. vic. Gorna Breznitsa, 5 km W Kresna, 8.6.2009, leg. Csősz, N 41.7523, E 23.1106, 350 m a.s.l., collection code: 188, (1 w, HNHM, Budapest).

Paratypes: B u l g a r i a: Maleshevska Planina Mts vic. Gorna Breznitsa, 5 km W Kresna,, 08.06.2009, leg. Csősz, N 41.7523, E 23.1106, 350 m a.s.l., collection code: 188, (7 w, 1 q, HNHM, Budapest);

Maleshevska Planina Mts. 2 km SW Mikrevo, 9.6.2009, leg. Csősz, N 41.6093, E 23.1806, 350 m a.s.l., collection code: 238, (6 w, HNHM, Budapest; 3 w, 1 q, UWPC, Wroclaw); Maleshevska Planina Mts 2 km SW Mikrevo, 09.06.2009, leg. Csősz, N 41.6093, E 23.1806, 350 m a.s.l., collection code: 239, (5 w, 1 q, HNHM, Budapest).

The other material examined is provided in Table 1.

For more recent localities in Greece, Peloponnese, see Borowiec & Salata (2017, as *T.* cf. *interruptus* sp. 2).

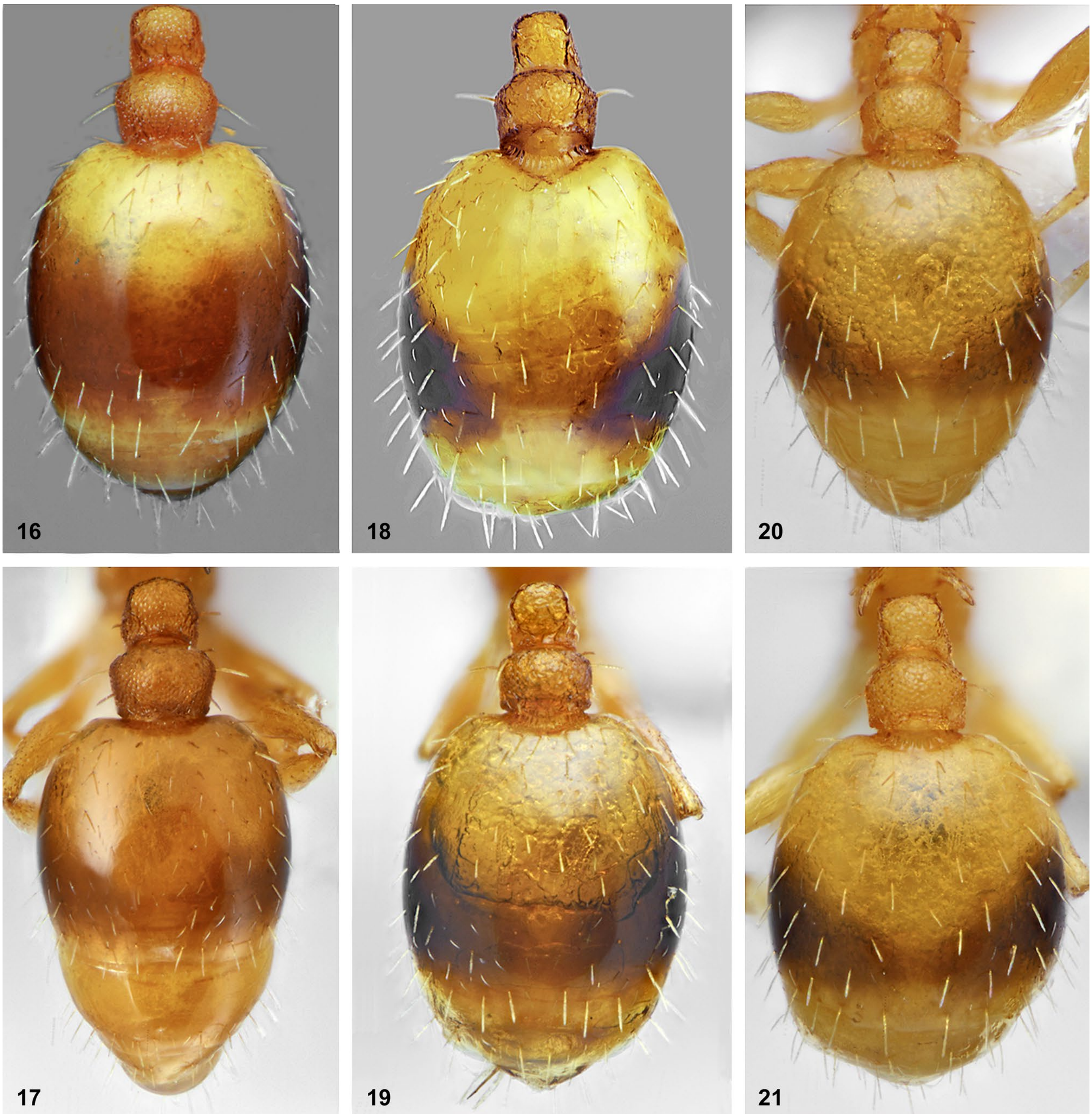
Etymology: This name refers to the ancient name of Struma River [Strymon]. Its valley is the locus typicus of this species.

