



A mixed colony of *Tetramorium immigrans* SANTSCHI, 1927 and the putative social parasite *Tetramorium aspina* sp.n. (Hymenoptera: Formicidae)

Herbert C. WAGNER, Celal KARAMAN, Volkan AKSOY & Kadri KIRAN

Abstract

Mixed ant colonies have long fascinated biologists since they are often examples of social parasitism. From the genus *Tetramorium* MAYR, 1855, two types of social parasitism are well known: dulosis and inquilinism. We present a nest record from Turkey comprising workers of *T. immigrans* SANTSCHI, 1927, workers and a single gyne of a new species, and brood in commonly used nest chambers. We interpret the new species as a social parasite and describe it as *T. aspina* sp.n. Three characteristics indicate a morphological degeneration of the worker caste: Workers of *T. aspina* sp.n. have strongly reduced propodeal spines, larger intranest morphological variability than workers of the *T. caespitum* complex sensu WAGNER & al. (2017: Myrmecological News 25: 95-129), and a larger proportion of these workers have an aberrant propodeum ("propodeal syndrome") compared with workers of the *T. caespitum* complex. The discovery of *T. aspina* sp.n. raises interesting questions concerning the characterization of its socially parasitic life history and its evolutionary origin.

Key words: Morphometrics, propodeal spine, intranest morphological variability, worker caste degeneration, new species, *Tetramorium caespitum* complex, non-cryptic pavement ant, Turkey.

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Herbert C. Wagner (contact author), Department of Ecology, University of Innsbruck, Technikerstraße 25, 6020 Innsbruck, Austria; ÖKOTEAM – Institute for Animal Ecology and Landscape Planning, Bergmannsgasse 22, 8010 Graz, Austria. E-mail: heriwagner@yahoo.de

Celal Karaman, Volkan Aksoy & Kadri Kiran, Faculty of Science, Department of Biology, Trakya University, 22030 Edirne, Turkey. E-mail: celalkaraman78@gmail.com, volkanaksoy@trakya.edu.tr, kadrikiran@trakya.edu.tr

Introduction

Symbioses among ant species have fascinated biologists for centuries (HUBER 1810, DARWIN 1859, FOREL 1874, FABRE 1879, HOFFER 1889, WASMANN 1891, EMERY 1909, FABER 1967, KUTTER 1968, HÖLLDOBLER & WILSON 1990, HEINZE 1996, SEIFERT 2007, BUSCHINGER 2009). According to HÖLLDOBLER & WILSON (1990), there are two types of ant symbioses: compound nests and mixed colonies. In compound nests, two ant species share a nest space or nest close to one another and occasionally interact, but they keep and rear their brood separately (GRAY & al. 2018). In contrast, in mixed colonies, two ant species share a nest space, interact frequently, and store brood in a common area where they are cared for by one or both species. Usually, myrmecologists explain the origins of mixed colonies via one of three types of social parasitism (HÖLLDOBLER & WILSON 1990, SEIFERT 2007, BUSCHINGER 2009): temporary social parasitism, dulosis (permanent social parasitism with slavery), or

inquilinism (permanent social parasitism without slavery). The latter two occur in the species-rich genus *Tetramorium* MAYR, 1855 leading to its central role in social parasitism research (FOREL 1874, EMERY 1909, CRAWLEY & DONISTHORPE 1913, EMERY 1913, KUTTER 1950, STUMPER 1951, KUTTER 1968, HÖLLDOBLER & WILSON 1990, SANETRA & al. 1999, SEIFERT 2007, BUSCHINGER 2009, WARD & al. 2015).

We describe *Tetramorium aspina* sp.n., a non-cryptic species belonging to the *T. caespitum* group sensu BOLTON (1995). We argue that the putative mixed colony indicates social parasitism using *T. immigrans* SANTSCHI, 1927, a member of the *T. caespitum* complex sensu WAGNER & al. (2017), as host.

Materials and methods

Sample: In 2012, 888 *Tetramorium* nest samples were collected from the East Black Sea Region in Turkey (leg. K.