Description of workers: Head yellow to dark orange with brown posterior part of gena or darker orange to brown posterior part of head. Scapes same colouration as head. Funicles same colouration as scapes or pale brown. Mesosoma, legs, petiole and postpetiole yellow to dark orange. Sometimes femora slightly darker than tibiae. Gaster yellow to dark orange with brown to black, transverse, band in the apical part of the first tergite, usually narrower than ⅓ length of tergite. In most specimens the band is tapering at the middle and gradually extending on sides (Figs. 6, 9, 12, 15, 20). Usually apical band with narrow interruption in the central part of parallel edges (Fig. 21) but often complete. In extreme form apical band is moderately broad, on sides reaching half-length of first tergite without or with median interruption but edges of the interruption more or less parallel (Figs. 20 - 21).

Head slightly longer than broad (CL / CWb: 1.237 [1.199, 1.267]), (Figs. 12, 15). Eyes small, oval, (EL / CS: 0.251 [0.234, 0.269]). Antennal scape moderately long (SL / CS: 0.856 [0.813, 0.890]), reaching occipital margin of head.

Mesosoma elongate (ML / CS: 1.222 [1.164, 1.382]), dorsal contour line in profile slightly rounded or straight. Propodeal spines long (SPST / CS: 0.384 [0.322, 0.429]), wide at base, slightly curved downwards with pointed apex.

Frontal carinae short, extending to ⅓ length of eye; antennal fossa shallow, with sparse rugosity, interstices punctate or microreticulate. Frontal lobes distinctly wider than frons (FL / FR: 1.090 [1.040, 1.146]), with sparse rugae or costae, interstices shiny. Frons shiny, longitudinally costulate or rugose, interstices punctate or microreticulate. Postocular area of head with sparse rugosity and sometimes longitudinally costulate. Genae sometimes with sparser sculpture. Interstices punctate or densely microreticulate and shiny. (Figs. 12, 15). Entire head bearing suberect to erect, pale and thin setae.



Figs. 16 - 21: Worker, gaster (in upper row the most common pattern, in lower row most distinct pattern). (16, 17) *Temnothorax interruptus*; (18, 19) *T. morea* sp.n.; (20, 21) *T. strymonensis* sp.n.

Dorsum of mesosoma sparsely rugulose. Lateral surface of promesonotum longitudinally costulate. Lateral surface of propodeum with weaker sculpture. Interstices shiny with dense microreticulation or micropunctation. Area between and below propodeal spines shiny and punctate, sometimes with transverse costae. Dorsal surface of mesosoma with sparse, erect, long, thick and pale setae (Figs. 6, 9). Entire surface of petiole and postpetiole with microrugosity to densely punctate.