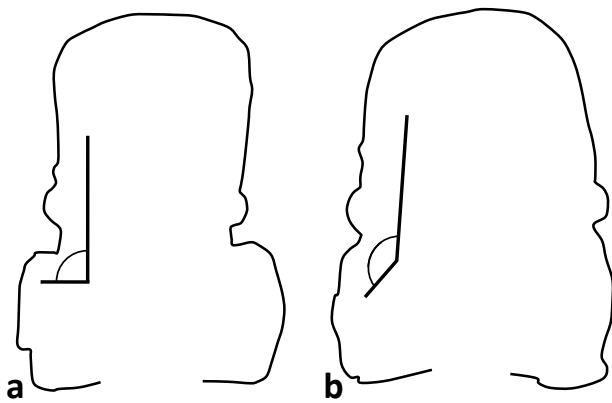


Fig. 1: Transversal section of mesosoma at level of propodeal spiracles. In workers with the “propodeal syndrome”, the propodeal narrowing leads to a step at meeting point of metapleuron and propodeum with an angle of around 90° (a). In normal workers, the step is missing or less pronounced and the angle is more obtuse (b).

Kiran, C. Karaman & V. Aksoy). This area of northeastern Turkey has thus far received little attention from myrmecologists (cf. KIRAN & KARAMAN 2012). Seven of the 888 samples were taken from near the Giresun-Dereli-Çamlı Village (50 km SSE Giresun, 40.4767° N, 38.5108° E, 1953 m above sea level). One of the seven samples proved to be a nest comprising two species. The nest was excavated thoroughly and a large number but not all of the available individuals of both the putative parasitic species and the putative host were collected.

Morphological investigation: Data were collected using a LEICA MZ16 A high-performance stereomicroscope with a magnification range of 80 - 294×. The host species was determined using the key of WAGNER & al. (2017). Morphometric and meristic data of 18 workers of *Tetramorium aspina* sp.n. from the type nest were taken. Most characters were defined by WAGNER & al. (2017); due to the partial lack of propodeal spines, SPWI could not be measured in workers. One morphometric character is newly introduced: PSW, which is the maximum outer distance between the edges of the left and right propodeal spiracles, measured in dorsal view. In the gyne, the depth of median petiole and postpetiole insection were also measured. Additionally, unilateral numbers of teeth and ommatidia were counted. All bilateral characters except PnHL (see definition in WAGNER & al. 2017) were measured from both sides and an arithmetic mean was calculated. In addition to morphometric measurements and meristics, qualitative morphological characters were collected. As “propodeal syndrome” we define an aberrant propodeal narrowing, which is found in workers of *T. aspina* sp.n. as well as in the *T. caespitum* complex. The propodeal narrowing leads to a step at the meeting point of metapleuron and propodeum with an angle of around 90° (Fig. 1a). In normal workers, the step is missing or less pronounced and the angle is more obtuse (Fig. 1b).

Statistics: Intranest morphological variability of *Tetramorium aspina* sp.n. was compared with that of the *T. caespitum* complex for 30 characters. In *T. aspina* sp.n., pairwise differences of morphometric and meristic character values of workers were calculated. By using 18 workers, there were $(18^2 + 18) / 2 - 18 = 153$ pair combinations. Negative difference values were multiplied by -1 to build arithmetic means of only positive values. The same was repeated with 478 intranest worker pairs of the *T. caespitum* complex (using data of WAGNER & al. 2017). The procedure described here was performed for absolute values and for indices (i.e., values divided by the head index CS). In a t-test (two-sided, type one), mean intranest character differences of *T. aspina* sp.n. and the *T. caespitum* complex were compared (Tab. 1). Frequency differences in the occurrence of propodeal syndrome between *T. aspina* sp.n. and the *T. caespitum* complex were evaluated using a chi-square-test. Statistics were done in SPSS Statistics v19. The alpha used was 0.05.

Treatment of species names: For all *Tetramorium* species listed for Europe, the Mediterranean Basin, North Africa, Middle East, Turkey, transcaucasian countries, Iran, and the Arabian Peninsula (BOROWIEC 2014), either recent taxonomic revisions (SANETRA & al. 1999, GÜSTEN & al. 2006, Csósz & al. 2007, Csósz & SCHULZ 2010, SHARAF & al. 2012, BOROWIEC & al. 2015, RADCHENKO & SCUPOLA 2015, SHARAF & al. 2015, BOROWIEC & al. 2016, SALATA & BOROWIEC 2017, SHARAF & al. 2017, WAGNER & al. 2017) or original descriptions were analyzed. Additionally, all *Tetramorium* type images available on AntWeb were investigated. Species that were neither yellowish nor lacked distinct propodeal spines were excluded from our list of possible conspecifics. The only species similar to *T. aspina* sp.n. was investigated by taking morphometrics of images on AntWeb.

Results and discussion

Mixed colony record: About 500 (56%) of the 888 *Tetramorium* nests sampled in the East Black Sea Region belonged to the *Tetramorium caespitum* complex. Near the Giresun-Dereli-Çamlı Village we found five nests of *T. cf. impurum* (FOERSTER, 1850), one of an unidentified *Tetramorium* species, and one nest containing the two species *T. immigrans* and *T. aspina* sp.n. Workers of the latter were distinguishable in the field from host workers by their yellowish color and smaller size. The nest was constructed under a stone that was 30 × 20 cm in diameter and 5 - 10 cm high. The colony comprised similar proportions of workers of each species. Workers of both species were evenly distributed over all nest chambers. The brood chambers comprised many larvae and one pupa. Based on the characteristic shape of the propodeum, the pupa could be assigned to *T. aspina* sp.n., but we could not assign the larvae to a species. If the larvae included individuals from *T. immigrans*, our observation could be interpreted as a case of a mixed colony. Alternatively, if the larvae only belonged to *T. aspina* sp.n., both species could be considered as co-inhabiting a compound nest. The only non-worker

Tab. 1: Mean intranest character differences of *Tetramorium aspina* sp.n. and the *T. caespitum* complex sensu WAGNER & al. (2017). Cases with larger differences in the *T. caespitum* complex in bold. Intranest differences in *T. aspina* sp.n. are significantly larger.

Characters	Absolute differences		Index differences	
	<i>T. aspina</i> sp.n. (n = 18)	<i>T. caespitum</i> complex (n = 478)	<i>T. aspina</i> sp.n. (n = 18)	<i>T. caespitum</i> complex (n = 478)
CL	35.4	30.2	0.0115	0.0081
CW	40.0	30.4	0.0115	0.0081
dAN	11.3	10.0	0.0073	0.0068
EL	10.6	7.6	0.0100	0.0062
EW	6.6	5.9	0.0066	0.0048
FL	15.6	13.3	0.0110	0.0080
HFL	38.5	31.8	0.0210	0.0169
MC1TG	1.4	2.4	0.0020	0.0034
ML	53.9	41.3	0.0247	0.0192
MPPL	17.2	12.5	0.0140	0.0083
MPSP	19.6	17.7	0.0207	0.0124
MPST	14.3	10.0	0.0142	0.0069
MtpW	32.4	17.6	0.0367	0.0102
MW	30.6	22.9	0.0173	0.0110
PEH	15.7	12.2	0.0121	0.0092
PEL	9.4	9.0	0.0094	0.0084
PEW	24.6	13.4	0.0269	0.0106
PLSP	18.7	11.4	0.0217	0.0123
PLST	14.6	10.6	0.0151	0.0094
PnHL	29.1	19.0	0.0374	0.0232
PoOc	10.8	12.5	0.0140	0.0097
POTCos	2.4	1.6	0.0037	0.0020
PPH	13.4	13.4	0.0162	0.0120
PPL	7.4	7.6	0.0091	0.0084
Ppss	17.1	15.0	0.0249	0.0206
PPW	22.9	15.8	0.0229	0.0135
PreOc	11.7	9.3	0.0086	0.0069
RTI	22.5	14.9	0.0157	0.0115
SLd	29.5	25.7	0.0209	0.0145
SPST	8.3	10.5	0.0128	0.0097

individual in the nest was a queen of *T. aspina* sp.n. found in a chamber 30 - 35 cm below the ground level. A *T. immigrans* queen was not found. The revelation of the parasitic biology of *T. aspina* sp.n. demands further investigation. Pure nest records of *T. aspina* sp.n., slave raids, or a lack of function of the worker caste would demonstrate temporary social parasitism, dulosis, or inquilinism with a worker caste, respectively (HÖLLDOBLER & WILSON 1990, BUSCHINGER 2009).

Morphology: The morphometric investigation of the new species revealed obvious differences from most other *Tetramorium* species known from Europe, the Med-

iterranean basin, and adjacent regions (for details, see **Taxonomic description of *Tetramorium aspina* sp.n.** below). The only similar species, *Tetramorium nitidissimum* PISARSKI, 1967 from Firyuza (25 km W Ashgabat, Turkmenistan), shares the character combination of very short propodeal spines and a yellowish color in workers. However, images of two workers from AntWeb (CASENT0904825, CASENT0917069) allowed a distinct differentiation from the new species described here (for details, see **Differential diagnosis**). Additionally, the type gyne of *T. nitidissimum* (CASENT0917070) is very different from the gyne of *T. aspina* sp.n. Thus, we consider



Fig. 2: A general view of the type locality of *Tetramorium aspina* sp.n.