Description of gynes: Head, mesosoma, antennae, petiole, postpetiole and legs orange or bright orange. Antennal club or whole funiculus darker. Sometimes scutum and scutellum darker or bright brown. Gaster with variable colouration. Most frequently first tergite in anterior half orange and posterior half brown, remaining tergites yellow-orange basally and brown apically but apical margins always pale. Sometimes first tergite on orange anterior surface with brown spot of diffused borders. The orange colouration can be limited to ⅓ length or can take the form of a spot. (Figs. 26, 27, 30).

Eyes big, oval [EL / CS: 0.3 ± 0.01]. Antennal scape long [SL / CS: 0.79 ± 0.02], reaching occipital margin of head. Propodeal spines long or medium length [SPST / CS: 0.4 ± 0.05], wide at base, triangular, straight or slightly curved downward, with rounded apex. Clypeus shiny with diffuse, longitudinal wrinkles, with smooth surface between carinulae. Its central area smooth and shiny; antennal fossa deep, with sparse rugosity. Surface between rugosity with micropunctation, shiny. Frontal lobes wide [FLS / CS: 0.4 ± 0.01], rugulose with thick longitudinal costae, shiny and with

Figs. 22 - 23: Gyne of *Temnothorax interruptus*. (22) Dorsal; (23) lateral.

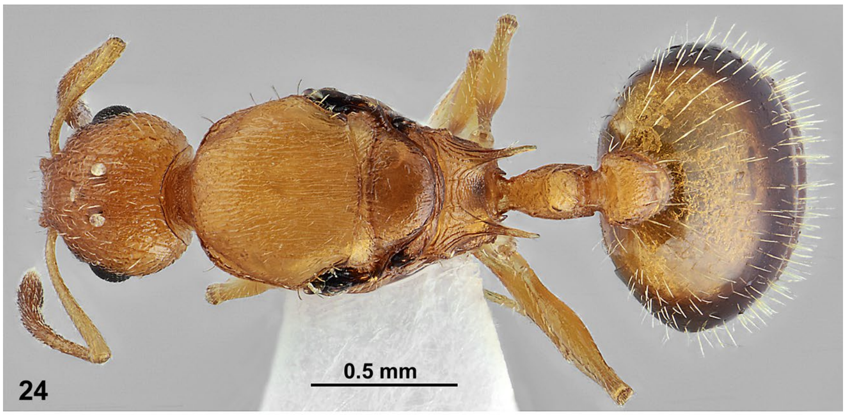
micropunctation between rugosities. Frons shiny, all surface longitudinally costate and rugose, interstices microreticulate, or micropunctate, shiny. Area above eyes and sides of head with sparse, thick rugosity and sometimes with sparse, thick, longitudinal costae. Surface between rugosity with dense microreticulation or micropunctation, shiny. Genae with reduced sculpture, with dense microreticulation, shiny (Figs. 26, 27, 30). Entire head bearing suberect to erect, pale and thin setae.

Pronotum with sparse rugosity on whole dorsal surface, surface between rugosity with sparse microreticulation, shiny. Sides with sparse, thick longitudinal costae or rugosity. Surface between rugosity with sparse microreticulation, shiny. Scutum with sparse, gentle longitudinal, and sometimes intermittent, costae, shiny. Sometimes main sculpture absent on the anterior surface and side edges. Scutellum entirely smooth and shiny, sometimes sides with sparse wrinkles. Metanotum smooth and shiny. Sometimes with few thick wrinkles (Figs. 26, 27). Propodeum with variable sculpture. Area above propodeal spines with very sparse, transverse and gentle costulae or sparse irregular rugosity, interstices microreticulate, shiny. Area between and below propodeal spines with dense punctation. Sides of propodeum with dense, gentle longitudinal costulae, interstices sparsely microreticulate or smooth, always shiny. Anepisternum, katepisternum, metaepisternum and metakatepisternum shiny, with dense, gentle, longitudinal costulae, interstices smooth or very finely microreticulate. Dorsal surface of mesosoma with sparse, erect, long, thick and pale setae (Figs. 26, 27). Petiole and postpetiole shiny, with sparse and gentle rugosity on the entire surface, thicker sculpture on the dorsal surface. Gaster smooth and shiny, bearing sparse, long, suberect to erect setae.