T. aspina sp.n. as a non-cryptic and non-described species. It belongs to the *T. caespitum* group sensu BOLTON (1995). Based on their yellowish color and small eyes, workers are probably subterranean foragers.

Morphological degeneration: We found three conspicuous characteristics of *Tetramorium aspina* sp.n. workers: (i) They are nearly the only *Tetramorium* workers in Europe, Anatolia, and adjacent regions lacking propodeal spines. Myrmecologists interpret propodeal spines often as defense against vertebrates (DORNHAUS & POWELL 2009, ITO & al. 2016, SARNAT & al. 2016, BLANCHARD & MOREAU 2017, SARNAT & al. 2017). There is a trade-off between defensive traits like the sting and spines. Interestingly, an evolutionary loss of spines is more than twice as likely as a gain (BLANCHARD & MOREAU 2017). In the *T. caespitum* complex, a relation between ecological niche and the evolution of propodeal spines has been discerned, and hence a selection pressure on this morphological structure and factors linked to ecology has been suggested (WAGNER & al. 2018). We speculate that the loss of spines in *T. aspina* sp.n. workers might represent a degeneration linked with their parasitic life history. (ii) Intranest morphological character differences (Tab. 1) were significantly higher than in the *T. caespitum* complex (absolute values, t-test, $p < 0.00001$; indices, t-test, $p < 0.00001$). Morphological characters with a high intranest variability were shown to be not under strong stabilizing selection pressure (IMAI & al. 2016). (iii) Eleven of 18 investigated workers (61%) had the propodeal syndrome. In contrast, in the *T. caespitum* complex, this syndrome was found only in four of 968 workers. Thus, it is more frequent in our sample of *T. aspina* sp.n. (qui-square-test, $p < 0.00000000001$).

To summarize, we propose three traits that at least partly indicate a morphological degeneration of workers: the lack of propodeal spines, the high intranest morphological variability, and the high frequency of workers with the propodeal syndrome. Future research should investigate if the parasitic biology and associated decrease of stabilizing selection on morphology (cf. IMAI & al. 2016) explains the



Fig. 3: Holotype worker of *Tetramorium aspina* sp.n. in (a) full face, (b) dorsal, and (c) lateral views (photographer Leo Kuzmits).

morphological degeneration of workers in *Tetramorium aspina* sp.n.

Outlook: Since all known parasites using *Tetramorium* as host show a more derived morphology than *T. aspina* sp.n. (see KUTTER 1968, HÖLLDOBLER & WILSON 1990, SEIFERT 2007, BUSCHINGER 2009, WARD & al. 2015), no species comparable with *T. aspina* sp.n. has ever been reported. Maybe, *T. nitidissimum* could be another example. Recent studies elucidated the evolutionary origins of

ant social parasites in distantly related genera (JANSEN & al. 2010, RABELING & al. 2014, LEPPÄNEN & al. 2015a, b, PREBUS 2017, SANLLORENTE & al. 2018), and inferring the evolutionary origin of *T. aspina* sp.n. is a high priority for future studies. Molecular studies should show if *T. aspina* sp.n. is evolutionarily related to morphologically similar species (e.g., *T. nitidissimum*), to the *T. caespitum* complex (the host; cf. EMERY 1909), to slave makers (and thus a dulotic species or the link in the evolution of dulosis; cf. KUTTER 1968), or to inquilines. Hopefully, field observations will also throw light on its parasitic biology and help determine which type of social parasitism applies to this enigmatic ant species.

Taxonomic description of *Tetramorium aspina* sp.n.

Etymology: Named after its strongly reduced propodeal spines. Because “*aspina*” is a noun in apposition, “a” is the correct ending.

Type locality: Giresun-Dereli-Çamlı Village (Turkey; Fig. 2), 40.4767°N, 38.5108°E, 1953 meters above sea level, leg. K. Kiran, C. Karaman, and V. Aksoy, 12.VI.2012, 425 workers and 1 gyne.

Type material: All type material from one nest, labeled “TUR: 40.4767°N, 38.5108°E, Giresun-Dereli-Çamlı Village, 1953 m, subalpine *Picea orientalis* forest, K. Kiran, C. Karaman & V. Aksoy, 12.VI.2012 [/] 12/0859b”. Holotype worker (Fig. 3a - c), 409 paratype workers, and 1 paratype gyne (Fig. 4a - c) in entomological collection of Biological Department of Trakya University, Edirne (Turkey), five paratype workers in private collection of H.C. Wagner (Graz, Austria), three paratype workers in Senckenberg Naturkundemuseum Görlitz (Germany), three paratype workers in Natural History Museum London (Great Britain), three paratype workers in Natural History Museum in Vienna (Austria), and one paratype worker in Tiroler Landesmuseum (Hall, Austria). Morphometric data of holotype in μm : CL = 703, CW = 691, dAN = 201, EL = 122, EW = 97, FL = 319, HFL = 538, ML = 861, MPPL = 252, MPSP = 267, MPST = 185, MtpW = 353, MW = 468, PEH = 250, PEL = 137, PEW = 237, PLSP = 150, PLST = 194, PnHL = 188, PoOc = 256, PPH = 244, PPL = 96, Ppss = 29, PPW = 278, PreOc = 182, PSW = 287, RTI = 274, SLd = 516, SPST = 108. Meristic data of holotype: MCITG = 7.8, unilateral number of ommatidia = 30, unilateral number of teeth = 10, POTCos = 7.5.

Putative host material: 150 workers of *Tetramorium immigrans* from same nest.

Worker: Size: Smaller than in *Tetramorium caespitum* complex, CS = 646 ± 32 [590, 699] vs. 749 ± 64 [561, 988] μm .

Dorsum of head light brown, ventralwards from level of frontal carinae continuously getting lighter and on eye level and ventral of eye yellowish. Appendices, mesosoma, petiole, and postpetiole yellowish. First 20 - 60% of first gastral tergite yellow, posteriorly continuously getting darker and last 10 - 50% light brown; remaining gaster yellowish with sometimes light brown caudal margins of tergites.

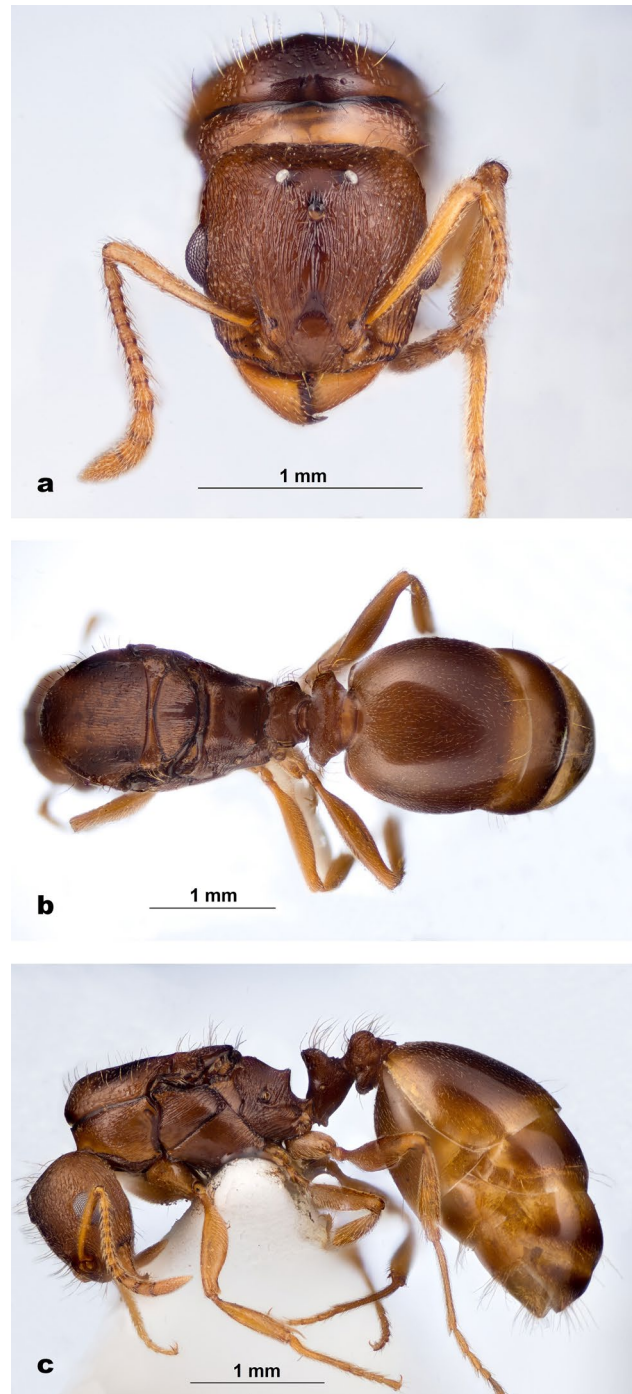


Fig. 4: Paratype gyne of *Tetramorium aspina* sp.n. in (a) full face, (b) dorsal, and (c) lateral views (photographer Leo Kuzmits).