Differential diagnosis: Workers and gynes of *Temnothorax strymonensis* differ remarkably from those of *T. interruptus* and can be easily separated on the basis of a couple of traits (see diagnosis of *T. interruptus*), but workers look very much like those of *T. morea*.

The most reliable features which help distinguish workers of *Temnothorax strymonensis* and *T. morea* are the FL / SL ratio (> 0.45 in *T. strymonensis* and < 0.45 in *T. morea*) and the shape of the transversal band on the first tergite. In *T. strymonensis*, the transversal band is the narrowest medially, and it gradually widens laterally. Usually, the apical band is intact, but if a narrow interruption in the central part of the band occurs, its edges are parallel. *T. morea* has a transverse band with a broad interruption in the central part. Interruption edges are never parallel; they are more or less V-shaped.

Gynes of *Temnothorax strymonensis* differ from *T. morea* in the following features: 1) propodeal spines (SPST / CS) are shorter than 0.3 (*T. morea* > 0.3); 2) the surface of the scutellum is smooth and shiny, sometimes with sparse wrinkles on its sides (*T. morea* has longitudinal costae, which are sparse and very gentle, covering the whole scutellum; sometimes, costae are absent on side edges); 3) very sparse, transverse, and gentle costulae and microreticulation is present above the propodeal spines (the surface above the



Figs. 24 - 25: Gyne of *Temnothorax morea* sp.n. (24) Dorsal; (25) lateral.

propodeal spines lacks transverse costae and is not microreticulated).

Biology: This species occurs in various habitats and can be found at altitudes between 10 and 1550 m a.s.l. Most samples were collected in stream valleys with deciduous or mixed forests, open oak woodlands, and mountain pastures with phrygana and oak shrubs. Three samples were collected in montane conifer forests. Single samples were found in a pine forest, shrubs overgrowing the old monastery, on marble tombs in the old cemetery, and on pastures and limestone rocks in the alpine zone. In all localities, ants were observed or collected on limestone rocks or in oak shrubs. Nests were located mostly in shaded areas under moss or in limestone crevices.

Geographic distribution: The *Temnothorax strymonensis* is an East Mediterranean (Vigna Taglianti & al. 1999) species. It most typically occurs in Greece and southern Bulgaria, but it can be found in Croatia along the Adriatic Sea coast as well. This species is known to penetrate deeply into the Anatolian territories of Turkey, where it syntopically co-occurs with *T. interruptus* in a single locality (Prov. Kayseri, Ziyarettepesi Geçidi, ca. 130 km E. Kayseri). Despite the extensive contact zone found for *T. strymonensis* and *T. morea* in southern and western Greece, true syntopic occurrence of these species has not been observed.

***Temnothorax morea* sp.n.**
(Figs. 5, 8, 11, 14, 18, 19, 24, 25, 29, Tabs. 1 - 3)

Type material examined: Holotype: Greece: Taygethos Oros, Trail to Profiti Ilias, 30.04.2011, leg. Schulz, N 36.948, E 22.377, 1400 - 1600 m a.s.l., collection code: 286, (1 w, HNHM, Budapest).