Sculpture on dorsum of head highly variable from nearly completely smooth with only few rudiments of rugulae to pronounced longitudinally rugulose. Vertex completely smooth. Praeoculo-temporal area of head pronounced longitudinally rugulose, postoculo-temporal area of head smooth or moderately rugulose, POTCos = 5.8 ± 2.2 [1.0, 9.3]. Dorsum of mesosoma smooth with only small parts of longitudinal rugae or moderately rugulose, lateral side of mesosoma with strongly pronounced rugae and only parts of pronotum sometimes smooth; smooth

and shiny area on lateral side of propodeum rather small, Ppss = 27 ± 17 [10, 79]. Dorsum of petiolar and postpetiolar nodes completely smooth. Small connected reticulate units scattered over 1st gastral tergite, MCITG = 6.0 ± 1.2 [4.2, 8.2].

No sinuous hairs on ventral head. No erect hairs on lateral side of head. A row of hairs at posterior margin of head. Mesosoma hairs shorter than in *Tetramorium caespitum* complex, PnHL / CS = 0.208 ± 0.032 [0.153, 0.270]. Moderately long erect hairs on dorsum of mesosoma, petiole, postpetiole, and first gastral tergite. Erect gaster hairs on further gastral segments only at caudal margins of tergites and sternites.

Head slightly elongated, CL / CW = 1.030 ± 0.020 [0.987, 1.059]. 8.3 ± 0.9 [6.5, 10] teeth. Palp formula as *Tetramorium immigrans*: Maxillary palp with 4 segments, labial palp with 3. Scape rather short, SLd / CS = 0.739 ± 0.018 [0.711, 0.770]. Twelve antennal segments. Distance between frontal lobes larger than in *T. caespitum* complex, between antennal fossae moderate, and between tops of ridges between antennal fossae smaller than in *T. caespitum* complex, FL / CS = 0.458 ± 0.010 [0.442, 0.484], dAN / CS = 0.288 ± 0.006 [0.273, 0.300], RTI / CS = 0.381 ± 0.013 [0.362, 0.399]. Eye small and number of ommatidia low, EL / CS = 0.165 ± 0.009 [0.147, 0.177], EW / CS = 0.133 ± 0.006 [0.121, 0.141], number of ommatidia 23.4 ± 3.7 [18.0, 30.0]. Preocular distance rather large, PreOc / CS = 0.268 ± 0.007 [0.258, 0.281], and postocular distance moderate, PoOc / CS = 0.403 ± 0.013 [0.375, 0.426].

Mesosoma longer and wider than in *Tetramorium caespitum* complex, ML / CS = 1.228 ± 0.021 [1.188, 1.274], MW / CS = 0.672 ± 0.015 [0.642, 0.698]. Promesonotal dorsum convex, metanotal groove moderately deep to deep. Propodeal syndrome common. Metapleuron and propodeum wider than in *T. caespitum* complex but (because of propodeal syndrome) highly variable, MtpW / CS = 0.508 ± 0.032 [0.446, 0.558], PSW / CS = 0.393 ± 0.050 [0.302, 0.471]. Hind femur short, HFL / CS = 0.751 ± 0.018 [0.718, 0.776]. Propodeal spine completely missing or rudimentary, MPSP / CS = 0.395 ± 0.018 [0.368, 0.430], SPST / CS = 0.166 ± 0.012 [0.155, 0.200], PLSP / CS = 0.206 ± 0.019 [0.177, 0.245]. Distance from anteroventralmost point of metapleuron to propodeal spiracle and propodeal lobe larger than in *T. caespitum* complex, MPST / CS = 0.269 ± 0.012 [0.252, 0.296], MPPL / CS = 0.374 ± 0.012 [0.358, 0.401]. Distance between propodeal lobe and propodeal spiracle larger than in *T. caespitum* complex, PLST / CS = 0.287 ± 0.013 [0.262, 0.312].

Postpetiole and petiole wider, higher, and shorter than in *Tetramorium caespitum* complex, PPW / CS = 0.421 ± 0.021 [0.392, 0.476], PEW / CS = 0.342 ± 0.025 [0.270, 0.380], PEH / CS = 0.373 ± 0.011 [0.358, 0.401], PPH / CS = 0.371 ± 0.014 [0.350, 0.407], PEL / CS = 0.211 ± 0.008 [0.196, 0.225], PPL / CS = 0.139 ± 0.008 [0.119, 0.154].

Gyne: Size: Smaller than in *Tetramorium caespitum* complex, CS = 1073 μm .

Dorsum of head medium brown, ventralwards from level of frontal carinae continuously getting lighter and on eye level and ventral of eye rather light brown. Appendices light brown. Mesosoma light brown, but with dark brown parts on mesonotum and scutellum, tegulae dark brown. Petiole and postpetiole medium to dark brown. First tergite of gaster medium brown, other tergites anteriorly light brown and posteriorly continuously getting darker and medium brown at caudal end.

Head frontal longitudinally rugulose, only area between ocelli and caudalmost part of head smooth and shiny. Lateral side of head with pronounced rugulosity, POTCos = 11. Around half of mesonotum smooth and half longitudinally rugulose, smooth regions anteriorly and laterally. Scutellum longitudinally rugulose. Lateral side of mesosoma with longitudinal rugae, pronotum, anepisternite, and mesopleuron partly smooth.

No erect hairs on lateral side of head, but long hairs at posterior margin of head and on dorsum of head. Moderately long mesosomal hairs, PnHL / CS = 0.242, short mesonotum hairs, long hairs on scutellum, metanotum, petiole (longest hair on petiole / CS = 0.305), and postpetiole (longest hair on postpetiole / CS = 0.287). Erect gaster hairs only at caudal margins of tergites and sternites.

Head broader than in *Tetramorium caespitum* complex, CL / CW = 0.878. Scape longer than in *T. caespitum* complex, SLd / CS = 0.795. 8 teeth. 12 antennal segments. Distance between frontal lobes larger than in *T. caespitum* complex, between antennal fossae and between tops of antennal fossae ridges moderate, FL / CS = 0.443, dAN / CS = 0.279, RTI / CS = 0.370. Eye larger than in *T. caespitum* complex, EL / CS = 0.288, EW / CS = 0.244. Preocular distance moderate, PreOc / CS = 0.202, and postocular distance smaller than in *T. caespitum* complex, PoOc / CS = 0.336.

Mesosoma shorter and narrower than in *Tetramorium caespitum* complex, ML / CS = 1.859, MW / CS = 1.067. Propodeal spiracle distance PSW / CS = 0.683. Hind femur moderately long, HFL / CS = 0.972. Propodeal spines shorter than in *T. caespitum* complex, MPSP / CS = 0.556, SPST / CS = 0.272, PLSP / CS = 0.269, SPWI / CS = 0.441. Distance from anteroventralmost point of metapleuron to propodeal spiracle and propodeal lobe smaller than in *T. caespitum* complex, MPST / CS = 0.344, MPPL / CS = 0.446. Distance between propodeal lobe and propodeal spiracle rather large, PLST / CS = 0.351.

Petiole and postpetiole wider, lower, and shorter than in *Tetramorium caespitum* complex, PEW / CS = 0.505, PEH / CS = 0.458, PEL / CS = 0.224, PPW / CS = 0.715, PPH / CS = 0.448, PPL / CS = 0.155. Median petiole insection depth / CS = 0.027, median postpetiole insection depth / CS = 0.008.

Differential diagnosis of workers: The character combination of yellowish color and strong reduction of propodeal spines allows differentiation from all *Tetramorium* species in Europe, Mediterranean basin, and adjacent regions. Differentiation from *T. nitidissimum* workers (type locality: Firyuza, 25 km W Ashgabat, Turkmenistan) possible by three steps: (i) *Tetramorium aspina* sp.n. exhibits