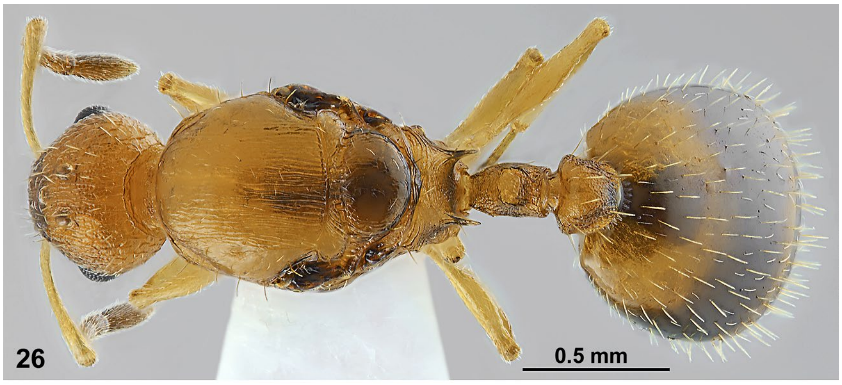
Paratypes: Greece: Taygethos Oros, Trail to Profiti Ilias, 30.04.2011, leg. Schulz, N 36.96, E 22.396, 1000 - 1200 m a.s.l., collection code: 276, (5 w, HNHM, Budapest); Taygethos Oros, Trail to Profiti Ilias, 30.04.2011, leg. Schulz, N 36.948, E 22.377, 1400 – 1600 m a.s.l., collection code: 286, (7 w, HNHM, Budapest); Taygethos Oros, Trail to Profiti Ilias, 30.04.2011, leg. Schulz, N 36.948, E 22.377, 1400 – 1600 m a.s.l., collection code: 295, (2 w, HNHM, Budapest; 3 w, UWPC, Wroclaw).

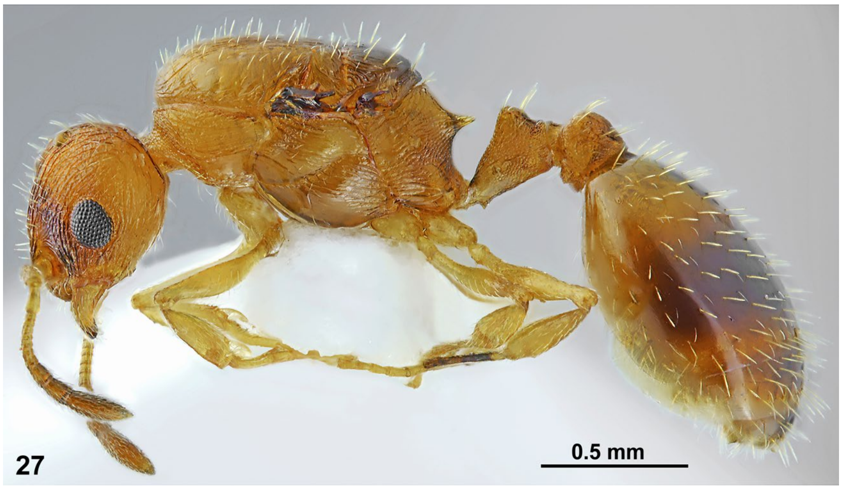
The other material examined is provided in Table 1.

For more recent localities in Greece, Peloponnese see Borowiec & Salata (2017, as *T.* cf. *interruptus* sp. 1).

Etymology: The name refers to Morea which was the name of Peloponnese peninsula in the Middle Ages. The species epithet is a noun in apposition.

Description of workers: Head orange to dark orange with brown posterior part of gena or darker orange to brown posterior part of head. Scapes same colour as head. Funicles same colour as scapes or pale brown. Mesosoma, legs, petiole and postpetiole yellow to dark orange. Sometimes femora darker. Gaster yellow to dark orange with brown to black apical band, widest laterally and gradually narrowing to the centre thus anterior margin of the band on sides runs obliquely forward. Transversal band on sides always reaching half length of tergite and usually has broad interruption in the central part (Figs. 5, 8, 11, 14, 18). The interruption edges never parallel thus yellow interruption appears more or less V-shaped (Figs. 24, 25).





Figs. 26 - 27: Gyne of *Temnothorax strymonensis* sp.n. (26) Dorsal; (27) lateral.

Head longer than broad (CL / CWb: 1.239 [1.201, 1.283]), (Figs. 11, 14). Eyes small, oval (EL / CS: 0.252 [0.234, 0.271]). Antennal scape long (SL / CS: 0.894 [0.845, 0.931]), surpassing occipital margin of head (Figs. 11, 14). Surface of the scape with very fine microsculpture, shiny, covered with short, moderately dense, suberect or adpressed setae.

Mesosoma elongate (ML / CS: 1.251 [1.214, 1.301]). Propodeal spines long (SPST / CS: 0.403 [0.358, 0.478]), wide at base, slightly curved downwards with pointed apex. Frontal carinae short, extending to ⅓ length of eye; antennal fossa shallow, with sparse thick rugosity, interstices microreticulate. Frontal lobes wider than frons (FL / FR: 1.087 [1.036, 1.146]), with sparse rugosity, shiny between rugosities. Frons shiny, all surface weakly, but densely longitudinally costulate and rugulose, interstices punctate or microreticulate. Postocular area of head densely rugulose and sometimes longitudinally costulate. Genae sometimes with sparser sculpture. Interstices densely microreticulate or punctate, shiny (Figs. 5, 8). Entire head bearing suberect to erect, pale and thin setae.

Dorsum of mesosoma finely rugose. Lateral surface of promesonotum longitudinally costulate. Lateral surface of propodeum with weaker sculpture. Interstices shiny with dense microreticulation or punctate. Dorsal surface of mesosoma with weaker rugosity, interstices microreticulate or punctate, sometimes longitudinally striate. Area between and below propodeal spines shiny and punctate, sometimes with transverse costulae. Dorsal surface of mesosoma with sparse, erect, long, thick and pale setae (Figs. 5, 8). Petiole and postpetiole shiny, on the entire surface with dense but weak rugosity or punctation.

Description of gynes: Head, mesosoma, antennae, petiole, postpetiole and legs orange or bright orange. Antennae club or whole funiculus darker. Sometimes scutum and scutellum slightly darker. Gaster with variable colouration. Most frequently first tergite in anterior half orange and brown in posterior half, remaining tergites yellow-orange basally and brown apically but apical margins always pale. The orange colouration can be limited to ⅓ length (Figs. 24, 25, 29).

Eyes big, oval [EL / CS: 0.29 ± 0.02]. Antennal scape long [SL / CS: 0.8 ± 0.01], reaching occipital margin of head. Propodeal spines long [SPST / CS: 0.52 ± 0.03], wide at base, triangular, straight, with rounded apex. Clypeus shiny and smooth or with few longitudinal wrinkles. Its central area smooth and shiny. Antennal fossa deep, with sparse rugosity. Surface between rugosity with dense microreticulation, shiny. Frontal lobes wide [FLS / CS: 0.4 ± 0.01], rugulose with thick longitudinal costae, interstices microreticulate, shiny. Frons shiny, all surface with sparse longitudinal costae or irregular rugosity, interstices microreticulate, shiny. Area above eyes and sides of head with very sparse, thick, irregular rugosity and sometimes with few longitudinal costae. Surface between rugosity with dense microreticulation, shiny. Genae with reduced sculpture, interstices microreticulate, shiny (Figs. 24, 25, 29). Entire head bearing suberect to erect, pale and thin setae.

Pronotum with punctation or sparse rugosity on whole dorsal surface, surface between rugosity with sparse microreticulation, shiny. Sides with sparse, thick longitudinal costae, interstices microreticulate, shiny. Scutum and scutellum with sparse, and very gentle longitudinal costae, shiny. Sometimes costae disappear on side edges. Surface between costae smooth and shiny. Metanotum with rugosity, shiny. Sometimes with few thick wrinkles (Figs. 24, 25). Propodeum with variable sculpture. Area above propodeal spines with very sparse, thick and irregular rugosity. Surface between sculpture smooth and shiny. Area below and between propodeal spines with dense punctation, shiny. Sides of propodeum with dense, gentle longitudinal costulae, interstices microreticulate, always shiny. Anepisternum, metaepisternum and metakatepisternum, shiny, with dense, gentle, longitudinal costulae, interstices smooth or with very gentle microreticulation. Katepisternum on its central surface smooth and shiny. Its edges with thick and dense reticulation. Dorsal surface of mesosoma with sparse, erect, long, thick and pale setae (Figs. 24, 25). Petiole and postpetiole shiny, with sparse and gentle rugosity on the entire surface, thicker sculpture on the dorsal surface. Gaster smooth and shiny, bearing sparse, long, suberect to erect setae.