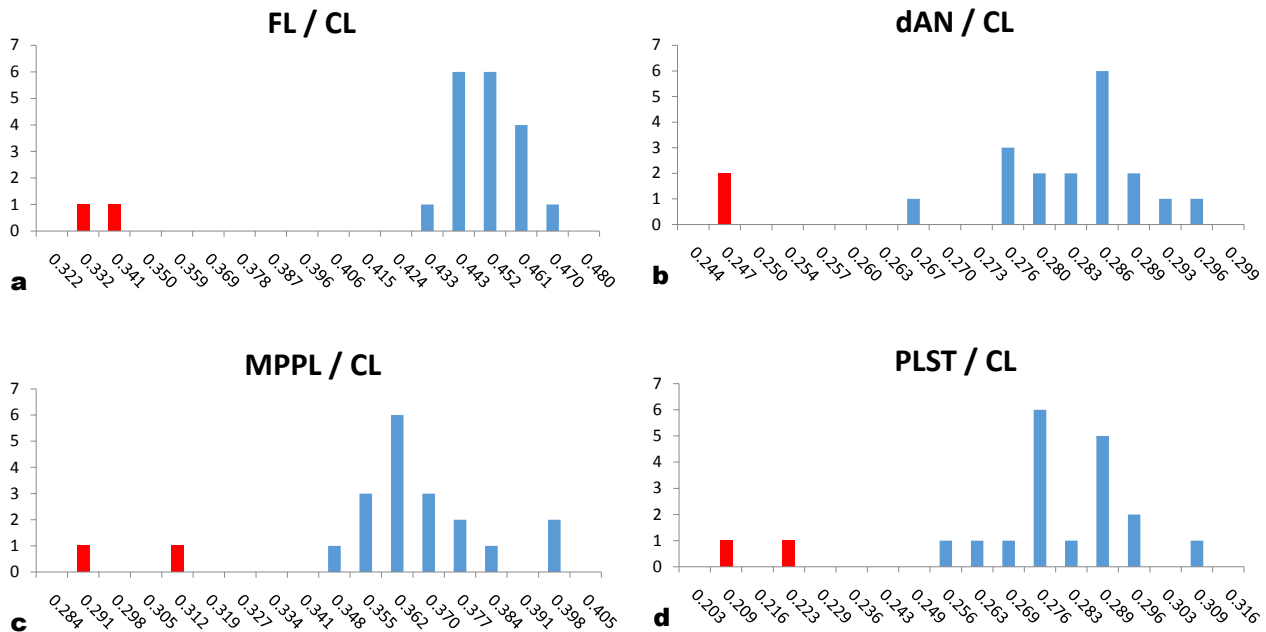


Fig. 5: Diagnostic characters of type workers of *Tetramorium nitidissimum* PISARSKI, 1967 (red; n = 2) and *Tetramorium aspina* sp.n. (blue; n = 18): (a) FL / CL, (b) dAN / CL, (c) MPPL / CL, and (d) PLST / CL.

a row of long hairs at posterior margin of head (see Fig. 3a). *Tetramorium nitidissimum* does not show such long hairs. (ii) Frontal carinae and antennal fossae of *T. nitidissimum* type-workers are narrower (FL / CL = 0.332 - 0.337, dAN / CL = 0.246 - 0.247, n = 2) than in *T. aspina* sp.n. (FL / CL = 0.451 ± 0.010 [0.435, 0.470], dAN / CL = 0.284 ± 0.007 [0.269, 0.296], n = 18; Fig. 5a, b). (iii) Distances from dorsocaudalmost point of propodeal lobe to most anteroventral point of metapleuron and to center of propodeal spiracle are smaller (MPPL / CL = 0.291 - 0.309, PLST / CL = 0.209 - 0.226) than in *T. aspina* sp.n. (MPPL / CL = 0.369 ± 0.013 [0.351, 0.398], PLST / CL = 0.283 ± 0.013 [0.259, 0.309] n = 18; Fig. 5c, d).

Distribution: Only known from type locality.

Biology: Putative social parasite of *T. immigrans*. Likely monogynous. Small eyes and yellowish color indicate subterranean activity.

Ecology: The type locality is a subalpine, sparse, and almost 100-year-old forest with large sun-exposed treeless areas. The nest was located on a stony and rocky east slope with a 50 - 55° inclination. Herb layer plants are *Anthemis* sp., *Daucus* sp., *Malva* sp., *Medicago* sp., *Myosotis* sp., Poaceae species, *Rosa* sp., *Rubus* sp., *Taraxacum* sp., *Trifolium* sp., *Verbascum* sp., and *Veronica* sp. *Camponotus aethiops* (LATREILLE, 1798), *Formica cunicularia* LATREILLE, 1798, *F. fusca* LINNAEUS, 1758, *Lasius alienus* (FOERSTER, 1850), *Lasius flavus* (FABRICIUS, 1782), *Manica rubida* (LATREILLE, 1802), *Messor structor* complex, *Proformica pilosiscapa* DLUSSKY, 1969, *Temnothorax artvinensis* SEIFERT, 2006, *Temnothorax unifasciatus* (LATREILLE, 1798), *Tetramorium immigrans*, *Tetramorium* cf. *impurum*, and a further non-identified *Tetramorium* sp. were also recorded from the same locality.

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