Differential diagnosis: Differentiation of *Temnothorax morea* from *T. interruptus* is detailed in the diagnosis of *T. interruptus*, from *T. strymonensis* is given in the diagnosis of *T. strymonensis*.

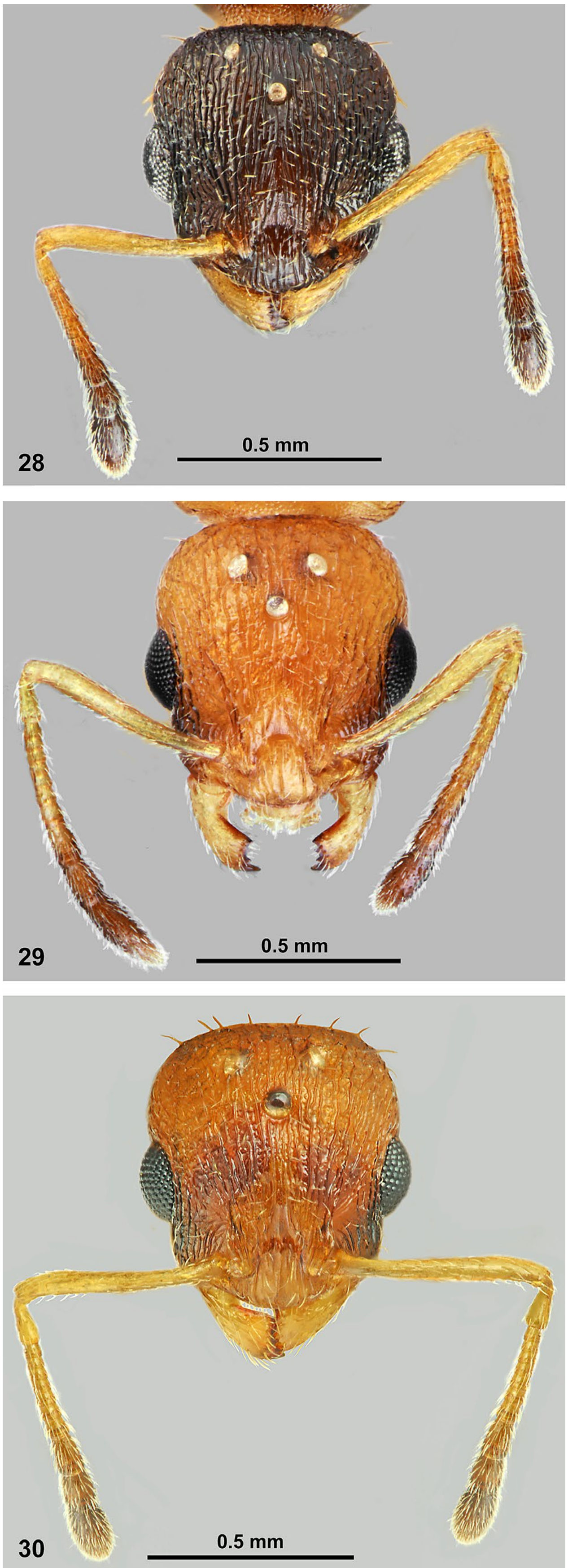
Biology: This species occurs in various dry habitats from altitudes of 110 to 2100 m a.s.l. Most samples were collected in deciduous forests (especially oak forests), in stream valleys with Platanus forests, and phrygana with oak shrubs. Two samples were found in coniferous forests, and single samples were taken from stream valleys in the alpine zone with Cyprus forests, olive orchards, pastures, and limestone rocks. In all localities, ants were observed or collected on limestone rocks or in oak shrubs. Nests were located under moss or in crevices in limestone rocks. Based on field observations, *T. morea* prefers more arid and sunny areas than *T. strymonensis*.

Geographic distribution: The *Temnothorax morea* is a typical East Mediterranean (Vigna Taglianti & al. 1999) species. It can be found in southern and western Greece, where an extensive contact zone with *T. strymonensis* is located. It also occurs in Croatia along the Adriatic Sea coast and in the western part of Turkey.

Taxonomic notes and associated taxa: There are several known taxa associated with the *T. interruptus* group. Below we list these names and discuss their positions:

Temnothorax nitidiceps (Dalla Torre, 1893) (= *Leptothorax tuberum interruptus nitidiceps* Forel, 1890, unavailable name) (terra typica: Algeria). Later, Forel (1890) mentions this taxon as a subspecies of *T. interruptus*. Cagniant (1970), basing his categorization on the shape of propodeal spines and thorax and head sculpture, identified it as a subspecies of *T. spinosus*. Its position was again changed by Baroni Urbani (1971), who restored its status as a subspecies of *T. interruptus*. Finally, Borowiec & Salata (2013) recognized it as a valid species. Its short petiole peduncle, the long propodeal spines, and the lack of mesopropodeal depression do not rule out its affiliation with the *interruptus* group. Hence, we considered this taxon as a potential member of this group.

However, our efforts to classify the only available, but beheaded type specimen using all available morphometric characters (excluding head traits) did not yield unequivocal results. The absence of the head hinders the classification of this specimen, therefore we no longer consider this taxon a potential synonym of either species treated in this revisionary work.



Figs. 28 - 30: Gyne, head and antennae. (28) *Temnothorax interruptus*; (29) *T. morea* sp.n.; (30) *T. strymonensis* sp.n.

Temnothorax junipereti (ARNOLDI, 1977) (terra typica: Ukraine) and *T. nikitae* (ARNOLDI, 1977) (terra typica: Ukraine) are considered junior synonyms of *Temnothorax knipovitshi* by RADCHENKO (1994). Their synonymy was confirmed by RADCHENKO (2016) in his monograph on ants in Ukraine. These taxa undoubtedly belong to the *interruptus* group, but because their type specimens were unavailable, we cannot confirm or contest their current position. Nonetheless, based on geographic information, their junior synonymy with *T. interruptus* represents the most likely scenario.

Temnothorax nassonovi (RUZSKY, 1895) (terra typica: Russia) is a member of the *interruptus* group. However, because of its central Asian distribution, which is far from the target region, we decided not to include this species in our investigation. Nevertheless, *Temnothorax nassonovi* differs remarkably from the Turano-European members of the *T. interruptus* group by its uniformly black or dark-brown head and abdomen, a colour combination which never occurs in any of the species treated in this work.

Conclusions

In this study, we revealed the diversity of a smaller fragment of the European *Temnothorax* fauna by evaluating continuous morphometric data. We recognized three morphologically distinct taxa: *Temnothorax interruptus* (SCHENCK, 1852) and two new species (*T. morea*, *T. strymonensis*) by using the highly automated protocol based on a fusion of two algorithms (CSŐSZ & FISHER 2016), the Nest Centroid clustering (NC clustering) and Partitioning based on Recursive Thresholding (PART).

The combination of the dimensionality reduction feature of NC clustering (SEIFERT & al. 2014) with the assignment of samples into clusters by PART (NILSEN & LINGJAERDE 2013) advances the automatization of morphometrics-based alpha taxonomy (CSŐSZ & FISHER 2016). The most important benefit of this procedure is that the determination of the optimal number of morphological clusters and sample assignments are no longer user defined, but rather is calculated by the algorithm based on statistical thresholds (TIBSHIRANI & al. 2001). This feature and the readily inferable display of the NC-PART clustering further help accelerate the taxonomic decision-making process.

Our research proves that Myrmicinae species considered in earlier years to be widely distributed in Europe and the Mediterranean Region are in fact groups of species. Mediterranean fauna appears to be more diverse and distinct from European fauna. In recent years, few other publications have presented similar results (BOER 2013, CSŐSZ & al. 2014, 2015, SALATA & BOROWIEC 2014, 2017). In addition to the differences that we had mentioned here, the fact that Eastern Mediterranean fauna differs from Western Mediterranean fauna also merits emphasis.

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